

INVESTIGATIONS OF MOULT CYCLES OF THE ANTARCTIC KRILL
EUPHAUSIA SUPERBA DANA IN CONCENTRATIONS
IN THE D'URVILLE SEA (EAST ANTARCTIC)

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Abstract: The krill (*Euphausia superba*) collected with the commercial trawl in the D'Urville Sea (off the Terre d'Adelie) in late January-early April 1989 was investigated for the moult stages, sex, length and maturity stages. From each catch, 41-80 (58 on the average) specimens were examined for moult stages according to BUHHOLZ's method with the identification of DRACH's moult stages.

Euphausia superba aggregating in concentrations appeared to be characterized by the specific phases of the moult cycle. Most of the animals were intermoult or early premoult stages regardless of the sex and age. The premoult krill may leave the aggregations before ecdysis (probably as swarms with synchronous moulting). Thus, the moult processes should strongly influence the size and density of the concentrations. In autumn the moult frequency decreased, so the krill in concentrations was mostly in the intermoult phases. A slow moult rate is connected with an increase of the aggregation density probably due to the decreased loss of the moulting krill or (and) moderation of the locomotor activity correlated with the moult state.

1. Introduction

A study of the moult activity of the krill (*Euphausia superba*) is required for understanding its growth, overwintering processes, reproduction and swarming (KILS, 1981; MAKAROV, 1983; BUHHOLZ, 1985). Several observations on the krill moulting have been done in aquaria (MORRIS and KECK, 1984; BUHHOLZ, 1985; CUZIN-ROUDY, 1987), in the field using random net samples (MORRIS and PRIDDLE, 1984; BUHHOLZ, 1985) and samples which targeted individual swarms of the krill (WATKINS *et al.*, 1986; BUHHOLZ *et al.*, 1988). Individual swarms form concentrations (aggregations and layers) of high density in certain places (CCAMLR, 1989). A "good" concentration is the principal subject of the krill fishery. Moult processes in the krill in such concentrations have not been studied before. We studied in the field (on board trawlers) the peculiarities of moult cycles in the krill which formed heavy aggregations and layers in the D'Urville Sea (off Terre d'Adelie) in the austral summer and autumn. The emphasis was laid on possible sexual, size-age and other differences in the moult cycles and also on the seasonal variability of the moulting activity of the krill in relation to seasonal changes in the concentration densities.

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2. Materials and Methods

This investigation was begun on board the factory-trawler (KKRT) 'KAPITAN OLEINICHUCK' (late January–early February 1989) and then it was continued on board FRS 'MYS JUNONY' (late February–early April 1989) which worked as a commercial vessel together with the former one. The krill was sampled during the fishery operations on the concentrations which were situated not far from each other in the outer shelf and inner slope zone. The dates, positions, some characteristics of the concentrations and the number of samples for each region of aggregations are listed in Table 1. From a catch, 41–80 specimens per sample (58 specimens on the average) were collected randomly. A total of 53 samples, 3072 specimens were examined. Microscopic examination of the uropod tissues was conducted following BUHHOLZ's method (1982) with the identification of DRACH's (1939) moult stages: A (postmoult), BC (intermoult), D_0 – D_{3-4} (premoult). Length (from the tip of rostrum to the end of telson), sex and maturity stage (MAKAROV and DENYS, 1981) were determined. About 100 specimens from each catch investigated for moult were measured in addition to the samples used for moult staging. Selected samples were examined for more detailed maturity staging using BARGMANN's (1945) and MAKAROV's (1983) systems.

It was difficult to identify an exact moult stage in some premoult specimens. The percentage of the unidentified stages decreased after the first week and then did not exceed, as a rule, 2–3%. This was obviously due to the staging experience. Samples with the percentage of unidentified stage more than 10% were not involved for the analysis of sexual and seasonal changes in the moult cycles. Seasonal variability of the density of krill concentrations was characterized on the basis of the fishery statistics from both ships. Catch per unit effort (CPUE) measures were calculated: mean

Table 1. Regions of krill concentrations, their positions, biological characteristics of krill and number of samples analyzed for moult.

Region number	Vessel	Dates in 1989	Coordinates south lat. east long.	TC/TFISHT (t/h)	Mean size of krill* (mm)	Percentage of females*	Number of samples
1	K	27.01–1.02	65.36–65.45 140.43–141.40	3.62	42.8 (3.60)	69.3 (3.0)	4
2	K	2.02–7.02	65.38–66.00 143.58–145.06	3.31	42.6 (3.62)	70.1 (1.4)	12
3	M	28.02	65.55–65.53 146.07–146.07	—	44.2 (3.48)	60.0 —	1
4	M	3.03–13.03	65.15–65.32 137.55–139.05	6.76	44.0 (3.89)	68.6 (6.9)	14
5	M	14.03–21.03	65.00–65.45 139.00–140.02	8.27	42.8 (3.57)	66.4 (8.0)	9
6	M	25.03–5.04	64.40–64.52 132.27–133.37	10.29	40.3 (3.37)	70.1 (8.2)	13

Vessels: K—"KAPITAN OLEINICHUCK". M—"MYS JUNONY". TC/TFISHT—total catch/total fishing time.

* Standard deviations are shown in parentheses.

catch per hour of trawling and TC/TFISHT (total catch/total fishery time) (CCAMLR, 1989; DOLZHENKOV *et al.*, 1990)

3. Results and Discussion

3.1. Composition on krill concentrations and differences of moult activity between sexes and developmental stages of the krill

The two main types in the length frequency distribution could be identified: a) one with two distinct size groups with the modal values in 39–40 mm and 44–46 mm; b) the other with single mode which fell in the mid-range of these two modes. These variants and the size distributions intermediate between them were found in every region of the krill concentrations (Figs. 1 and 2). Average size of the krill varied little among the regions of concentrations (Table 1). We suppose that the krill aggregations and layers consisted mainly of the two overlapping size-age groups. Modal values of

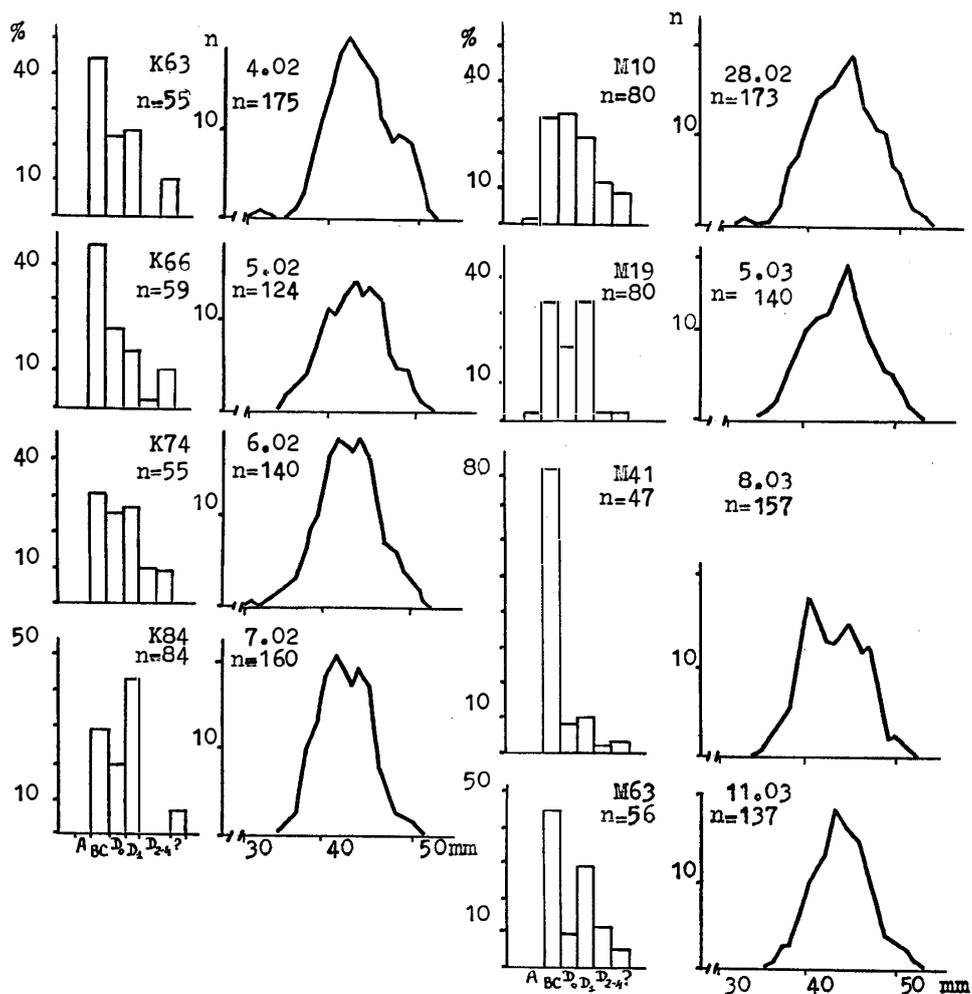


Fig. 1. Examples of moult stages and length frequencies of *Euphausia superba* in the regions 1–4 (see Table 1). K—Samples from factory-trawler “KAPITAN OLEINICHUCK”, M—samples from FRS “MYS JUNONY”. ?—unidentified stages.

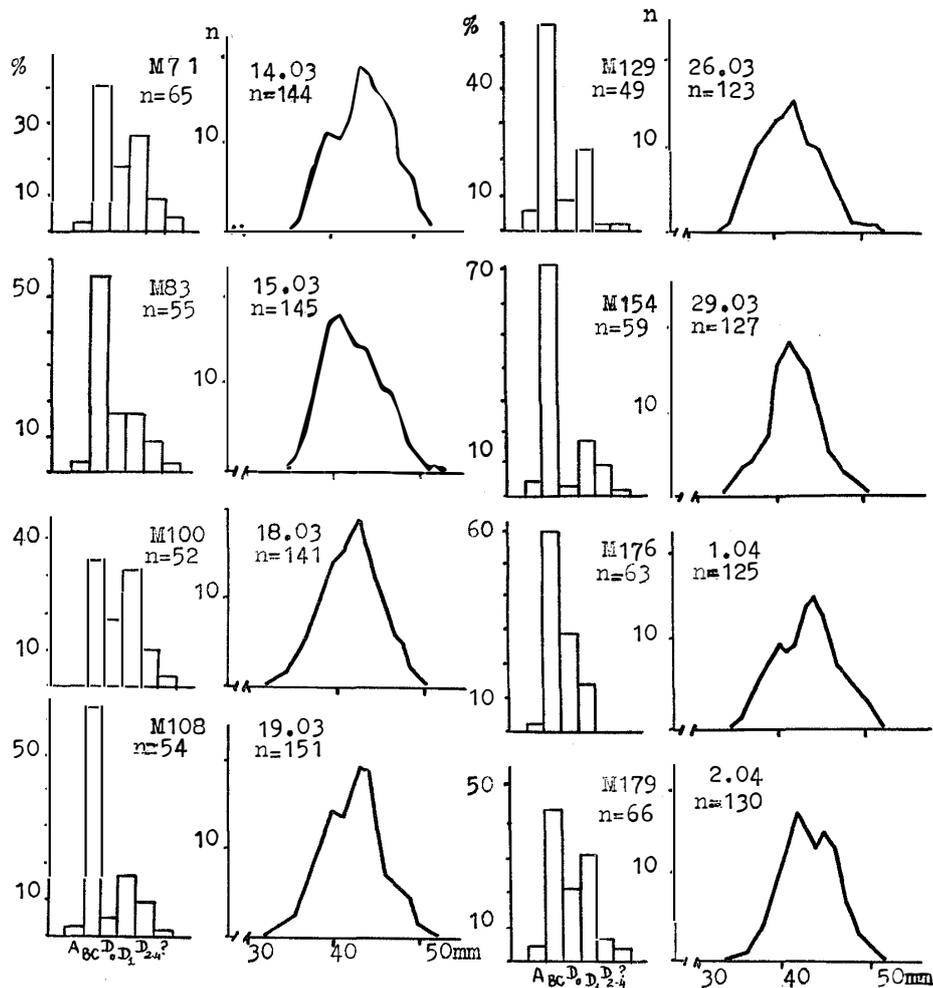


Fig. 2. Examples of moult stages and length frequencies of *Euphausia superba* in the regions 5 and 6. Abbreviations M, ? as in Fig. 1.

the small size krill correspond well to the summer size of 2+ year krill while the larger one to 3+ year animals off the Antarctic Peninsula (SIEGEL, 1986; SPIRIDONOV, 1987) and in the Prydz Bay region (HOSIE *et al.*, 1988). The environmental conditions of these regions (*e.g.* seasonal ice covering, water temperature, the duration of the phytoplankton vegetation) are comparable with the conditions of the D'Urville Sea. So we believe that the krill caught here comprised mainly of 2+ and 3+ age classes. Of course there were the krill of older than 3+ years in the concentrations studied. They were scarce, however, as in the Prydz Bay region (HOSIE *et al.*, 1988) and did not appear as a distinct size peak.

An interesting feature of our aggregations was a shift in the sex ratio: females distinctly predominated over the whole area and period of the investigation (Table 1). In late January–early February the females were mainly spent or immature but the gravid females also occurred. From late January to 7 February the percentage of gravid females dropped from 15–20 to 1–3 percent. In March such females were not observed at all. Most of the males were immature for the whole period of the present investigations.

The composition of the krill in various concentrations studied was similar in relation to size, sex ratio and maturity stages. Some differences observed in the maturity state were rather due to the seasonal variation. The concentrations studied were formed on the common hydrological background, *i.e.* the quasi-stationary eddy off the Terre d'Adelie (DOLZHENKOV *et al.*, 1990). So we suppose that the krill in these concentrations belongs to the same population division.

Differences in the moult stage composition between sexes were examined with chi-square test (Table 2). Significant difference was found in only one case. Although the males were scanty in the samples, it appeared that the animals of both sexes within dense aggregations were similar in terms of the moult stage composition.

Let's consider size-related differences in the moult stage composition with some examples. In late January one case of the predominance of the D_0 -stage was noted (Fig. 3A; chi-square test shows significant differences in stage composition between the krill smaller and larger than 42 mm ($\chi^2=7.69$, $p<0.05$, d.f. =2). But there was apparently no correspondence between size and stage in other samples from the same region 1 (Fig. 3B). In early February (region 2) some cases of unevenness in the stage distribution within length classes were observed but no significant differences were revealed by chi-squares between the krill smaller and larger than 43 mm (Fig. 3D). Usually there was no predominance of certain stages at certain size intervals (*e.g.* Fig. 3C). In early and mid-March (regions 3–5) some cases of apparent unevenness in the stage distribution within sizes were noted as well (Fig. 3E, H, I). But other samples obtained close in space and time did not indicate such differences in moult stages between the krill of dissimilar sizes (Fig. 3F, G). In late March–early April (region 6) the moult stages were rather evenly distributed within length frequencies (Fig. 3J, K). So, size-related differences in the moult stages were observed in few cases and we failed to delineate any regularities of them even within the same concentration of the krill.

It is known that individual swarms of *E. superba* consists of the specimens of similar size (MARR, 1962; SPIRIDONOV *et al.*, 1985; WATKINS *et al.*, 1986) and this is obviously interrelated with moult cycle synchronization within swarms (BUHOLZ, 1985). There is an evidence that mixing of the randomly caught groups of the krill takes place in the trawl cod end. Obviously individual swarms may be characterized both by specific size and moult stage compositions. But these specific features should be likely smoothed in the characteristic scale of the large krill concentrations.

Table 2. Comparison of the moult stage composition in the males and females of *Euphausia superba*. Region numbers are as in Table 1.

Region	Number of samples checked	Number of cases of significant difference	Range of chi-square values when differences are not significant d.f.=1 or 2	Chi-square $p<0.05$ d.f.=1 or 2
1+2	7	—	0.11–2.63	5.99
3	1	—	0.10	5.99
4	11	1 ($\chi^2=6.35$)	0.004–5.35	3.84–5.99
5	7	—	0.003–1.71	3.84–5.99
6	9	—	0.006–3.53	3.84

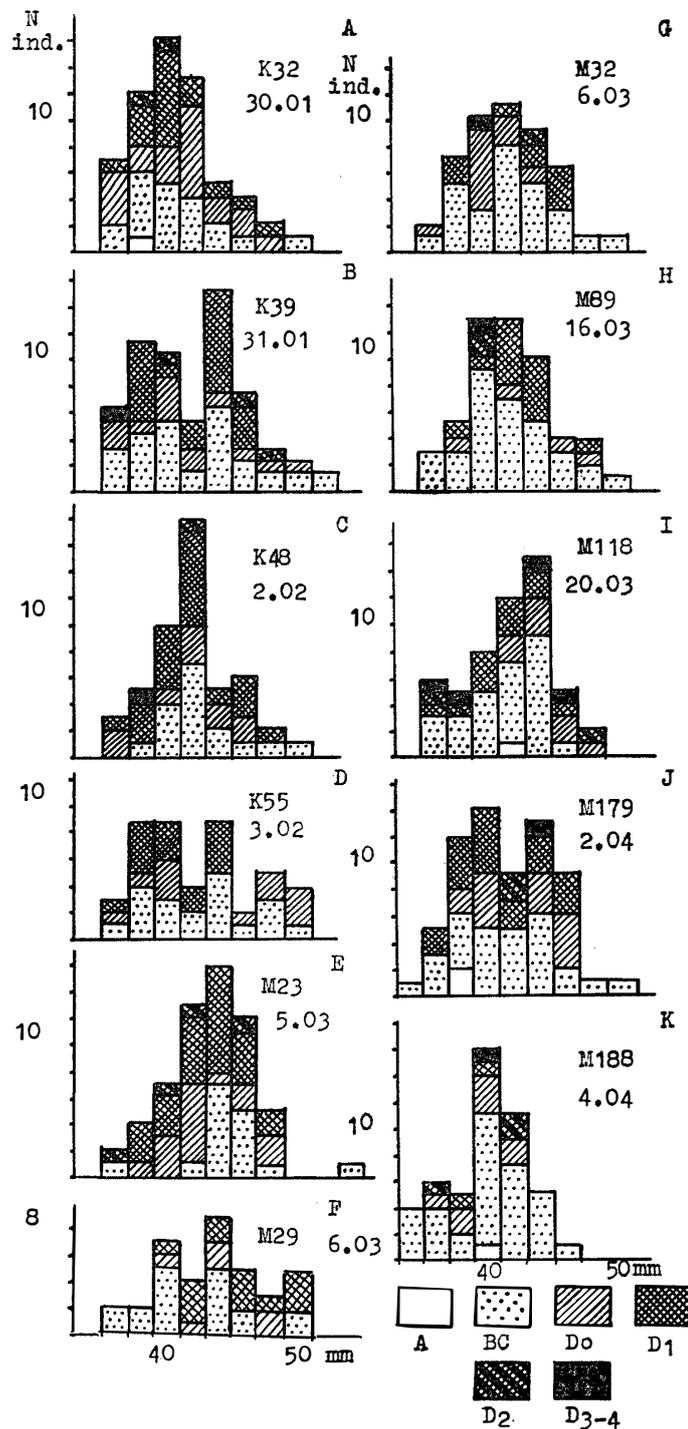


Fig. 3. Examples of moult stages distributions within length frequencies. Unidentified stages are not shown.

Mature krill, as we already noted, was not numerous in our material. It seems, however, interesting to discuss their moult activity. Mature males and gravid (IIIC, D —MAKAROV and DENYS, 1981) females consisted both of the intermoult and premoult animals in January–early February (Fig. 4A, B). It suggests that the krill continues to

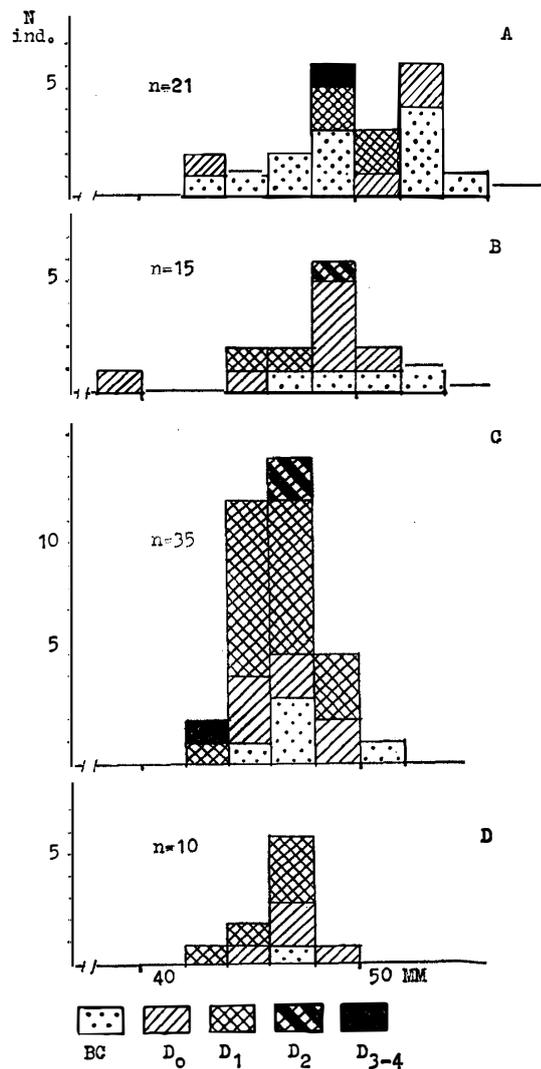


Fig. 4. Moult stages distribution within selected groups of the krill. A—gravid females, B—mature males in the regions 1, 2. C, D—spent females with spermatophores, region 4 (C), region 5 (D).

moult when maturing as other authors pointed out (CUZIN-ROUDY, 1987; BUHHOLZ *et al.*, 1988; NICOL, 1989).

In March spawning of *E. superba* was apparently completed. Several large (at least 3+ year) females carried spermatophores. As a rule such specimens were in the early stage of the postspawned reorganization of the gonads (stage 5—MAKAROV, 1983; see also MAKAROV, 1975; DENYS and MCWHINNIE, 1982). These spent females were mainly premoult (Fig. 4C, D) contrary to the predominance of the BC-stages in the immature specimens and the krill which became spent long ago (Figs. 1–3; see below) (84% of the D-stages in the females with spermatophores and 47% in the females without spermatophores in the regions 4 and 5).

It is known that a female krill throws off the spermatophores when moulting (MAKAROV, 1983). Though some females had sperm mass in their thelycum (stage G—BARGMANN, 1945), and repeated copulation after final spawning could not be excluded, the presence of the spermatophores rather means that these animals did not moult in spent condition. But the breeding of *E. superba* has been completed in the concentrations studied about mid-February (see above). CUZIN-ROUDY (1987) ob-

served krill spawning to take place mostly in the D_0 -stage. So if females have spent in this stage remaining at the same place they should have conspicuous prolongation of the premoult phase. Spermatophore-bearing females were rarely observed after 25 March, so this prolongation should be about a month. This seems doubtful since an intermoult period rarely exceeds a month even in the starved krill (IKEDA *et al.*, 1985; BUHHOLZ, 1985).

But if these females did not spawn in a certain moult stage, as NICOL's (1989) results indicated, it should be difficult to explain the observed predominance of the D-stages among spent specimens. Another explanation suggests that the spawning continued somewhere outside the concentrations studied until at least early March and spermatophore-bearing spent females were included into the krill concentrations in the slope zone. It is shown for the Antarctic Peninsula region that an important krill spawning area there is the southern periphery of the Antarctic Circumpolar Current where the season of reproduction is longer than in the coastal zone (MAKAROV and SPIRIDONOV, 1988). Then the spent krill from the former oceanic area may be partly included into the concentrations in the latter one (SIEGEL, 1986; SOLYANKIN and SPIRIDONOV, 1987). Similar processes can take place in the D'Urville Sea region. If it is so we are not to suppose very long delay of the moult after spawning among 3+ year females.

3.2. *Moult activity in the krill concentrations and its seasonal changes*

In late January–early March (regions 1, 2, 3, partly 4) the principal moult stages in the krill concentrations were BC, D_0 and D_1 (Fig. 1). The percentage of each of them varied from 15% to 50%. Postmoult and ready-to-moult (D_{2-4}) specimens were rare (not more than 5% each). The consecutive samples were sometimes similar in the moult stage composition (Fig. 1). From 6 March to early April the BC-stage was distinctly dominant (more than 50%) (Figs. 1 and 2). The percentage of the D_0 -stage decreased in March sometimes to less than 5%. In early April some increase of percentage of this stage was noted (Fig. 2). Both the A and D_{2-4} stage specimens were scanty for the whole autumnal period (not more than 5 and 15%) (Figs. 1 and 2).

The data were grouped by nearly weekly intervals (to obtain equal numbers of samples in each of them) and every interval means of the individual percentages of the BC-, D_0 -, and D_1 -stages were calculated. As shown in Fig. 5A the mean percentage of the BC-stage increased over the whole period especially from early February to mid-March, and the percentage of D_0 -stage accordingly decreased. The one-way variance analysis confirmed significant seasonal influence on the percentages of BC- and D_0 -stages (Table 3). Differences in the mean D_1 -stage's percentages are not significant.

The previous workers showed that the predominance of postmoult or ready-to-moult krill was not rare in the samples from the water column or separate swarms (BUHHOLZ, 1985; BUHHOLZ *et al.*, 1988). A question may arise why such specimens were rare in the dense aggregations and layers of the krill examined in this study. Two explanations are possible. Because euphausiids of the stages A and partly D_{3-4} are soft (BUHHOLZ, 1982), they may be rumbled in the trawl and are lost in the sample. Mechanical deformation of such kind is not the case for the D_2 -stage, but this stage also is not numerous in the samples.

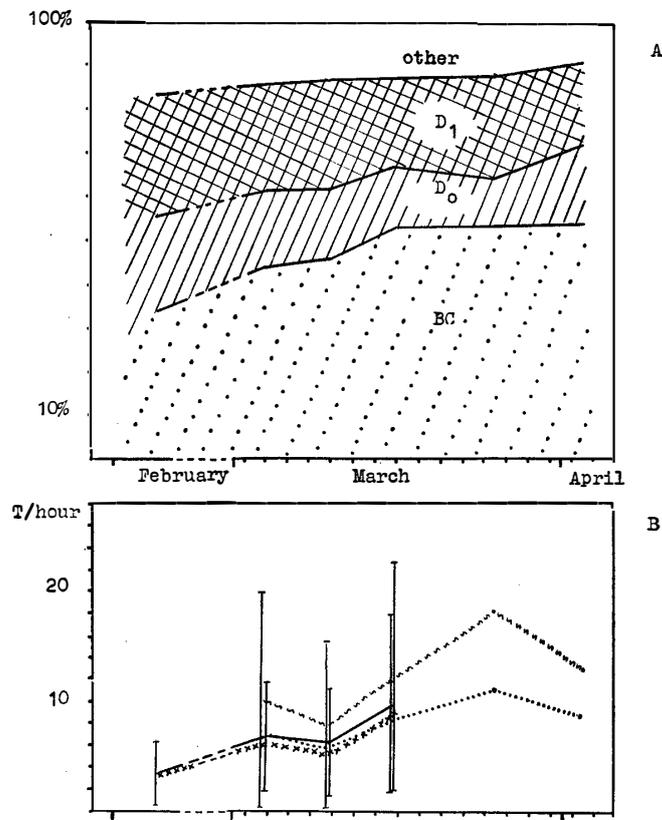


Fig. 5. A—Percentages of the main moult stages in the krill concentrations averaged by approximately weekly intervals. B—CPUE-indices: solid line—"KAPITAN OLEINICHUCK" mean catch per hour, crossed line—the same vessel's TC/TFISHT, s-line—"MYS JUNONY" mean catch per hour, dotted line—the same vessel's TC3/TFISHT (bars—standard deviations for means).

Table 3. One-way variance analysis of seasonal variation of the percentage of the main moult stages in the krill concentrations.

Date	Mean percentage of a stage			Rank values of TC/TFISHT indices
	BC	D ₀ %	D ₁	
2– 7.02	33.9	21.7	27.8	1
28.02– 7.03	44.3	17.4	24.3	3
8–13.03	45.6*	16.0	25.1	2
14–20.03	53.6*	13.1*	20.8	4.5
21–30.03	53.9*	10.9*	23.8	6
31.03– 5.04	54.3*	17.6	18.6	4.5
Errors	4.8	2.0	1.1	
F	2.77	3.64	1.10	
p	<0.05	<0.05	not significant	

* Significantly different from the value of 2–7 February.

The second explanation suggests that the concentrations of the krill of high density consisted mainly of the intermoult and early premoult individuals. Individuals or their swarms which are ready to moult may leave the concentrations, so the ecdysis takes place outside them. This moult-related behavioral pattern should have an adaptive value since soft animals can reduce a chance to be eaten by the conspecifics as KILS (1983) observed in aquaria. Various behavioral ways are adopted by the crustaceans for avoiding intraspecific attacks when moulting or just moulted (PASSANO, 1960; REAKA, 1976; LIPCIUS and HERRNKIND, 1982). As known also for the crustaceans, the oxygen consumption increase during the premoult phase (NOVALES *et al.*, 1978). But the oxygen pressure is evidently a limiting factor for the maintenance of krill aggregations (JOHNSON *et al.*, 1984). So the oxygen deficiency may force the krill to go away from the aggregations during a preparation for ecdysis.

Returning to the seasonal changes in moult activity one must note that the BC-category includes resting stage C_4 (DRACH, 1939). So, the autumnal increase of the BC-stage percentage indicates a decrease of the moult activity. A drop of the D_0 -stage percentage probably reflects the mass transition to the next stages but this transition is not compensated by corresponding start of the preparation for moult in the intermoult krill.

In late winter almost all the krill off Elephant Island (in the ice-free waters) were in the intermoult condition (MORRIS and PRIDDLE, 1984). Our recent observations (Winter Weddell Gyre Study, 1989) showed that *E. superba* actively moulted in the similar season under the ice (4% postmoult, 45% intermoult and 51% premoult animals). Obviously the changes in the moult activity of the krill in autumn and winter depend on what habitat it uses. When *E. superba* survives under unfavorable conditions, being aggregated in the ice-free waters, the moult cycles may be more prolonged than in dispersed swarms under the ice. This is due to be possible availability of the ice-algae (SPIRIDONOV *et al.*, 1985; MARSCHALL, 1988). BUHHOLZ *et al.* (1988) also demonstrated a variability of the moulting activities within and between years in the Scotia Sea and its dependence on the feeding conditions.

3.3. *Moult and seasonal variability of krill concentrations*

Densities of *E. superba* concentrations in the D'Urville Sea, as well as in the other areas of the Antarctic, vary seasonally, which is reflected by CPUE-measures (DOLZHENKOV *et al.*, 1990; see Table 1). Obviously the density of the concentrations reaches the maximum in autumn. CPUE-indices for the time intervals analyzed for mean percentages of the moult stages are shown in Fig. 5B. Their increase coincides well with the increase of the percentage of the intermoult krill (Fig. 5A, B). Unfortunately, fishery statistics for each one of the trawlers did not cover the whole period of the investigations. Combining the values of the least varied index (TC/TFISHT) (Fig. 5B) for both ships, we got Spearman's rank correlation coefficient of 0.83 between this index and the BC-stage percentage ($p < 0.05$; rank values are shown in Table 2).

We suppose that the moult activity really influences the density of krill concentrations. *E. superba*, as has been noted, may moult outside the concentrations. Consequently the higher the moult frequency, the more krill would leave the aggregations. This loss would not be necessarily compensated by the arrival of new animals

with hardened cuticle. When moults become rarer in autumn the advection of other krill from the surrounding waters to the concentrations should be greater than the loss of the moulting krill, and aggregation density should increase.

Probably the relations between moult and density of the krill aggregations are more complex. It is known for *E. superba* that the decrease of its food availability forces them to seek the more economical regime of living (KAWAGUCHI *et al.*, 1986; BOYD *et al.*, 1988). This may be expressed in slow moult rates and a decrease of the locomotory activity of the krill. LIPCIUS and HERRNKIND (1982) showed that the locomotor activity of the spiny lobster *Panulirus argus* is influenced by the moult cycle and it decreases from the B₂-stage to the ready-to-moult phase. We speculate that it is also true for *E. superba*. In late summer–autumn the krill concentrates in the areas of the slow mesoscale circulations (DOLZHENKOV *et al.*, 1990, in the D'Urville Sea) where the currents are weak enough for allowing the station-keeping of the krill but they bring the food particles to them. Our data on the krill feeding (V. A. SPIRIDONOV, in preparation) revealed that the krill in the concentrations fed actively in spite of the scarcity of net phytoplankton. In such a situation the limited locomotor activity should favour the station-keeping of the krill and leads to the accumulations of more animals in certain places.

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