

Reproductive characteristics of Antarctic Krill, *Euphausia superba* Dana, in the Prydz Bay region

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Abstract Experiments and observations on reproduction of Antarctic krill, *Euphausia superba* Dana, were conducted on board ship of R/V "JIDI" during the austral summer of 1993 in the Prydz Bay region. The development of ovaria oocytes in gravid females, spawning episodes, and brood size were studied. The sexual maturity process and spawning season were discussed. Fifty-three live gravid females captured at two stations in January, 1993 were cultured in a cool-room on board. They spawned within 1 to 16 days after capture. Most of them spawned only once except two, that spawned secondly on the 5th and 7th day after first spawning. The brood size of first spawning ranged from 225 to 5919 eggs with the average of 2132 eggs. The second brood was rather small, about 500 eggs. There were 0~213 (mean 32) mature oocytes remained in the post-spawn ovaries, and revitellogenesis was not observed. Brood size increased with the increasing of body length, but the correlation was not good. The number of ovarian oocytes in gravid female ranged from 2188 to 9263 with a mean of 5283. The composition of oocytes of different type varied in different samples. That all oocytes become completely matured seems to be an indication of pre-spawning. Spawning could take place through the summer with the peak spawning occurring from late January to late February. Interannual variation in peak spawning season might be significant.

Key words reproduction, Antarctic krill, the Southern Ocean.

1 Introduction

Antarctic krill, *Euphausia superba* Dana, is thought to be an important component of the Antarctic marine ecosystem considering its huge standing stock and its key position in Antarctic marine food web (Marr, 1962; Mauchline, 1980; Hempel, 1983). Year to year variations in distribution and abundance of Antarctic krill will influence both primary production and predators of high trophic level, and further the entire ecosystem. Antarctic krill is considered to be the important potential source of protein and becoming the object of a developing fishery. The knowledge about the mechanisms of recruitment is important for a good understanding of population dynamics of this species and provide basements for fishery managements. But until now, there are many uncertainties on reproductive characteristics of this species, especially in the Prydz Bay region.

Fecundity is an important index of reproduction of *E. superba*. It is defined as the number of eggs laid during any one breeding season (Mauchline, 1968). Size and the

number of broods produced in a breeding season determine the fecundity of euphausiids during the spawning season (Mauchline and Fisher, 1969), but there is no agreed opinion on it (Harrington and Ikeda, 1986). Timing of the peak spawning may be an important factor which influence the recruitment of this species, since the survival of early larval stages is closely related to the availability of food in the environment and the productive season is short in the Southern Ocean. So year to year variations in peak spawning season may be a direct factor influencing the krill population dynamics.

This paper presents some results on broods size, spawning episodes and post-spawn ovarian development, as well as breeding habit of krill observed on board ship during the summer cruise of 1992/1993, in the Prydz Bay region. Ovarian oocytes development and spawning season were also investigated based on the data collected in 4 summer cruises, from 1989/1990 to 1992/1993, in this area.

2 Materials and methods

2.1 Laboratory observation on spawning and brood size

Live female *E. superba* which used in laboratory spawning and brood size experiments were collected during the 9th Chinese National Antarctic Research Expedition cruise of R/V "Jidi" in the Prydz Bay region in January, 1993. Krill were from two samples: sample A was collected by a 0~35 m oblique tow with the high-speed zooplankton sampler at site of 66°10'S, 62°55'E in January 14; sample B was collected by 0~100 m oblique tow with the 6 feet Issacs-kidd midwater trawl (IKMT) at site of 67°06'S, 73°10'E in January 30, 1993.

Active females with swollen carapace by enlarged ovary (3DF of maturity stages defined by Makarov and Denys, 1980) were picked out without prejudice and kept individually in 5-litre glass jars in refrigerator at temperature of 0~1°C. One-third of the seawater in jar was replaced by newly collected and filtered seawater everyday. Krill was fed with natural phytoplankton assemblage collected. Jars were checked at 00 : 00, 06 : 00, 12 : 00 and 18 : 00 local time regularly and more frequently when spawning started. All eggs found in the jar were removed and preserved in 5% formalin in seawater. Females after the first spawning was completed were kept in jar to observe the possible second and third time spawning and the rematuration until they died or be killed for other purpose. The died or killed post-spawn krill were preserved in 10% formalin in seawater. Overall 16 females from sample A and 37 females from sample B were observed for this study.

Later in the laboratory, the number of eggs for each brood and the number of oocytes remained in the ovary were counted. The diameter of eggs (mean of 40 eggs), diameter of eyes and length of uropod exopodite of the post-spawn females were measured under a dissecting microscope.

2.2 Observations on oocytes development in gravid female

Krill samples were collected during the routine summer cruises of R/V "JIDI" from

1989/1990 to 1992/1993, in the Prydz Bay region. These samples provide us plentiful data for analysis of breeding habits of *E. superba*. The sampling times of the 4 cruises were: Jan. 7 ~ Mar. 3, 1990; Dec. 28, 1990 ~ Jan. 11, 1991; Dec. 30, 1991 ~ Jan. 28, 1992; Jan. 11 ~ Feb. 5, 1993. 2 samples in 1989/1990, 3 samples in 1990/1991, 2 samples in 1991/1992 and 3 samples in 1992/1993 were selected for the analysis of oocytes development of gravid females. Table 1 lists the sampling data of the 10 samples.

Table 1. Summary of sampling data of samples for observation of oocytes development in gravid females

Sampling years	Sampling No.	Sampling position	Sampling time (day/month/year)	Sample size	Mean TL $M \pm SD$ (mm)
1989/1990	Sample 1	64°58'S, 75°00'E	Feb. 18, 1990	10	49.49 ± 0.84
	Sample 2	64°57'S, 79°56'E	Mar. 3, 1990	10	53.06 ± 0.84
1990/1991	Sample 3	62°00'S, 72°00'E	Jan. 8, 1991	5	54.31 ± 1.36
	Sample 4	66°03'S, 77°57'E	Jan. 6, 1991	5	49.97 ± 1.09
	Sample 5	63°55'S, 84°45'E	Jan. 4, 1991	10	50.85 ± 0.08
1991/1992	Sample 6	64°01'S, 78°01'E	Jan. 5, 1992	11	51.36 ± 0.52
	Sample 7	66°39'S, 67°41'E	Jan. 25, 1992	10	48.76 ± 0.88
1992/1993	Sample 8	65°02'S, 73°08'E	Jan. 31, 1993	15	51.53 ± 0.82
	Sample 9	67°06'S, 73°10'E	Jan. 30, 1993	32	49.41 ± 0.43
	Sample 10	64°57'S, 77°54'E	Feb. 3, 1993	33	50.88 ± 0.39

For each samples, 5 to 33 gravid females (3DF) were selected randomly. Length of uropod exopodite and diameter of eyes were measured under dissect microscope. For samples of 1992/1993, wet body weight were measured. The ovary of each female was dissected out and the number of type 1 (oc1), type 2 (oc2), type 3 (oc3) and type 4 (oc4) oocytes were counted according to Cuzin-Roudy (1987a) and Cuzin-Roudy and Amsler (1991). Oc1 and oc2 were counted together.

2.3 Development stage composition in females

Development stage composition in females for the 4 cruises were analysed. The sexual maturity stages of female were classified based on the external sexual characters described by Makarov and Denys (1980).

3 Results

3.1 Spawning habits in laboratory on shipboard

The measurements and spawning information of individual females from sample A and B incubated on board ship for the observation of spawning habits were summarised in Table 2.

Table 2. Body measurements and spawning information for females from sample A and sample B maintained on board the ship. ED=eye diameter; UL=uropod length; Oc4=type 4 oocytes remained in spawned females; * indicate second spawning

Sampling No.	ED (mm)	UL (mm)	Spawning date		Brood size	Death date (day/month)	Oc4
			day	time			
A-1	-	6.5	Jan. 19	0600	566	24/01	-
A-2	1.875	5.8	Jan. 19	1400	1650	07/02	31
			Jan. 26 *	1200	516 *		31
A-3	-	6.4	Jan. 20	0000	5919	30/01	-
A-4	-	-	Jan. 21	1000	1802	-	-
A-5	-	-	Jan. 21	1800	893	-	-
A-6	-	-	Jan. 21	1800	1102	27/02	-
A-7	2.325	6.5	Jan. 22	0000	3550	-	8
A-8	-	-	Jan. 23	0600	1019	07/02	-
A-9	2.275	6.4	Jan. 23	0600	665	-	5
A-10	-	-	Jan. 24	1200	3475	-	-
A-11	-	-	Jan. 25	0800	2265	-	-
A-12	-	6.7	Jan. 25	1800	850	26/01	-
A-13	1.9	5.3	Jan. 26	2200	1216	04/03	2
A-14	1.85	5.9	Jan. 28	0000	846	10/02	45
A-15	2.15	5.55	Jan. 28	0000	2794	05/03	1
A-16	2.2	6.25	Jan. 30	1800	2509	09/02	1
B-1	-	-	Jan. 30	1800	603	-	-
B-2	2.1	6.35	Feb. 01	0000	-	13/02	0
B-3	2.225	6.1	Feb. 01	1100	590	15/02	3
B-4	1.95	5.65	Feb. 01	1200	822	10/02	35
B-5	-	-	Feb. 01	1600	1114	-	-
B-6	2.175	6.1	Feb. 01	2200	3052	11/02	32
B-7	-	-	Feb. 01	2200	3488	07/02	-
B-8	2.175	6.2	Feb. 01	0400	3036	05/02	22
B-9	-	5.8	Feb. 01	0400	1161	10/02	-
B-10	-	6.7	Feb. 01	0800	2160	09/02	-
B-11	-	6.7	Feb. 01	1400	-	12/02	-
B-12	-	6	Feb. 01	1400	896	-	-
B-13	2.025	6.15	Feb. 01	1600	3400	-	1
B-14	-	6.3	Feb. 01	1600	1003	11/02	-
B-15	-	5.4	Feb. 01	2200	1690	12/02	-
B-16	-	-	Feb. 02	0000	225	-	-
B-17	-	5.6	Feb. 02	0000	2650	10/02	-
B-18	-	5.6	Feb. 02	1000	1916	14/02	-
B-19	-	6.2	Feb. 02	1000	3333	09/02	-
B-20	-	6.2	Feb. 02	1200	1544	-	-
B-21	-	-	Feb. 02	2200	2440	-	-
B-22	2.25	6	Feb. 03	0000	3885	14/02	19
B-23	-	6.1	Feb. 03	0000	3756	13/02	9
B-24	2.25	6.45	Feb. 03	0000	1399	-	1
B-25	2.2	6.15	Feb. 03	0400	-	13/02	9
B-26	2.215	5.7	Feb. 03	1200	2030	09/02	213
B-27	2.25	6.45	Feb. 04	1200	3124	12/02	141
B-28	1.925	5.7	Feb. 05	0600	2394	05/02	163
B-29	-	-	Feb. 06	0400	1000	-	-
B-30	2.325	6.6	Feb. 08	0600	3640	14/02	0
B-31	-	-	Feb. 08	1200	568	-	-
B-32	2.275	6.1	Feb. 08	2000	2082	15/02	0
B-33	2.3	6.7	Feb. 10	1000	2101	18/02	0
			Feb. 15 *	2000	492 *		
B-34	2.2	5.65	Feb. 10	1600	4790	-	1
B-35	2.755	6.9	Feb. 10	2200	4867	10/02	1557
B-36	2.2	6.15	Feb. 11	1200	2580	21/02	13
B-37	2.3	6.5	Feb. 13	2200	-	27/02	-

3. 1. 1 *Spawning time*

16 gravid females with swollen carapace from sample A, which collected on 14 January spawned first time from 19 to 30 January, 5 to 16 days (mean 9.4 days) after capture. Sample B which collected on 30 January contained 37 gravid females, which spawned first time from 1st to 15 February, 1 to 15 days (mean 5.7 days) after capture (Table 3).

Table 3. Frequency(%) of first spawning of gravid females after capture, from two samples in the Prydz Bay region, in January 1993

Sample No.	No. of females	Day after capture															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
A	16	0	0	0	0	12.5	6.25	18.75	6.25	12.5	6.25	12.5	6.25	0	12.5	0	6.25
B	37	2.7	0	37.84	18.92	8.11	2.7	2.7	2.7	0	10.81	0	8.11	2.7	0	2.7	0

3. 1. 2 *Spawning episodes and ovary development of spent female*

Most of the females spawned only once. Spawned females had been incubated for 1 to 39 days (mean of 12.3 days) before death or being killed. During this period, only 2 females released eggs second time after first spawning 5 and 7 days separately (Table 2). For the first spawning episode, it was observed that females released almost all or a large fraction of eggs, and this process lasted less than 4 hours since the beginning of spawning. Some of the observed females released a small fraction of eggs within the following 24 hours.

26 post-spawn females were dissected for observation of remained oocytes in ovary and maturity development. There were 0~213 (31 by average) mature oocytes (oc4) remained in ovaries, except one female which died immediately when spawning with 1557 oc4 remained in the ovary (Table 2). An negative correlation was found between the number of oc4 remained in spent ovary and time of days after spawning ($R=0.447$, $F[1,15]=3.747$, $p=0.072$). The compositions of oocytes in spent ovaries were only oc4 for most of the spent females, only three females had a few oc1 and oc2 remained in spent ovaries.

3. 1. 3 *Brood size and egg diameter*

The first brood size of 49 females ranged from 225 to 5919 eggs (mean = 2132, s.d. = 169). The number of eggs released by two females secondly were 516 and 493 separately. The mean diameter of eggs released ranged from 534.38 μm to 607.19 μm (mean = 562.88 μm , s.d. = 2.39 μm).

Table 4 gives the measurements of uropod length, brood size, egg diameter of sample A and sample B and the comparison between them. The average of uropod length (6.09 mm), brood size (1945) and egg diameter (537.19 μm) of female krill in sample A were slightly smaller than those of females in sample B (uropod length = 6.13 mm, brood size = 2237, egg diameter = 563.65 μm separately). But the results of analysis of

variation (ANOVA) indicated that there were no significant differences of uropod length ($F[1, 38]=0.0045$, $p=0.9465$), brood size ($F[1, 47]=0.5312$, $p=0.2697$) and egg diameter ($F[1, 22]=1.9798$, $p=0.1734$) between the two samples.

Table 4. Mean length of uropod exopodite, brood size and egg diameter and ANOVA analysis in sample A and sample B obtained from the Prydz Bay region, Antarctica, in January 1993

	Uropod length (mm)	Brood size	Egg diameter (μm)
Sample A	6.09 ± 0.16	1945.06 ± 372.14	537.19 ± 6.02
Sample B	6.13 ± 0.07	2237.21 ± 216.69	563.65 ± 3.64
ANOVA	$F(1, 38)=0.0045$ $P=0.9465$	$F(1, 47)=0.5312$ $P=0.4697$	$F(1, 22)=1.9798$ $P=0.1734$

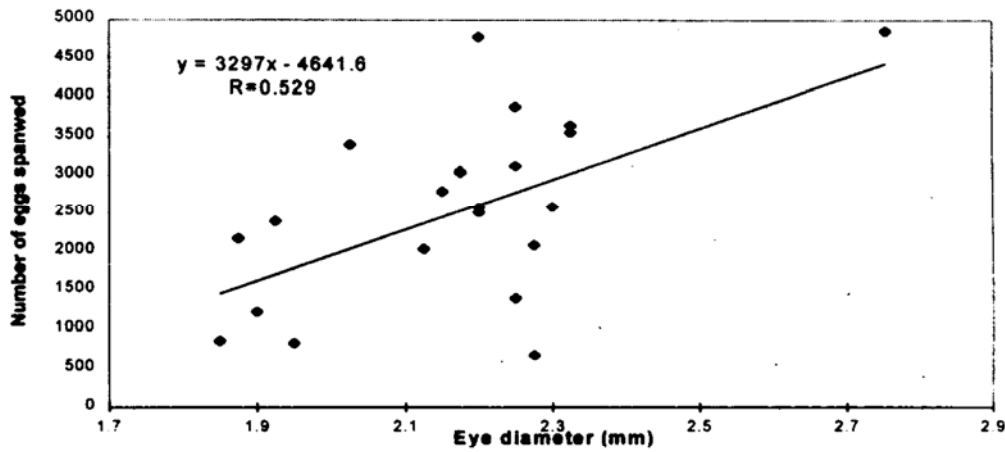


Fig. 1. Relationship between brood size (total number of eggs spawned) and eye diameter (mm) for females from two samples in the Prazy Bay region.

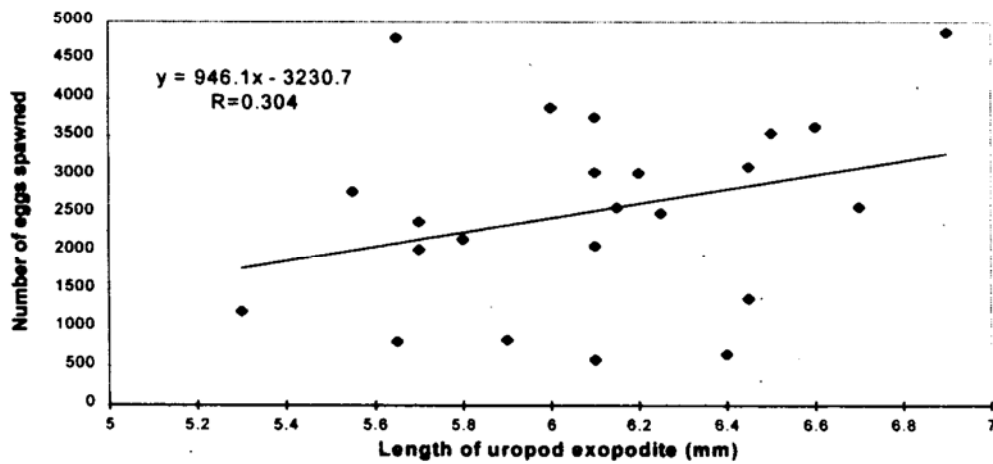


Fig. 2. Relationship between brood size (total number of eggs spawned) and length of uropod exopodite (mm) for females from two samples in the Prazy Bay region.

The total number of eggs spawned by females both in sample A and sample B were plotted against diameter of eyes in Fig. 1 and against length of uropod exopodite in Fig. 2. A significant positive correlation of brood size (BS) against eye diameter (ED) in mm was found by linear regression analysis: $BS = 3297 \times ED - 4641.6$ ($R = 0.529$, $F[1,21] = 8.144$, $P = 0.0095$). The correlation efficiency between brood size and uropod length (UL) in mm was not as good as that between brood size and eye diameter, but the correlation was still statistically significant: $BS = 946.1 \times UL - 3230.7$ ($R = 0.304$, $F[1,21] = 2.2089$, $P = 0.1521$).

The regression analysis indicated that there was no significant correlation between egg diameter and uropod length ($R = 0.186$, $F[1,17] = 0.6106$, $P = 0.4453$).

3.2 Ovarian oocytes in gravid females

3.2.1 The number of oocytes in relation with body weight and length

The numbers of oocytes in ovaries of gravid females captured during austral summer of 1992/1993 were plotted against their wet body weights in Fig. 3. Ovarian oocytes (OC) increased with the increase of wet body weights (WW , g). The relationship between OC and WW was expressed as the following: $OC = 5172.1W - 1121.6$, $R = 0.856$. Analysis of variation for regression and residual showed that the correlation was significant (ANOVA: $F[1,78] = 14.665$, $P = 0$).

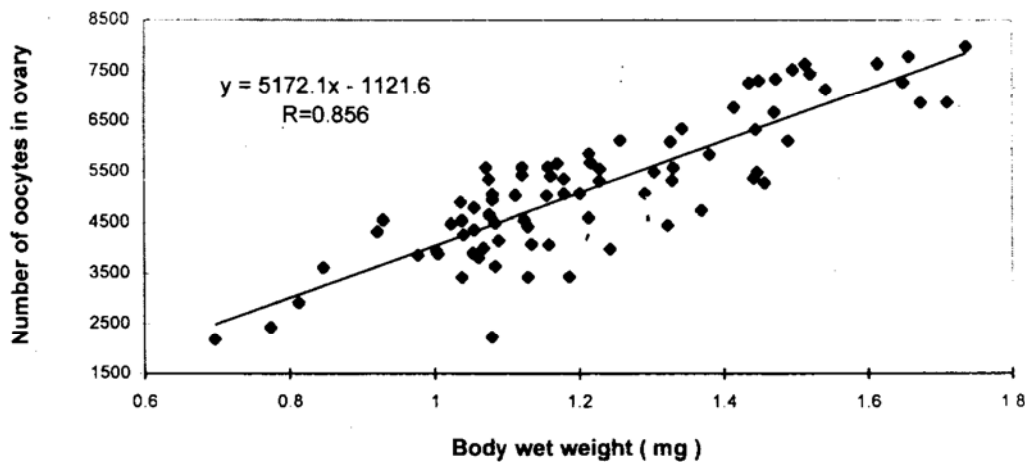


Fig. 3. Relationship between ovarian oocytes and body wet weight of gravid female captured during austral summers of 1992/1993 in the Prazy Bay region.

Fig. 4 showed the relationship between the number of oocytes in ovary and eye diameter (ED , mm) of gravid females collected in the summer of 1992/1993. This relationship was expressed by the equation: $OC = 3799.1 \times ED - 3175.6$, $R = 0.431$. Although the correlation efficiency ($R = 0.431$) was not as significant as that between ovarian oocytes and body weight ($R = 0.856$), ANOVA analysis for regression and residual revealed that the correlation was also statistically significant (ANOVA: $F[1,62] = 14.148$, $P = 0.0004$).

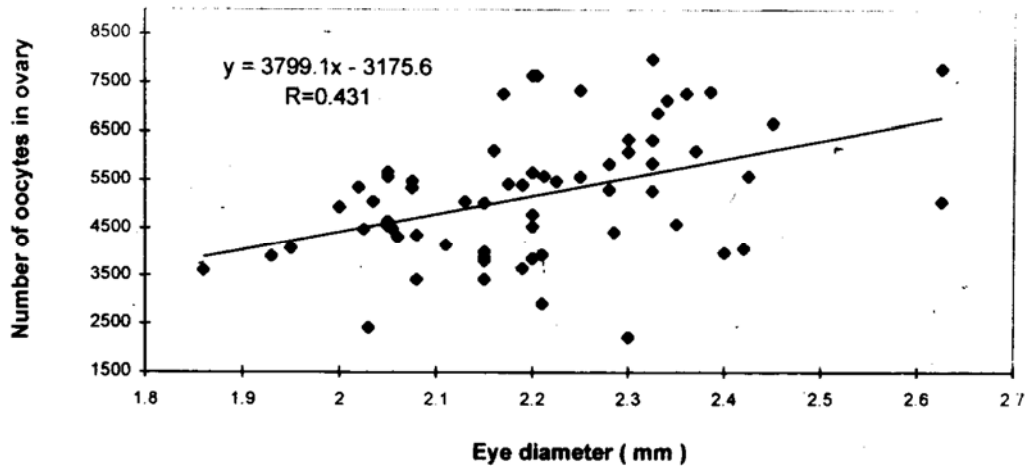


Fig. 4. Relationship between ovarian oocytes and eye diameter of gravid female captured during austral summer of 1992/1993 in the Prazy Bay region.

For female *E. superba* obtained during the austral summer from 1989/1990 to 1991/1992, relationships between ovarian oocytes and eye diameter, ovarian oocytes and uropod length (UL, mm) were shown in Fig. 5 and Fig. 6 separately. The results of regression and ANOVA analysis were as follows:

$$OC = 2718.1 \times ED - 850.22, R = 0.266, F(1, 59) = 4.509, P = 0.038$$

$$OC = 813.2 \times UL - 35.98, R = 0.243, F(1, 59) = 3.166, P = 0.08$$

3.2.2 Oocytes composition

Table 5 showed the percentages of the number of oc1, oc3, oc4 to the total number of ovarian oocytes in gravid females ovaries in the ten samples. Sample 1 and 2 were collected in February and March of 1990 separately. Compositions of oocytes from these two samples were dominated by oc4 (98.7%), there were few oc3 and oc1~2. Oocytes compositions of sample 3~5 which collected in the early January 1991 were also dominated by oc4 (59.2~72.7%), but there were a certain amount oc3 (18.5~30.3%) and oc1~2 (1.9~10.6%). Sample 6 which collected in the early January and sample 7 which collected in the late January, 1992, had different ovarian oocytes compositions. Sample 6 had almost the same percentages of oc4, oc3 and oc1~2 (31.0, 38.4, 30.6% separately), but sample 7 was dominated by oc4 (90.3%). Sample 8~10 were collected in the late January and early February. The fraction of oc4, oc3, oc1~2 were 59.4~97.6%, 1.6~19.9% and 0.8~20.7% separately. The fraction of oc4 in sample 9 was higher than that in sample 8 and sample 10.

It seemed that the maturity stage composition of oocytes was related with the sampling time, e.g. the percentages of oc4 collected in late February and early March were higher than that collected in January.

Table 5. Number and composition of oocytes in gravid females from 10 samples (see Table 1)

Sample No.	Total oocytes		Oocytes composition (%)		
	Range	M±SD	oc1~2	oc3	oc4
Sample 1	4602~8046	5809±346	0.7	0.6	98.7
Sample 2	2672~6150	4313±350	1.1	0.2	98.7
Sample 3	3657~6393	4989±487	10.5	30.3	59.2
Sample 4	5145~7317	6164±358	1.9	25.4	72.7
Sample 5	2724~6635	4598±371	10.6	18.5	70.9
Sample 6	3552~9263	6477±528	30.6	38.4	31.0
Sample 7	3135~6951	4919±353	5.0	4.7	90.3
Sample 8	2188~7796	5135±380	20.7	19.9	59.4
Sample 9	2228~7537	4965±224	0.8	1.6	97.6
Sample 10	2924~7989	5462±238	10.8	14.2	75.0

oc1~4; type oocytes; M; mean; SD; standard error.

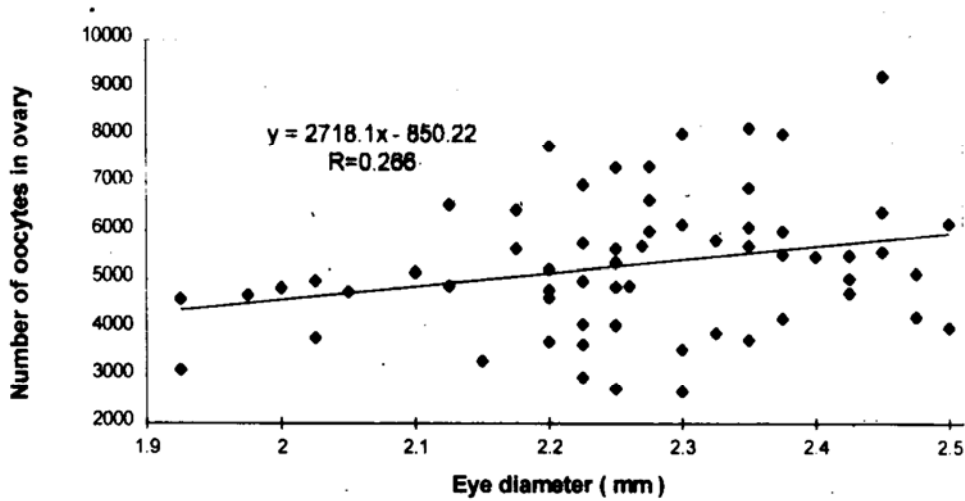


Fig. 5. Relationship between ovarian oocytes and eye diameter of gravid female captured during austral summers of 1989/1990, 1990/1991, 1991/1992 in the Prazy Bay region.

3. 2. 3 Variability of ovarian oocytes

The numbers of oocytes in ovary of gravid female ranged from 2188 to 9263, with average of 5283. The mean numbers of ovarian oocytes of each sample ranged from 4313 to 6477.

Year-to-year variability of the number of ovarian oocytes in gravid female were tested by ANOVA with the results shown in Table 6. The differences in numbers of ovarian oocytes between different years were not significant ($F(3,137)=1.123$, $p=0.342$).

3. 3 Development of sexual maturity stage and estimation of spawning time

The percentage-frequency distribution of maturity stage of sub-adult and adult female krill were shown in Fig. 7~10 for each sampling year.

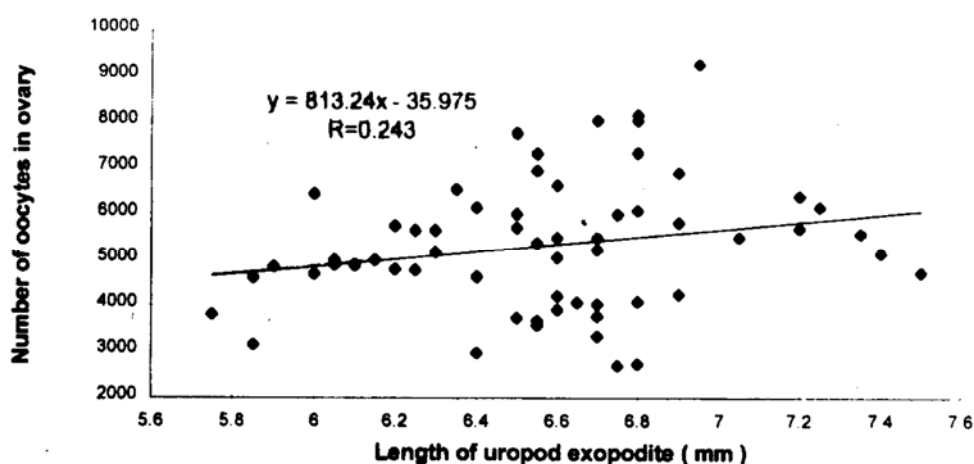


Fig. 6. Relationship between ovarian oocytes and uropod exopodite length of gravid female captured during austral summers of 1989/1990, 1990/1991, 1991/1992 in the Prydz Bay region.

Table 6. Data of ANOVA for the number of ovarian oocytes in gravid female sampled in different years in the Prydz Bay region

Anova single factor							
SUMMARY	Groups	Count	Sum	Average	Vanance		
	1989/1990	20	101216	5060.8	1736947		
	1990/1991	20	101736	5086.8	1469610		
	1991/1992	21	120434	5735.0	2729236		
	1992/1993	80	416128	5201.6	1818051		
ANOVA	Source of variation	S	df	MS	F	P-value	F crit
	Between groups	6370936	3	2123645	1.122732	0.342177	2.670689
	Within groups	2.59E+08	137	1891498			
	Total	2.66E+08	140				

In 1989/1990 austral summer sampling was made in three separated months: 7~8 January, 16~20 February, and 7~8 March. Fig. 7 showed that, in early January, most of the females were in stage 2F (32.48%) and 3AF (55.41%) which had not mated. There was only a small fraction of gravid female (3DF, 4.49%). In the mid February, females were dominated by 3DF (56.59%). In early March, the difference of frequency of each maturity stage from 2F to 3DF was not obvious, but 3DF took the largest portion (29.41%). The situation in March might have less representative because only 68 females were captured, but at least it was shown that there were still a certain amount of gravid females in early March.

In 28 December~11 January of 1990/1991 summer cruise, the percentage composition frequencies of different maturity stage (from 2F to 3EF) were 10.06, 32.31, 14.60, 26.63, 13.34 and 3.06% respectively (Fig. 8). Similar to that in early January of last year, the frequency of 3DF was not high. Fig. 9 gave the situation in 5~25 January

of 1991/1992 summer cruise which indicated that 3DF dominated the female population (38.42%). From 11 January to 5 February, 1993, 75.5% of the captured females were 3DF (Fig. 10).

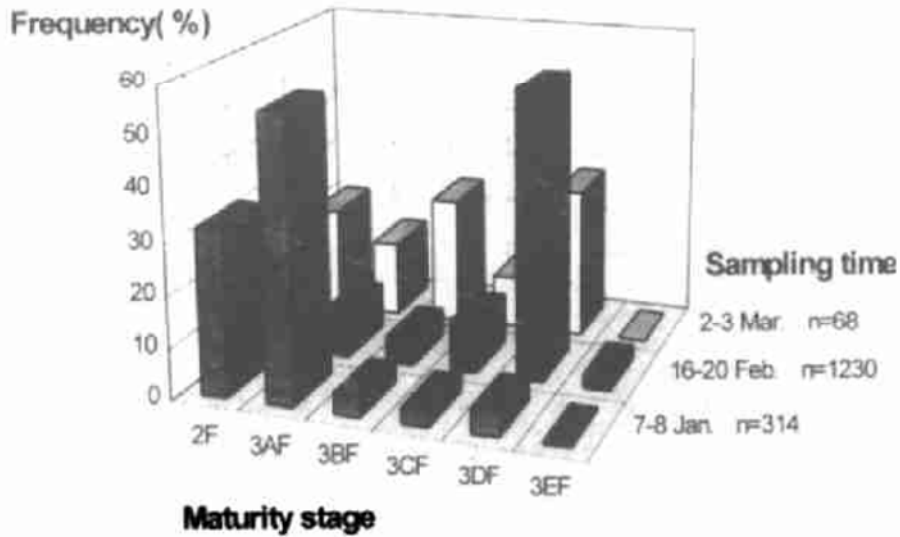


Fig. 7. Development of Maturity stage composition of females in the summer of 1989/1990 in the Prazy Bay region.

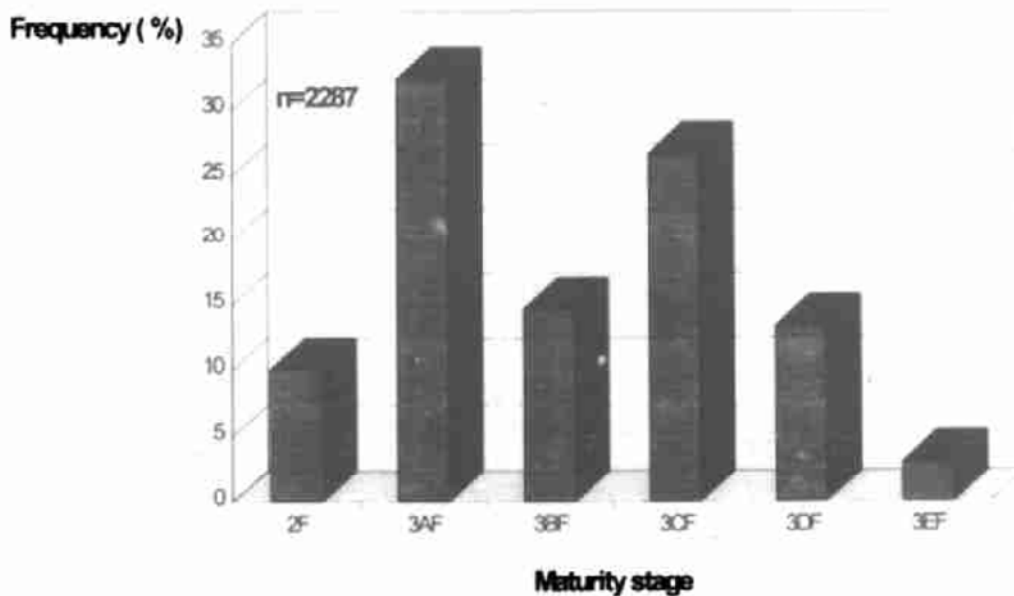


Fig. 8. Maturity stage composition of females in 28 December, 1990~11 January, 1991 in the Prazy Bay region.

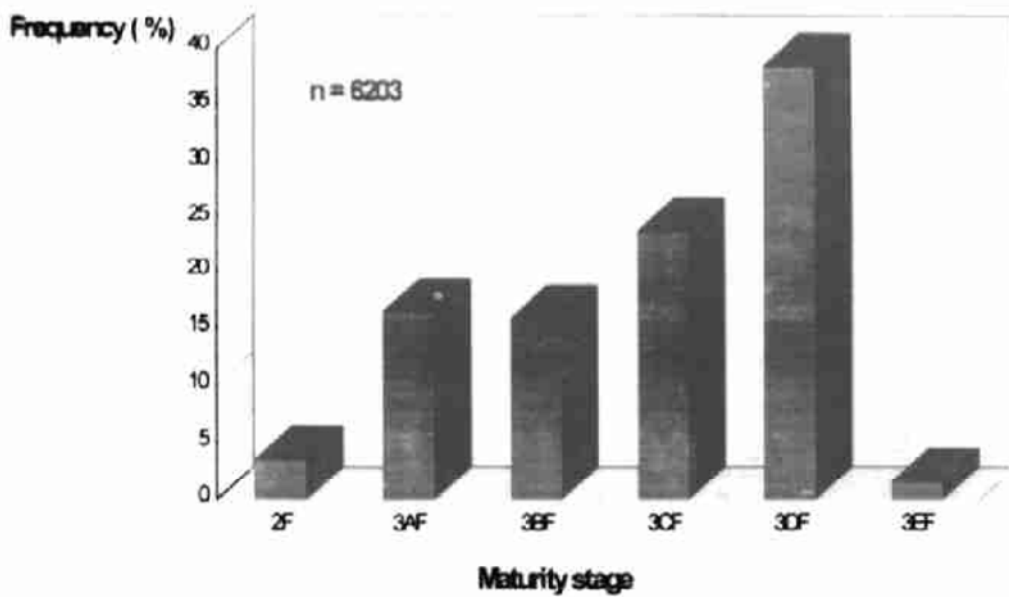


Fig. 9. Maturity stage composition of females in 5~25 January, 1992 in the Prazy Bay region.

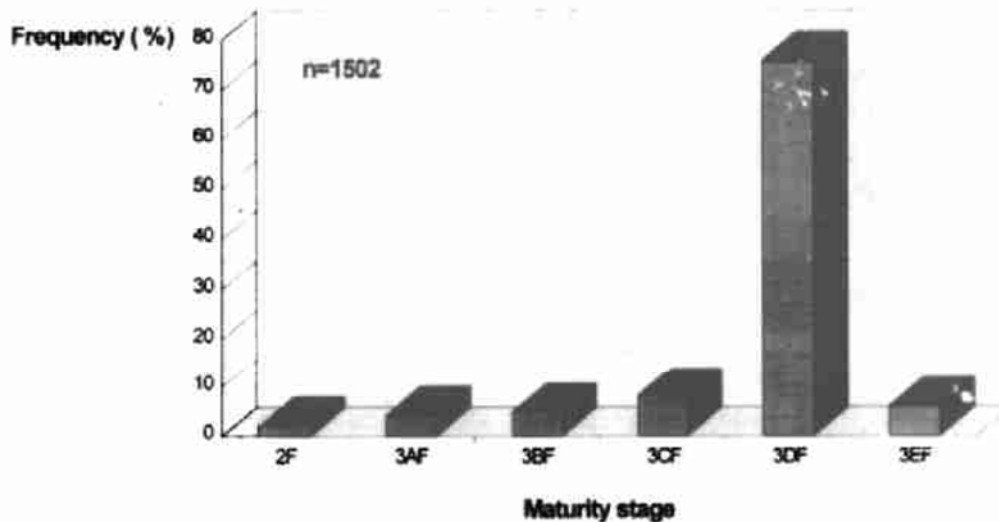


Fig. 10. Maturity stage composition of females in 15 January~5 February, 1993 in the Prazy Bay region.

4 Summary and discussion

(1) Most of the females spawned only once incubated on ship board, and revettilogenesis was not observed. The second spawning with comparatively small brood size seems to be continuation of the first spawning. Our observation supports that of Harrington and Ikeda (1986) and Nicol (1989) by the same method and in the same area. Regarding to the number of spawning episodes, some workers (Bargmann, 1945; Ivanov,

1970; Kikuno and Kawamura, 1983, cf. Harrington and Ikeda, 1986) suggested only one for each spawning season, some (Denys and McWhinnile, 1982; Cuzin-Roudy, 1987) thought there might be two or three, and even 9 to 10 (Ross and Quetin, 1983). Cuzin-Roudy (1987) studied the gonad history of *E. superba* maintained on board ship and observed three different batches of oocytes (type 1, 2, 4) at the same time in krill ovary, so she concluded that female *E. superba* could mature successive batches of eggs and spawn repetitively at least three times and presumably more during a single reproductive season. The observation of ovarian oocytes in gravid female (Table 3) indicated that different development phases of oocyte existed, the completely mature of almost all oocytes in ovary seemed to be an indication that spawning could happen soon. Krill of sample 9 with 97.6% oc4 in ovary came from the same sample of sample B used in laboratory spawning experiment would spawn in the following 1~15 days (Table 3). The sampling time of sample 1 and sample 2 which characterised by dominated oc4 and few oc3 and oc1~2 corresponded well with the February to early March peak spawning season in summer of 1989/1990 in the field (Wang and Zhong, 1993; Wang *et al.*, 1993).

Since the successive spawning were not observed for most females in laboratory spawning experiment of this study, and histological study of spent ovary showed that there were only few, if any, oocytes remained in spent ovaries, we can assume that the oocyte development is synchronously but, krill don't spawn until almost all of the oocytes become mature (stage oc4). When all oocytes develop to oc4, krill will release all eggs at one time.

(2) The brood size for this experiments ranged from 225 to 5919 eggs, with average of 2132. The brood size measured by former workers are: Denys and McWhinnile (1982), 1592~4054; Kikuno and Kawamura (1983), 627~3115 (cf. Nicol, 1989); Ross and Quetin (1983), 500~8000; Harrington and Ikeda (1986), 89~6167; Nicol (1989); 263~3662. The number of total oocytes in ovary of gravid female ranged from 2188 to 9263 with average of 5283 for this study, also close to the published data: 2000~14000 (Naumov, 1964; Jazdzewski *et al.*, 1978; Nemoto *et al.*, 1981, cf. Harrington and Ikeda, 1978); 2457~10977 (Wang and Chen, 1989); 11000~11500 (Bargmann, 1937). There was a distinct difference between the number of eggs spawned and that in ovary of gravid female. It seems that the majority of the oocytes in ovary will be released and the remains probably be resorbed (Zelikman, 1958; Mauchline, 1968, 1980). In our experiments, there might be loss by feeding of females on their own eggs right after spawning. Further works are need to ascertain what fraction of eggs is fully developed and released.

(3) The brood size and the number of ovarian oocytes had positive correlations with body length, although the correlation efficiencies were not very strong. Generally speaking, the fecundity of krill increases with the increasing of body length or age. It is widely accepted that krill may live for 4~5 years or even longer (Ettershank, 1983; Ikeda, 1987; Siegel, 1987). Regression and redeveloping of ovarian oocytes in post-spawn females were observed both in laboratory and field (Makarov, 1975; Denys and McWhinnile, 1982; Cuzin-Roudy, 1987). Siegel (1987) suggested that Antarctic krill spawned at least in three successive years in the Antarctic Peninsula areas.

(4) Our data collected in the 4 successive years indicated that, in the Prydz Bay region, spawning of Antarctic krill could take place through the summer, at least from early January to early March. The peak spawning might occur from late January to late February. As we do not have monthly data through the whole summer, it is difficult to say the peak spawning season exactly and discuss the year-to-year variability of it. However we could get some idea about the year-to-year variability based on the data we had. In early January of 1989/1990, most of the females were still remained very early stages of maturity (2F, 3AF), mating had not taken place yet by then, but in mid February, about 40 days later, the dominated stage move to 3DF which indicated the immediate peak spawning. The occurrence of peak abundance and composition of developmental stages of *E. superba* larvae also demonstrated that in 1989/1990, *E. superba* could spawn through the whole summer but with peak spawning in mid and late February (Wang and Zhong, 1993). Krill data of 1992 came mainly from two samples collected in 5 January and 25 January. Females in sample of 5 January were also dominated by 3DF (Fig. 10) similar to that in sample of 25 January, but there was large fraction of young oocytes in ovaries (Sample 6 in Table 5). 3DF is characterised by its swollen carapace caused by enlarged ovary, but the extent of swollen is different. Swollen carapace might not an indication of immediate spawning. Laboratory experiment showed that a few 3DF krill spawned as long as 15 days after their capture. As we have proposed that gravid females don't spawned until most of the ovarian oocytes become mature. The females captured in 5 January might spawn 10 to 20 day later, corresponding with the krill in the sample of 25 January, of which 90% ovarian oocytes were in mature stage oc4 (Sample 7 in Table 5). In late January and early February, 1993 females were dominated by 3DF. So the peak spawning season in 1991/1992 and 1992/1993 probably occurred in late January and early February, about 20 to 30 days ahead of the peak spawning suspected for 1989/1990.

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