

Environmental Variability and Its Impact on the Reproductive Cycle of Antarctic Krill¹

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SYNOPSIS. “Recruitment potential” in Antarctic krill in the Palmer Long-Term Ecological Research (LTER) study region west of the Antarctic Peninsula varied significantly over the 7-yr time series between January 1993 and January 1999. Timing of ovarian maturation, the percent of the population reproducing, and individual reproductive output (batch volume, embryo diameter) were measured. Indices have been developed to quantify the timing and intensity of reproduction in Antarctic krill. One finding important to estimates of population fecundity for this long-lived species is that the percent of the population reproducing can vary widely, from 10 to 98%. Each season was characterized as having delayed, average or advanced ovarian development. In this study we relate these indices to direct and indirect indicators of spring or annual food availability. The timing of the spring sea ice retreat and the extent of sea ice in the spring (September through November) appear to significantly affect the intensity and timing of reproduction in the population. Intensity of reproduction was highest under “average” conditions, and oöcyte development fastest with conditions of a late retreat and high spring sea ice extent.

INTRODUCTION

The premise underlying this study of interannual variability in the reproductive output of Antarctic krill, *Euphausia superba*, is that the quantity and quality of food available to female krill affects the rates of maturation and the reproductive output of both the individual and the population. The resulting variation in reproductive output will lead to differences in population fecundity and the potential strength of a year class. Although large differences in recruitment success in *E. superba* are well documented (Siegel and Loeb, 1995; Loeb *et al.*, 1997), recruitment success reflects the combined effects of variation in reproductive output and in survival of the early life history stages their first winter (Ross and Quetin 1991). In a study of early larval and gravid female abundances in the 1980s, Brinton *et al.* (1986, 1987) suggested that differences in the abundance of early furcilia stage larvae in late summer were a re-

flection of variation in ‘recruitment potential’ or reproductive output over that season. However, rarely is reproductive output, either of the individual or the population, directly investigated.

The reproductive cycle for *Euphausia superba* alternates between a resting period in fall and winter, and a maturation and spawning period in spring and summer. During the spawning season a reproducing female produces multiple batches (Ross and Quetin, 1983; Cuzin-Roudy, 1987*a,b*; Cuzin-Roudy and Labat, 1992), with each cycle of the ovary yielding three batches of embryos. After reproduction there is a period of reorganization, and subsequent regression of the ovary and thelycum to an immature state in fall and winter (Poleck and Denys, 1982). Maturation or rematuration of the ovary occurs in the spring. The energetic demands of reproduction in *E. superba* are high (Ross and Quetin, 1986; Nicol *et al.*, 1995), and occur over a prolonged period. Reproduction in these primarily herbivorous euphausiids depends on the food available during the reproductive season (Hagen *et al.*, 1996) since lipid stored during the previous season is used over the winter. Food is needed for ovarian

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TABLE 1. Palmer LTER cruises: Name, sampling dates, and transect lines surveyed.

Cruise	Sampling dates	Transect lines	No. Stations
93 Jan	8 Jan to 6 Feb	200.* (partial), 300.*, 400.*, 500.*, 600.*	37
93 Mar	28 Mar to 12 May		
94 Jan	11 Jan to 6 Feb	300.*, 400.*, 500.*, 600.*	35
95 Jan	7 Jan to 6 Feb	200.*, 300.*, 400.*, 500.*, 600.*	46
96 Jan	8 Jan to 9 Feb	200.*, 300.*, 400.*, 500.*, 600.*	46
97 Jan	11 Jan to 13 Feb	200.*, 300.*, 400.*, 500.*, 600.*	46
98 Jan	28 Jan to 13 Feb	200.*, 300.*, 400.*, 500.*, 600.*	42
99 Jan	9 Jan to 11 Feb	200.*, 300.*, 400.*, 500.*, 600.*	46

development and initiation of oöcyte development in spring, and for final maturation of the oöcytes and possible recycling of the ovary to produce additional batches in summer.

This study is part of the Palmer Long-Term Ecological Research (LTER) program, sited on the shelf and continental slope region west of the Antarctic Peninsula. The region is swept by the advance and retreat of seasonal sea ice each year, with maximum sea ice extent in August or September (Stammerjohn and Smith, 1996). In this region, ovarian maturation begins in September, and spawning is most intense in late January and February. The seven-year time series on the reproductive cycle in *Euphausia superba* is based on the annual summer (January/February) Palmer LTER cruise. Indices have been developed to quantify the timing and intensity of reproduction in individual Antarctic krill and in the population as a whole. In this study we relate these indices to direct and indirect indicators of seasonal or annual food availability. The extent of the sea ice and the timing of retreat represent variation in food resources associated with seasonal sea ice dynamics, and seasonal primary production represents variation in food resources in the water column in late spring and summer. In some years populations of salps and krill co-occur across the shelf, whereas in other years salps are only found near the shelf slope (Ross *et al.*, 1996, 1998). Thus this time series can be used to test the hypothesis that salps are direct competitors with Antarctic krill for food (Loeb *et al.*, 1997). If salps do out-compete krill for food, the prediction is that reproduction in krill will be delayed and less intense in years when

salps and krill occur than in years when salps are absent.

MATERIALS AND METHODS

At the initiation of the Palmer LTER a sampling grid with fixed geographic station locations (Waters and Smith, 1992) was established. Standard alongshore transects are 100 km apart, and standard stations on transects 20 km apart running from the coast to 200 km offshore. Each grid location is identified with 6 digits, 3 for the transect and 3 for the station, *i.e.*, 200.020 refers to the 200.* transect and the *.020 station. The 000.* or base transect is at the far southwest end of the grid, and the *.000 stations are the furthest inshore. The time-series reported in this study is based on 7 summer cruises from 1993 to 1999 with either the MV *Polar Duke* or the ARSV *Laurence M. Gould* (Table 1). The summer study region encompasses the 200.* to 600.* transects, on the continental shelf and slope between the southern ends of Anvers and Adelaide Islands. Due to weather and time constraints, not all of the 46 possible stations have been occupied every year (Table 1). The sampling and experimental design included net tows at each station. Analysis of the ovarian physiological maturity of krill yielded data on the timing and intensity of the reproductive season. At selected stations spawning experiments were conducted on board and the reproductive output of individual female krill measured.

Macrozooplankton collection

At each station macrozooplankton were collected with a 2-m square fixed-frame net (net of 700 µm stretch mesh) as described in Ross *et al.* (1998). Trawl contents were

TABLE 2. *Yearly relationships between total length (TL) in mm and wet weight (Wwt) in g for mature female Antarctic krill with red thelycums: Wwt = a · TL^b.*

Year	a	b	n	r ²
1993	$2.95 \cdot 10^{-6}$	3.283	92	0.98
1994	$4.10 \cdot 10^{-6}$	3.191	140	0.95
1995	$0.86 \cdot 10^{-6}$	3.641	103	0.92
1996	$0.66 \cdot 10^{-6}$	3.700	163	0.84
1997	$5.92 \cdot 10^{-6}$	3.098	41	0.95
1998 and 1999*	$1.06 \cdot 10^{-6}$	3.540	171	0.90

* The relationship found in 1999 was used for spawning females in 1998.

analyzed for macrozooplankton abundance either on board or from preserved subsamples. Either a subsample or the entire catch was preserved in 10% formalin. The abundance of the salp *Salpa thompsoni* at a station was expressed as numbers per 1,000 m³ of water filtered. Mean abundances for the grid were calculated with a log transformation and adjusted for zero values according to the method of Pennington (1983). A subset of krill encompassing the full size and sexual maturity stage range of krill collected was frozen in pre-weighed vials for wet weight determinations. Before freezing, the total length (Standard length 1, from the tip of the rostrum to the end of the uropods) (Mauchline, 1981) and sexual maturity stage of each krill was recorded: subadult (not able to determine sex), immature female or male, mature female (clear or red thelycum) or male. The red thelycum indicates a female in the reproductive cycle, either committed to reproduce that season or

reorganizing after reproducing that season. Wet weights of individual krill were determined on station within a week of the end of the cruise (weight of vial plus krill - weight of vial), and the relationship between total length and wet weight of female krill with red thelycums determined (Table 2).

Ovarian physiological maturity stages

Female krill were later analyzed for ovarian physiological maturity (Cuzin-Roudy and Amsler, 1991) (Table 3). Stages 4 to 9 are in the reproductive cycle, and have red thelycums. Stages 2, 3 and 10 are non-reproducing females. Large females still in oogenesis (stages 2 and 10) or early previtellogenesis (stage 3) in late January or February are unlikely to complete a cycle of maturation and release of oocytes before the end of the reproductive season. Stage 8—continuing females will recycle the ovary and produce a second group of three spawning episodes; stage 8—final will not (Cuzin-Roudy and Amsler, 1991). The spatial distribution of the different physiological stages each year was determined. Three preserved samples from each transect line were chosen for analysis, one inner (000 to 080), one middle (100 to 140) and one outer (160 to 200) shelf station. The stage composition was calculated as numbers of a stage per 1,000 m³ of water filtered.

In this study we used the percent of females actively spawning (stage 7) and post-spawn (stage 9) of all reproducing females (stages 4 to 9) to compliment experimental

TABLE 3. *Physiological phases of ovarian development for female Euphausia superba, according to Cuzin-Roudy and Amsler (1991).*

Ovarian Development	Stage
Non-Reproducing—subadult or resting	
Oögenesis and gametogenesis—immature thelycums	2, 10
Initiation of ovarian maturation	
● early previtellogenesis; no mating activity; clear mature thelycum	3
Reproductive cycle—all females with red thelycums	
Oöcyte development—prespawning—yolk accumulation	
● previtellogenesis (proteic yolk); mating activity begins	4
● vitellogenesis (lipidic yolk accumulation)	5 and 6
Oöcyte maturation and egg release	
● mature oöcytes ready to release in a few days	7
● recently spawned (8—continuing, recycle; or 8—final, complete)	8
Post-spawn, ovary in regression	9

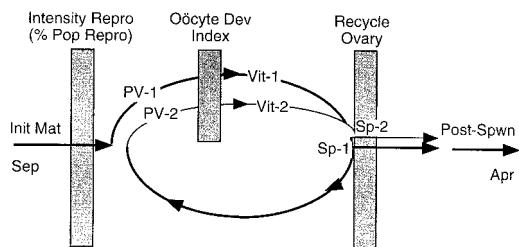


FIG. 1. Cycle of ovarian maturation in spring and summer (September to April) in *Euphausia superba*, with shaded bars indicating the postulated plateaus during the reproductive cycle. The postulated plateaus are after initial maturation (Init Mat), before vitellogenesis (Vit), and prior to the release of the embryos (Sp or spawning episodes). After the first three spawning episodes (Sp-1), the ovary may recycle, repeating the cycle of pre-vitellogenesis (PV-2), vitellogenesis (Vit-2) and spawning (Sp-2) before starting reorganization of the ovary for the winter (post-spawn = Post-Spwn).

determinations of spawning frequency. The presence of stage 7 females means that spawning is ongoing, and the absolute percent of stage 7 females is related to the spawning frequency (Quetin *et al.*, 1994). The higher the percentage of post-spawn females the greater the proportion of females that have completed spawning for the season. Differences among the composite of each transect line revealed spatial variation in the timing of reproduction. Details of the spatial distribution are described in Shaw (1997) for 1993 to 1997, and additional years will be presented in Shaw *et al.* (in preparation).

In most non-brooding eucarid crustaceans there are three more or less brief plateaus during maturation, the first after proliferation of oöcytes in the germinal zones of the ovary, the second at the beginning of vitellogenesis, and the third before actual release of the embryos (Nelson, 1991). A plateau is terminated after a stimulus, such as photoperiod, copulation or accumulation of a source of energy for oöcyte maturation, is received. Based on the assumption that Antarctic krill probably have a similar cycle of ovarian maturation, we developed two indices based on ovarian physiological maturity stages (Fig. 1). The first index is the percent of females reproducing in a season, *i.e.*, stages 4–9/stages 2–10, or the intensity of reproduction in the population. Although

TABLE 4. Characterization of a reproductive season in Antarctic krill in January/February.

Oöcyte			
Dev Index	% spawn (7s)	% post-spawn (9s)	Season
low	low	low	delayed
high	high	low	ongoing
low	high	low	recycling
high	—	high	nearing completion

some females reproduce in their third summer, first reproduction may be delayed a year or even skipped in subsequent years if nutritional conditions are not conducive to successful completion of a cycle. Thus not all females of a particular size will reproduce every summer, a concept supported by almost complete overlap of the size range of non-reproducing and reproducing females (Shaw, 1997). The plateau after initial proliferation of young oöcytes is not always terminated. The second index represents the rate of oöcyte development during yolk accumulation, and is the ratio of females in vitellogenesis (stages 5 and 6) to those in late previtellogenesis and vitellogenesis (stages 4, 5 and 6). Oöcyte development will proceed more rapidly when food is plentiful, and a higher proportion of females will be in vitellogenesis in January/February when food availability is high. The oöcyte development index in conjunction with the percentages of spawning (7s) and post-spawn (9s) females allowed us to characterize a season in January/February as delayed, ongoing, recycling or nearing completion (Table 4).

Spawning frequency and egg production rates

Spawning frequency experiments were attempted on at least one northern transect line (500.* and 600.*) and one southern transect line (400.*, 300.* and 200.*) each year to compare alongshore differences in spawning frequency or embryo production rates. We followed the protocol for spawning frequency experiments described in Ross and Quetin (1983). Briefly, between 35 and 50 females were randomly chosen from all female krill with red thelycums in a catch and placed into individual 2-L glass

vessels, and checked for released embryos every 12 hr. If embryos were seen, the female was allowed to finish the spawning event, then the total length measured before preservation in 10% formalin or freezing in a preweighed vial. Embryos were collected by attaching a funnel with a 20-ml glass vial to the neck of the experimental vessel. The vessel was inverted, and the embryos sank into the vial. The embryos were preserved within 25 hr to avoid the period of rapidly changing embryo size at gastrulation (Quetin and Ross, 1984). In the laboratory the diameters of 30 embryos from each spawning female were measured under a dissecting microscope to the nearest 10–20 μm . The total volume of the batch (embryos from one spawning episode) was measured to the nearest 0.025 ml in a narrow diameter (0.4 mm ID) calibrated glass tube. Due to variation in female size among years, batch volume was scaled to female wet weight in order to compare the individual reproductive output among years (Somers, 1991). The relationship between total length and wet weight of mature females with red thelycums generated for each cruise (Table 2) was used to estimate the wet weight of individual spawning females for that cruise.

Environmental parameters

Sea ice indices for the Palmer LTER region were derived from multi-frequency passive microwave satellite data supplied by the National Snow and Ice Data Center and analyzed by Stammerjohn *et al.* (1997) and Stammerjohn and Smith (personal communication, for April 1997 to December 1998) with the NASA Team algorithm. Sea ice extent was defined as the area enclosed by the 15% ice concentration contour as consistent with previous studies (Zwally *et al.*, 1983). For this study the sea ice extent for the months of September through November was chosen to reflect the area affected by the retreat and melting of sea ice, and thus enhancement of productivity in the region. Standard deviates were calculated by subtracting the time series mean from each annual value, then dividing the anomalies by the standard deviation for the time series. Years in which the spring

sea ice extent was within 0.5 standard deviates of the mean were considered average, and those greater than 0.5 of a standard deviate either high or low years of ice-associated productivity. Initiation of retreat was taken to be the month before the first month in which sea ice extent was below the average for the climatology.

Smith *et al.* (2001) and Dierssen (2000) compared annual primary production in the water column in the Palmer LTER area as estimated from experiments conducted throughout the spring and summer at Palmer Station, modeled from chlorophyll *a* measurements, and modeled from SeaWiFS satellite ocean color data. These estimates reflect interannual variability in water column production from November–March and thus late spring through summer food availability for female krill.

RESULTS

Ovarian physiological maturity stages

Spatial distribution. In 5 of the 7 years nearly half of the reproducing females were in pre-spawning stages (stages 4–6) in January/February, except on the 200.* transect line where only 14–27% were still in pre-spawning stages (Table 5). In 1997, most female krill on the 200.* line were also still in pre-spawning stages. In the summer of 1996, however, very few females remained in pre-spawning stages. The percent of females actively spawning was highly variable, from 0 to 92% (stage 7, Table 5). Usually the percent of actively spawning females was higher on the three southern transect lines (>10%), than the two northern lines (<10%). The exception was again 1996 when most females were spawning on the 300.*, 400.*, 500.* and 600.* transect lines. Generally only a minority of females had completed spawning in January/February (stage 9, Table 5), with about the same percent of post-spawn females on all lines. However, there are some north/south differences that imply that the duration or intensity of the season may vary spatially. The combination of no or a low (<3%) percent of spawning females and a significant proportion (15–30%) of post-spawn females is more often seen in the northern

TABLE 5. Frequency of pre-spawning (stages 4–6), actively spawning (stage 7), and post-spawn (stage 9) *Euphausia superba* on each transect line.

Year	600.*			500.*			400.*			300.*			200.*		
	Pre	Act	Post	Pre	Act	Post	Pre	Act	Post	Pre	Act	Post	Pre	Act	Post
1993	69	0	31	100	0	0	99	1	0	62	21	15	22	78	0
1994	84	0	16	76	0	24	42	23	35	46	24	28	—	—	—
1995	92	2.5	5	70	0	30	28	45	1	46	10	5	16	3	1
1996	15	85	0	7	92	0	0	58	17	11	45	0	14	21	23
1997	93	3	4	92	0	8	76	5	19	96	0	0	92	8	0
1998	66	11	23	40	21	39	31	4	64	74	12	9	27	4	66
1999–1	64	5	31	66	19	15	47	26	27	22	70	8	16	27	56
1999–2	19	0	78	—	—	—	—	—	—	9	60	31	—	—	—

region. In four years, the low percentage of post-spawn females supported the conclusion that spawning was ongoing (1993, 1995, 1996, 1997). For three years (1994, 1998, 1999), a significant proportion had completed spawning, suggesting that the spawning season was drawing to a close.

Population indices. The intensity of reproduction (% of the population reproducing) ranged from a low of 10% in 1995 to a high of 98% in 1996 (Table 6). The oöcyte development index ranged from 0.06 in 1997 to 0.96 in 1996 (Table 6). The intensity of reproduction was negatively correlated with the oöcyte development index, except for 1996 when both were at a maximum (% repro = 36.6–32.5% oöcyte dev. index, $r^2 = 0.63$ for all but 1996). Thus in general oöcyte development in females in the reproductive cycle is most advanced in January when the intensity of reproduction is low.

Spawning frequency and embryo production rates

Timing of spawning. Spawning frequency varied from 0–22% over the 7 yr (Table 7). When actively spawning females were a small proportion of the population (<5%), spawning frequency usually ranged from 0–2% (Table 4 vs. Table 7). In most years, the low spawning frequencies and low percentages of actively-spawning and post-spawn females (Table 5) on the 500.* and 600.* transects suggested that spawning was just beginning in the northern part of the study region in mid- to late January. However, in 1996, high spawning frequencies across the entire grid coincided with a high proportion of stage 7 female krill on all transect lines. In 1998, spawning was observed on the 500.* line, and inferred on the 600.* line from the high proportion of stage 7s (Tables 5 and 7). In comparison,

 TABLE 6. Reproductive characteristics of *Euphausia superba* from 1993–1999, with sea ice dynamics during the previous spring (standard deviate of sea ice extent and the timing of retreat), annual primary production, and the abundance of salps throughout the region.

	1993	1994	1995	1996	1997	1998	1999
Reproductive Characteristic							
Oöcyte development index	0.31	0.71	0.75	0.96	0.06	0.57	0.19
Intensity of reproduction (%)	16	21	10	98	40	14	34
Embryo diameter (μm)	576	595	613	636	603	621	627
Weight-specific batch vol (ml g^{-1})	0.50	0.48	1.02	1.10	0.85	1.12	0.89
Environmental Conditions							
St deviate ice extent	-0.6	+0.4	+0.9	+0.1	-0.5	+0.7	-0.9
Timing retreat	Aug	Nov	A&N	Sep	Aug	Nov	Sep
Annual primary prod (g C m^{-2})	100	50	150	350	110	75	75
Percent sta with both krill & salps	11	80	22	7	74	7	89
Salps ($\text{number } 1000 \text{ m}^{-3}$)	0.25	11.50	0.14	0.03	8.04	0.12	17.99

TABLE 7. Spawning frequency (% females spawning $d-1$) collected at Palmer LTER grid locations during January/February from 1993 to 1999.

Year	600.*		500.*	400.*			300.*			200.*	
1993	nd		nd	0.0%			6.1%			5.6%, 5.1%	
				*.140			*.200			*.200	
				29 Jan			31 Jan			2 Feb	
1993-fall	12.5%	17.3%	nd	nd			nd			nd	
	600.040	700.040									
	13 Apr	3 Apr									
1994	nd		0.0%	6.4%			2.5%			12.0%	
			*.180	*.160			*.180			*.140	
			14 Jan	2 Feb			3 Feb			4 Feb	
1995	0.0%		0.0%	22.4%			nd			nd	
	*.160		*.060	*.060							
	10 Jan		16 Jan	27 Jan							
1996	4.8	13.0	5.5	5.6	12.8	21.5	nd			8.0	
	*.180	*.040	*.220	*.180	*.160	*.080				*.160	
	12 Jan	16 Jan	11 Jan	26 Jan	26 Jan	27 Jan				30 Jan	
1997	0.0		0.0	14.6			nd			nd	
	*.160		*.180	*.160							
	18 Jan		13 Jan	28 Jan							
1998	nd		7.5	43.8			nd			0.8	
			*.180	420.015						*.100	
			1 Feb	11 Feb						7 Feb	
1999	0.0		1.3	2.9			7.8			11.5 5.8	
	*.100		*.160	*.180			*.120			*.040 *.160	
	20 Jan	10 Feb	11 Jan	26 Jan			16 Jan			6 Feb 5 Feb	
										12.0 *.140 17.5 *.040	
										3 Feb 29 Jan	

females collected from the southern transect lines were always actively releasing embryos in January, with spawning frequencies varying from 5 to 15%. In most years, the low percentage of post-spawn females in the southern region suggested that the reproductive season was still ongoing. In 1998 and 1999, the higher proportion of post-spawn females, particularly on the 200.* transect line, suggested that the season was near completion.

Batch volume and embryo diameter. There was no correlation between weight-specific batch volume and wet weight (Fig. 2A), which allows us to compare means across year and location. In both 1996 and 1999 data on weight-specific batch volume and embryo diameter were available from grid locations spaced 300–400 km apart which allowed us to test for the effect of location. In neither year did embryo diameter differ with location (ANOVA-1996, $F = 2.03$, $P = 0.067$, $n = 125$; ANOVA-1999, $F = 1.67$, $P = 0.139$, $n = 82$). In 1999 there were no significant differences in batch volume with location (ANOVA, $F = 1.11$, $P = 0.36$, $n = 83$). Wet-specific

batch volume, however, varied with location in 1996 (ANOVA, $F = 36.99$, $P \ll 0.001$, $n = 122$). In 1996 the frequency distribution of weight-specific batch volume was bimodal (Fig. 2B). A group of 27 females released small batches (mean 0.118 ml g^{-1} , $SD = 0.079$), and a larger group of 95 females released batches averaging 1.38 ml g^{-1} ($SD = 0.385$). Most females releasing small batches were collected at the three outer shelf stations (200.160, 400.180, and 500.220).

There were significant interannual differences among years in both measures of individual reproductive output. Embryo diameter differed significantly with year (ANOVA, $F = 81.994$, $P = 0.0000$, $n = 338$) (Table 6), as did weight-specific batch volume (ANOVA, $F = 11.54$, $P = 0.0000$, $n = 329$) (Table 6). Weight-specific batch volume and embryo diameter of individuals were not correlated within a year, but there was a positive correlation between mean annual weight-specific batch volume and mean annual embryo diameter:

Weight-specific batch volume = -5.956

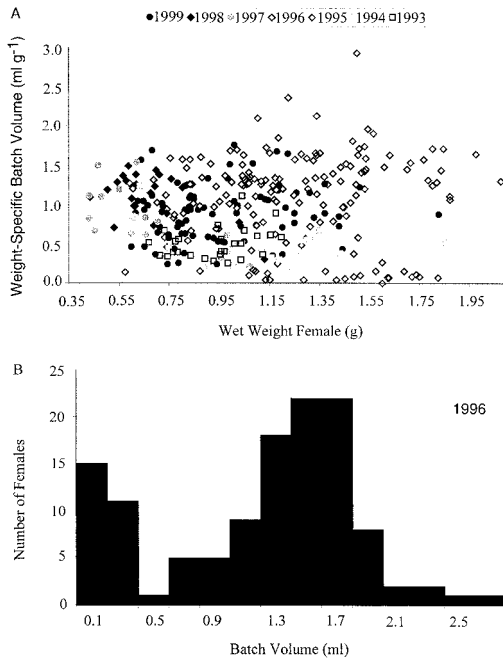


FIG. 2. A. Weight-specific batch volume of *Euphausia superba* in the Palmer LTER study region during 7 summer cruises from 1993 to 1999. Different symbols are used for batch volumes of individual females from different years. B. Frequency distribution of weight-specific batch volumes in Jan/Feb 1996, $n = 123$.

+ 0.0112*Embryo diameter ($r^2 = 0.684$, $n = 7$).

Thus, the two measures of individual reproductive output co-varied on large temporal scales. Neither was significantly correlated with intensity of reproduction, a measure of population reproductive effort.

To test whether the north/south differences in ovarian maturity stages and spawning frequency were due to a lack of synopticity in either sampling or experiments, we repeated two of the five transect lines during the 1999 annual cruise. Samples were collected and experiments conducted within a few days of each other for the 300.* and 600.* transect lines (16–20 Jan), and the effort repeated 3 wk later (5–10 Feb). For both transects the percent of females in pre-spawning stages decreased during the 3 wk interval, and the percent post-spawn increased (Table 5). But both the proportion of females actively spawning (Table 5) and the spawning frequency (Table 7) remained

about the same. The results were more similar within a transect line within sampling periods, suggesting that the timing of the reproductive cycle does vary from north to south, and that the annual cruise captured those differences.

Environmental parameters

Indices of food availability. The standard deviate of the spring sea ice extent within the Palmer LTER study region is the index used to represent the area conditioned for phytoplankton blooms by sea ice retreat, and assumed to be correlated with ice-associated primary productivity during the spring. Standard deviates of spring sea ice extent ranged from -0.9 in 1999 to $+0.9$ in 1995, with only one year close to the average (1996) (Table 6). The month prior to below average sea ice extent was an index of the initial availability of ice-associated production, and ranged from August to November (Table 6). In 1995, sea ice retreated to below average extent in August, but subsequently advanced to above average extent, retreating for the final time in November. The latter retreat time was used in further analyses. Annual primary production was estimated to be two to seven times higher in 1995–1996 than in any other year (Table 6). Annual primary production was lowest in the 1993–1994 season. Annual primary production generally ranged from 75 to 150 g C m^{-2} (Smith *et al.*, 2001).

Presence of other grazers. During three of the seven years in this time series, salps were abundant across the grid (Table 6). Krill and salps co-occurred at $>70\%$ of the stations in 1994, 1997 and 1999 (Table 6). In other years salps and krill co-occurred at $<22\%$ of the stations.

Environmental effects on the reproductive cycle of Antarctic krill

The intensity of reproduction (% population reproducing) was consistently low, $<20\%$, when sea ice retreat began in late spring (November) (Fig. 3A). Initiation of retreat in September appeared to foster a greater intensity, $>30\%$. The intensity of reproduction during summers after a late winter (August) retreat of sea ice was in-

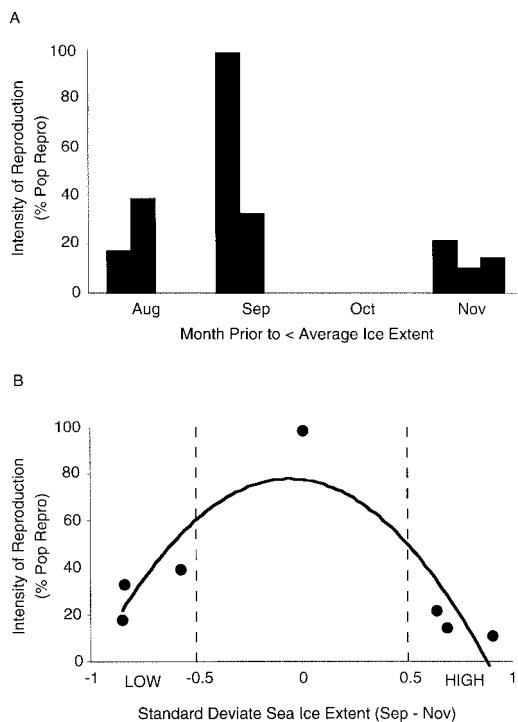


FIG. 3. Percent of population reproducing and seasonal sea ice dynamics. A. Timing of retreat, month prior to month with sea ice extent below average. B. Standard deviate of sea ice extent between September and November. Dotted lines divide low (-0.5 to -1.0 standard deviates) and high ($+0.5$ to $+1.0$ standard deviates) spring ice years. Line fitted by eye.

consistent, but in general higher than in summers following a late spring retreat. The pattern with standard deviates of spring sea ice extent showed a marked optimum at an average spring sea ice extent (Fig. 3B). The percent of the population reproducing in years when spring sea ice extent was high was lower than in years when sea ice extent was low.

The oöcyte development index was consistently above average (>0.5) when sea ice retreat began in late spring (Fig. 4A). In years when sea ice retreat begins in late winter oöcyte development was delayed. Retreat in early spring (September) can result in either few females in vitellogenesis or most females in vitellogenesis. The standard deviate of the spring sea ice extent is a better predictor of rates of oöcyte development (Fig. 4B). When the extent of spring sea ice is below average, the oöcyte

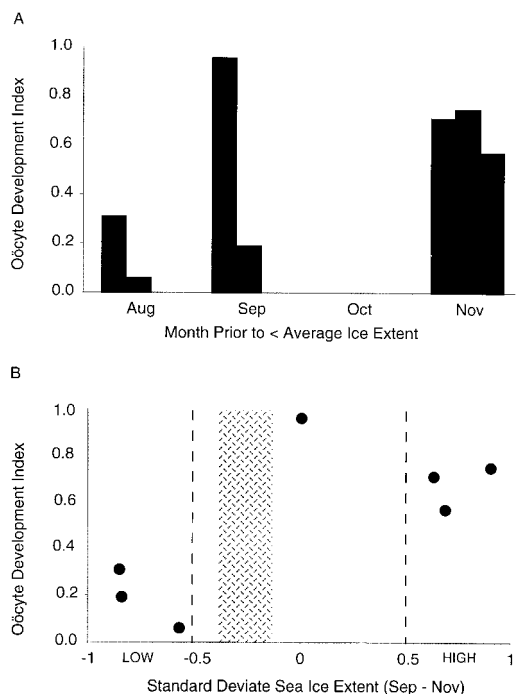


FIG. 4. Oöcyte development index and seasonal sea ice dynamics. A. Timing of retreat, month prior to month with sea ice extent below average. B. Standard deviate of sea ice extent between September and November. Dotted lines divide low (-0.5 to -1.0 standard deviates) and high ($+0.5$ to $+1.0$ standard deviates) spring ice years. Flecked area represents possible threshold between delayed and advanced seasons.

development index is low. In all years of above-average sea ice extent, the oöcyte development index was 0.5 or greater. Thus the rate of ovarian maturation appeared to be related to a threshold area of enhanced productivity, not the absolute ice area. In years of below-average sea ice extent, ovarian maturation was delayed, *i.e.* oöcyte development indices <0.3 .

The intensity of reproduction was the only population index significantly correlated with annual primary production in the water column (0.86) (Table 8). Measures of individual reproductive effort, batch volume and embryo diameter, were not significantly correlated with the standard deviates of spring sea ice extent ($r < 0.35$) or with water column annual primary production ($r \sim 0.5$). The abundance of salps was not significantly correlated with any of the measures of variation in the reproductive cycle.

TABLE 8. Correlation matrix of reproductive indices and environmental indices.*

	Oöcyte Dev Index	Inten (% Pop Repro)	Wt-Spec Bat Vol	Emb Diam	Ann Prim Prod	SD Spr Sea Ice	Salp Abund
Oöcyte Dev	1						
% Pop	0.334	1					
Wt-Spec Bat Vol	0.291	0.361	1				
Emb Diam	0.361	0.569	0.858	1			
Ann PP	0.581	0.864	0.499	0.525	1		
SD Sea Ice	0.725	-.226	0.305	0.209	0.031	1	
Salp Abund	-.488	-.062	-.313	0.074	-.469	-.372	1

* Critical value = 0.75.

DISCUSSION

The reproductive cycle in Antarctic krill appears to follow the same pattern of ovarian maturation as found in most eucarid crustaceans (Nelson, 1991). For *Euphausia superba*, the first plateau during maturation may occur in early previtellogenesis (Stage 3), before mating has occurred. At stage 3, the small ovary contains only small (<200 µm) oöcytes, and the energetic investment has been minimal. A “fat body,” documented in two species of euphausiids, has the same placement, tissue characteristics, and development as the insect fat body, and is hypothesized to have the same function, *i.e.*, synthesis and transfer of carbohydrates, lipids and protein compounds into growing oöcytes during previtellogenesis and vitellogenesis (Cuzin-Roudy, 1993). Development of this “fat body” parallels ovarian development early in the season, *e.g.*, November for *E. superba* in the Scotia-Weddell Confluence region (Cuzin-Roudy and Labat, 1992). The capacity of the “fat body” for long-term storage of resources that can be mobilized during vitellogenesis may be part of an efficient strategy to buffer female krill against short-term temporal variability in food supplies in the Southern Ocean. We hypothesize that the “fat body” in stage 3 females must develop sufficiently by late spring (November) or ovarian development will not continue and those females will not reproduce that season. We suggest that our index for the intensity of reproduction, the percent of the population reproducing, represents females that have been able to ingest enough food in early to late spring to build up adequate reserves in

their “fat bodies” to continue ovarian maturation.

The second plateau for *Euphausia superba* may occur at the beginning of vitellogenesis. If so, energetically demanding yolk accumulation will not proceed until sufficient resources are available to complete the process. Again, the cue may be development of the “fat body.” The oöcyte development index represents the proportion of the population that has passed the postulated second threshold that allows the female to initiate lipidic yolk accumulation. Slow or variable rates of accumulation during the spring and early summer will lead to a low oöcyte development index, and high rates to rapid oöcyte development and a high index. Thus passing this threshold by late January/early February is postulated to be a function of both spring and early summer resources.

We suggest that the third plateau for *Euphausia superba* occurs prior to the release of the last batch of embryos of a pulse of oöcyte production. If resources are adequate, the ovary will recycle, and a second pulse of oöcytes will be produced. Although the “fat body” is a likely storage spot, the source of food is probably water column production in late spring and summer just prior to the first spawning. In summary, we suggest that successful transition of the three plateaus would involve food availability during different parts of the spring/summer continuum. Thus population indices that represent these different plateaus will not necessarily co-vary, as spring and summer food availability may not co-vary in any one year. In this study the in-

tensity of reproduction and the oöcyte development index did not co-vary, and are thought to depend on food availability at different times.

Spatial and temporal variability in rates of ovarian maturation

The combination of the oöcyte development index, the frequency of actively spawning and post-spawn females, and the presence of recycling females allows us to characterize the timing and duration of spawning in a particular reproductive season. Shaw (1997) documented the presence of recycling (stage 8–continuing) females in the Palmer LTER study area in both 1995 and 1996. Evidence of recycling was not found in any of the years with a low oöcyte development index. The 1993 spawning season was delayed. Both the oöcyte development index and the proportion of post-spawn females were lower than average. Some females continued to develop and spawned late, in April of that year (Table 7). In 1994, the higher oöcyte development index and the greater proportion of post-spawn females than in 1993 indicated that the season was further advanced. The state of ovarian maturation in 1995 was similar to that in 1994, the presence of recycling females and fewer post-spawn females indicated that the 1995 season was advanced and prolonged. The 1996 season was also both advanced and prolonged, with a high oöcyte development index, few pre-spawning or post-spawn females and recycling females present. Ovarian maturation was most retarded in 1997, with nearly all females still in pre-vitellogenesis in January/February. The 1998 season was one of average duration, timing and intensity. A low oöcyte development index in 1999 indicated slower ovarian maturation rates than in any season but 1996–1997.

From the early review of Mauchline and Fisher (1969) and the more recent review of Ross and Quetin (2000), the timing and duration of spawning in euphausiids were known to vary with location and species. As a general rule, earlier and longer spawning occurs at lower latitudes. These observations led to the hypothesis that timing and duration of spawning are keyed to the pe-

riod of elevated food production, *i.e.*, earlier in the year and longer at lower latitudes. Spiridonov (1995) confirmed this pattern for *Euphausia superba* in a study of euphausiids from both the Weddell Sea and waters west of the Antarctic Peninsula. At the fringe of the extent of seasonal sea ice, spawning was early (late November/early December), and tended to be long (3–3.5 mo) but variable in duration. In contrast, in coastal areas at higher latitudes, spawning began later and was of shorter duration (~1.5 mo). Spiridonov (1995) concluded that low sea ice extent coincided with early spawning, and a slow (late) retreat resulted in a delayed and less intense spawning season. However, the polyna or ‘oasis’ effect, described in the Weddell Sea by Makarov and Men’shenina (1992) can reverse the normal north to south gradient in timing of reproduction. When polynas open early in the spring, simulating an early retreat, reproduction starts earlier than in ice-covered waters to the north. In contrast, Siegel and Loeb (1995) found that low sea ice extent in winter and/or early sea ice retreat leads to a delay in spawning for krill at the tip of the Antarctic Peninsula. In this study west of the Antarctic Peninsula, a reverse gradient usually exists in the timing of the spawning season, with spawning earlier and more intense at higher than lower latitudes.

Reconciling these disparate views of the influence of seasonal sea ice on the timing and intensity of spawning of Antarctic krill (Spiridonov, 1995; Siegel and Loeb, 1995; Makarov and Men’shenina, 1992; this study) requires us to understand the link between food production and spawning. When sea ice retreats, the melting sea ice conditions the water column for ice edge blooms (Lizotte, 2001). Cuzin-Roudy and Labat (1992) suggest that Antarctic krill do not come into reproductive condition under the ice, so the extent and timing of these ice edge blooms may play an important role in the rate of ovarian development and timing of spawning. Because seasonal sea ice dynamics are region-specific, “early” retreat in one region may lead to blooms prior to the peak demand for food for oöcyte development, whereas in another region “early” retreat may create ideal conditions. The

physiological status of the female krill is a function of when sea ice retreat conditioned the water relative to the timing of food requirements. In regions at the edge of the extent of seasonal sea ice, *e.g.*, the Elephant Island area, the extent of sea ice will have a larger effect than in regions swept each year by the advance and retreat of the seasonal pack ice, *e.g.*, the southern part of the Palmer LTER grid (Stammerjohn, 1993). At the northern edge of the influence of seasonal sea ice, if sea ice in winter is low, little of the region will be conditioned for an ice edge bloom, and the area of enhanced food availability will be small. With an early retreat, bloom conditions may occur prior to the time of maximum need for food for ovarian development. Thus low winter sea ice extent and/or early retreat mean lower food availability in the spring, and will be associated with delayed spawning, such as found by Siegel and Loeb (1995) for the Elephant Island region. In the Palmer LTER region, the reverse latitudinal gradient was also a function of the combination of sea ice extent and timing of retreat. The 1997 season showed the slowest ovarian development and delays across the entire grid. Not only was the retreat early (August) so any ice-associated blooms were prior to peak demand, but the low spring sea ice extent meant the areal extent of conditioning was low. In contrast, the optimal combination seen in 1996 appeared to be average sea ice extent and an average month of retreat. In general sea ice retreats from the northern regions first, so conditioning may occur prior to peak need, creating a situation where the female krill will be more dependent on water column primary production than ice-associated primary production. With fewer food resources, ovarian maturation will be slower than at higher latitudes where the water column is routinely conditioned by sea ice retreat, and both ice-associated and water column food resources are available. In the Palmer LTER region rates of maturation are often slower and spawning intensity lower at lower latitudes, *e.g.*, the low spawning frequency and low percentage of stage 7 females on the 500.* and 600.* transect lines. Females in the northern sector may initiate

ovarian maturation earlier based on photoperiod, but early retreats and inconsistent sea ice coverage lead to low ice-associated food resources, and slower ovarian maturation. Seasonal sea ice dynamics mediates the areal extent and timing of spring food for ovarian development, and it is the interaction of that timing with the timing of the needs of the krill population that drives rates of ovarian maturation and timing of spawning.

Reproductive output—Population and individual

Population fecundity in euphausiids is a product of both population characteristics, such as female abundance and the percent of the population reproducing, and the reproductive output of an individual. Individual reproductive output includes the number of embryos per spawning episode and the number of spawning episodes, itself a function of spawning frequency and whether the ovary recycles during the season. A separate index of individual reproductive effort is embryo diameter. In this time series we documented the intensity of reproduction, embryo diameter, and the volume of embryos produced per spawning episode (batch volume). These measures of individual reproductive output only refer to those females that are in the reproductive cycle. Thus individual reproductive output and the percent of the population reproducing do not necessarily co-vary.

Intensity of reproduction (% of population reproducing). Most euphausiid species only reproduce for one year, with a small percent surviving to reproduce a second season (Ross and Quetin, 2000). For *Euphausia superba*, the assumption has been that all females larger than the size at maturity will reproduce during that reproductive season (Siegel and Loeb, 1994). Shaw (1997) has refuted that assumption for *E. superba* in the Palmer LTER region west of the Antarctic Peninsula by showing that some females larger than the size of maturity are in immature or resting stages (stages 2, 3 and 10) during January/February. In this paper we added to her 5-yr time series to show that the percent of the population

reproducing can range from 10 to 98%. This strategy of delayed reproduction or diverting energy to growth instead of reproduction for a season can potentially enhance the total number of larvae produced in a lifetime.

Individual reproductive output. Over the past 20 yr, studies of ovarian cells and spawning frequency experiments with live euphausiids have demonstrated that multiple spawning episodes are characteristic of euphausiids in general (Ross and Quetin, 2000). In this study we do not estimate either interbrood period (the inverse of spawning frequency) or the number of spawning episodes per season because the duration of the spawning season is unknown. However, analysis of ovarian maturity stages does provide additional information on whether the ovary recycles in a specific season and thus is an indication of increased individual fecundity. Based on the presence of recycling females, a high oöcyte development index, and a low percent of post-spawn females, both 1995 and 1996 were considered prolonged spawning seasons due to recycling of the ovary. Recycling of the ovary was predicted to depend on late spring and summer food availability, *i.e.*, water column production. Estimates of annual primary production in the water column for 1995 and 1996 were the two highest of the 7-yr time series, supporting this prediction.

Numbers of embryos released per spawning episode varies both within and among species of euphausiids (Ross and Quetin, 2000). Although fecundity is predicted to increase with increasing female size, multiple investigators have found that the correlation of batch size with total length is low (for *Euphausia superba*: Ross and Quetin, 1983; Harrington and Ikeda, 1986; Nicol *et al.*, 1995). However, Xuefeng and Rong (1995) and Cuzin-Roudy (2000) have shown that the relation between female volume (wet weight or length cubed) and ovarian oöcytes is linear for both *E. superba* and *Meganctiphanes norvegica*. In this study we have shown that weight-specific batch volume is not a function of size, and that the interannual variability in weight-specific batch volume is significant. Siegel (1985)

also saw interannual variability in the number of oöcytes in *E. superba* in the early 1980s at the tip of the Antarctic Peninsula.

However the variability within a year is still high, suggesting that size of the female is not the only factor affecting the number or volume of embryos released per spawning episode. There are several possible sources of this variability. Studies of both *M. norvegica* and *E. superba* have shown that an individual female does not release the embryos from a pulse of oöcyte production in three equal successive spawning episodes (Harrington and Ikeda, 1986; Nicol 1989; Cuzin-Roudy and Buchholz, 1999). The number or volume of embryos released per spawning episode can also vary among geographical sites, as shown here for 1996 and by Harrington and Ikeda (1986). Presumably food availability both prior to and during the reproductive season is one factor determining the size of the batches, but in this study the correlation of mean annual weight-specific batch volume with annual primary production (0.5) was not significant.

Embryo size. Interannual and geographic differences in embryo size have been well documented for euphausiids (Ross and Quetin, 2000). Although no studies have explicitly addressed the question, these differences imply that energy reserves available for non-feeding larvae vary, and that those with more reserves will survive longer through the fall and winter. Thus embryo diameter may be a factor in recruitment success of that year class. Weight-specific batch volume and embryo diameter were both significantly different among years, and co-varied. However, they were not closely correlated with any one index of food availability. Further investigation is merited.

Presence of competing grazers

Siegel and Loeb (1995) hypothesized that feeding by salps during the spring bloom period could result in reduced food availability for krill, and thus slow ovarian development and spawning. Their hypothesis was based on both high salp abundance and delayed reproduction in krill seen after winters of low sea ice. Subsequently Loeb

et al. (1997) hypothesized that a low sea-ice winter would create conditions favoring extensive salp blooms developing in October and November, strong grazing competition for limited resources, and delayed krill spawning which is presumed to be less successful than earlier spawning. Kawaguchi *et al.* (1998) questioned whether significant competition for phytoplankton exists between salps and krill. If salps are strong competitive grazers, the degree of greenness (a measure of the amount of phytoplankton eaten) in krill is predicted to decrease with increasing salp abundances. However, Kawaguchi *et al.* (1998) found no correlation between salp densities and the proportion of green krill in catches west of the Antarctic Peninsula. Kawaguchi *et al.* (1999) did find that the greenness of krill is strongly associated with the size composition of the phytoplankton community, with the larger cells (>20 μm) promoting higher ingestion rates. As an alternative explanation for the correlations previously found, they suggested that salps bloomed in oceanic waters with phytoplankton communities composed of smaller particles in low concentrations. Fatal clogging of salps is more apt to occur in dense concentrations of large particles (Harbison, 1986). Krill production is enhanced in waters with high phytoplankton concentrations composed of larger cells (diatoms). Recently Ross *et al.* (2000) showed that growth rates of young krill increase as a function both of total chlorophyll *a* concentration and the phytoplankton community composition, supporting the concept that the two species fare best with different phytoplankton communities. Nicol *et al.* (2000) also suggest that the co-variance of krill and salps with sea ice may be a function of oceanic circulation and water masses and their association with sea ice and not of direct competition.

In the Palmer LTER study region krill and salp distributions overlap in some years, and are mutually exclusive in others. If salps are strong competitors for krill in this region, we would predict that the percent of population reproducing or the oöcyte development index or weight-specific batch volume would be correlated with salp abundance. However there were no signif-

icant correlations of any of our indices with salp abundance. Thus the data do not support a direct competitive interaction between salps and krill in our region. The differences in proximity of the southern boundary of the Antarctic Circumpolar Current (Orsi *et al.*, 1995) and differences in seasonal sea ice dynamics may underlie the differences seen in the krill–sea ice–salp interaction in the Palmer LTER region and the Elephant Island region.

In summary, timing of reproduction and reproductive output of *Euphausia superba* varied significantly in the Palmer LTER study region during the 7-yr time series from 1993 to 1999. The impact of this variation on estimates of population fecundity depends on the scales of variation. The intensity of reproduction has a much higher coefficient of variation (0.91) than either measure of individual reproductive effort. The intensity of reproduction varied by a factor of 10 whereas the weight-specific batch volume only varied by a factor of three, and embryo diameter by 3%. Thus for Antarctic krill, one important factor in calculations of total population fecundity (number of embryos produced by a population during the entire reproductive season) is the numbers of females in the reproductive cycle. The 10-fold variation must be factored into estimates of population fecundity. From this study this proportion appears to depend on food resources in the spring, primarily ice-associated resources. The impact of low food resources early in the spring can be mitigated by increasing food later in spring and summer, but never fully redressed. Therefore any changes in spring sea ice dynamics due to climate change will seriously impact the “recruitment potential” of Antarctic krill.

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