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Seasonal Distribution, Egg Production and Feeding by the Marine Copepod *Calanus sinicus* in Asan Bay, Korea

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Seasonality in abundance and egg production was investigated for *Calanus sinicus* in Asan Bay, Korea, and feeding effort was measured in the laboratory condition. Although abundances of this species in this bay showed only one peak in spring, egg production showed two peaks, spring and fall, in this bay. Potential of year-round egg production was also found. Food availability judged by the particulate organic carbon (POC) concentration was usually more than enough in this bay. High egg production in fall resulted in spring peak in abundance. But high egg production in spring did not result in summer or fall peak in abundance. Low abundances in summer and fall were believed to be the result of long range horizontal migration out to the central part of the Yellow Sea. The highest average egg production by the population of this species was 16.3 eggs female^{-1} day^{-1}. Maximum egg production by an individual was 39.0 eggs female^{-1} day^{-1}, which yielded 30.7% of specific egg production rate in terms of body carbon content with the carbon contents of 44.44 μgC and 0.35 μgC for individual adult female and egg, respectively. Clearance rate (F) measured in the laboratory condition decreased exponentially with the increase of food concentrations, as expected. The asymptote of F was 3.17 ml copepod^{-1} h^{-1}. When this value and the minimum concentration of POC measured in the field were applied under the assumption of continuous feeding in the nature, the calculated gross efficient of egg production was 41.6% in case of average egg production of the population. Violation of the assumption of diurnal feeding rhythm and application of the minimum concentration of POC may offset the influence on calculation each other.

INTRODUCTION

Copepods are one of the most abundant zooplankton taxa in the coastal areas off Korean peninsula (Park *et al.*, 1991; Choi and Park, 1993), and among them *Calanus sinicus* is one of the major herbivores that plays an important role as energy linker between the primary producers and the consumers in higher trophic levels (Zhang, 1995). Therefore, dynamics of this species is crucial for better understanding of energy flow in the coastal ecosystem as well as for the monitoring of the possible environmental changes.

Asan Bay is known to be a spawning and nursery ground for various commercial fishes, and abundances of *Calanus sinicus* were shown to fluctuate seasonally in this bay. High abundances up to 300 individuals m^{-3} in spring and low abundances less than 30 individuals m^{-3} in other seasons were typical in this bay (Choi and Park, 1993). However, the reason for this seasonal variation was not clearly known yet. Without any direct evidences some physical environmental factors such as temperature and salinity were often mentioned as reasons for the found seasonal abundance variation in that they also fluctuated seasonally. There may be several ways in finding why a certain species shows seasonal abundance fluctuations. One of the better methods that can be adopted to figure out the mechanism for the population dynamics of zooplankton is to measure the egg production, which is an important aspect of the ecology from both population dynamics and individual energetic perspectives. It is because egg production is a measure of the population recruitment of new individuals at the population level and it is a sensitive measure of the growth rate of adult females at the level of individual energetics.

In this context Park and Lee (1995) suggested a hypothesis that seasonal distribution pattern of this species was partially coupled with life history pat-

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tern. They showed two peaks in egg production in a year, fall and spring. The fall peak in egg production coincided with the spring peak in abundance of adults assuming the growth rate shown by Uye (1988). But the spring peak in egg production did not result in following peak abundance of adults. They cautiously reasoned that this might be due to the predation pressure on eggs and early stages of this species by demersal fishes which were most abundant during summer in this bay. However, they could not show any direct evidence of high predation pressure such as food selectivity of the fishes.

On the contrary, Huang *et al.* (1993) reported that this species could reproduce year-round, and Lin and Li (1984, 1986) and Chen (1964) reported that there were three major spawning seasons. But those periods of the spawning events previously reported were not the same. To find out reasons for the contradictory reports, second series of egg production measurements, following those of Park and Lee (1995), were done from May 1995 till May 1996. Here I report the results of the follow-up experiments along with the contents of Park and Lee (1995). In addition, gross efficiency of egg production was inferred from laboratory measurements of feeding rate of this species.

MATERIAL AND METHODS

Seasonal zooplankton samples have been collected in Asan Bay, Korea (Fig. 1) for seven years since fall of 1989. Either a conical net with mouth diameter of 76 cm or a "Bongo" net with mouth diameter of 60 cm was used in collection, and both net were fitted with 0.333 mm mesh nets. The net was towed obliquely from near bottom to the surface with the tow speed and tow duration of about 1 m sec^{-1} and 5 minutes, respectively. At least three replicate samples were intended for each sampling unit.

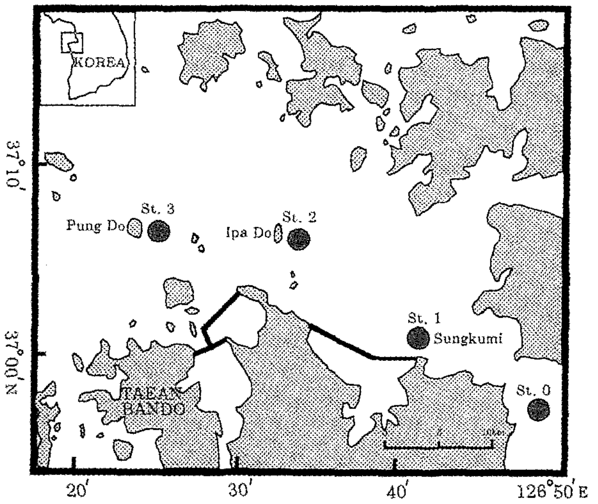

Fig. 1. Map of sampling sites.

Samples for the distribution data were fixed and preserved with buffered formalin (pH 8, final concentration about 5%). Subsamples split with a Folsom Plankton Splitter were examined under a dissecting microscope and specimens were counted with identification to the lowest possible taxa.

To see the statistical significances of the differences in abundances (individuals m^{-3}) and percent compositions of *Calanus sinicus* with respect to the sites of collection, inner bay versus outer bay, seasons, and the interaction of these two, analyses of variances (ANOVA) were done with the model, $Y_{ijk} = \mu+\alpha_i+\beta_j+(\alpha\beta)_{ij}+\varepsilon_{ijk}$, where Y_{ijk} was the abundance (or percent composition) obtained by kth replicate sample (year was pooled in replicate so that k ranged up to 21) of ith season and jth site, μ was the overall mean, α_i and β_j were effects of season and site, respectively, $(\alpha\beta)_{ij}$ was the interactive effect of season and site, and finally ε_{ijk} was error term. Data from the period from fall (Nov.) of 1990 till winter (Feb.) of 1997 were used in the analyses.

Egg production was measured for two series of experiments. The first set of experiments, which included 9 measurements of one to two months intervals, were done from September 1993 till August 1994, and the second set, 11 measurements of one to two months intervals from May 1995 till May 1996. Live target species, *Calanus sinicus*, were sorted on board the ship and transferred to the laboratory within 4 hours after capture. During the transfer, live specimens in a jar with filtered seawater were kept in ice-box filled with seawater to minimize the change in water temperature.

Incubation containers for the laboratory experiments were designed to collect eggs with minimal loss to cannibalism. That is, egg-separation containers consisted of inner plexiglas cylinders (about 0.7 or 3-liter volume) with 300 μm screened bottom suspended in 1 or 5-liter glass beakers (Park and Landry, 1993). The screen was used to separate the produced eggs from adults. One to five adults were placed into each of 1-liter containers and up to 50 female adults were placed into 5-liter beakers. The former was used in determining the maximal egg production by one individual and the latter was used in determining average population egg production rates. Incubation containers were kept in incubators of which temperature was set to be the seawater temperature. Dim light inside the incubator was on and off for 12-hour intervals.

Chaetoceros simplex and *Chlorella ellipsaidea* were added sufficiently to the experimental containers as food. Sufficiency was checked by examining the production of fecal pellets. Aeration was done every 6 hours to prevent the food from sinking.

Dry weight of adult females was measured using a Perkin-Elmer AD-4 Autobalance after being rinsed with isotonic ammonium formate (6.0% w/v) and dried for 24 hours at 70°C (Omori and Ikeda, 1984). Carbon and nitrogen contents of egg and adult female of *Calanus sinicus* were measured with a Perkin-Elmer 2400 CHN analyzer. Usually 5 adults and more than 200 eggs were used for each measurement.

Filtering effort for feeding in terms of volume swept clear by each individual copepod (clearance rate) was measured in the laboratory condition by the method of Frost (1972) independently from egg production measurements for three times in Nov. 1996 and Jan. 1997. *Stichococcus bacillaris* (about 4 μm in size) cultured in the laboratory was used as food at different levels of concentrations in 2,000～9,000 cells ml^{-1}. Cell counts were done using a Coulter counter (model Z1) every two hour during the measurements. To minimize the containment effect, fast growing of phytoplankton cells in the experimental jars compared with in the control jars due to the excretion by zooplankton in the experimental jars (Roman and Rublee, 1980), ammonium chloride was added enough to both experimental and control jars. The jars with filtered seawater and food were slowly rotated on a wheel to prevent the food from sinking during the experiments. Usually 3 females were located in an experimental jar of 500 ml volume. Particulate organic carbon concentrations at the collection sites were measured during the first series of egg production measurements.

RESULTS

Seasonal distribution of Calanus sinicus

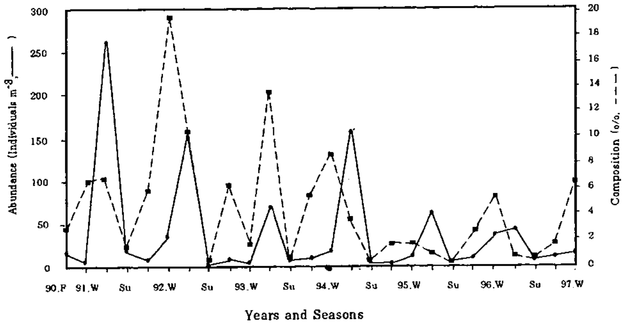

Fig. 2. Seasonal abundance (individuals m^{-3}) and percent composition of *Calanus sinicus* in Asan Bay, Korea from fall of 1990 till winter of 1997.

In case of abundance, interaction of the season and site was not significant (p=0.3) in the anaysis of variances. Effect of the site was not significant (p=0.27), either. However, seasonal effect was significant (p<0.01). Spring abundance was the highest with up to 264 individuals m^{-3}. Abundances in other seasons were low with tens of individuals m^{-3} or even less. Fluctuation of averaged abundances at different sites were shown in Fig. 2. It showed annually decreasing trend suggesting the malicious effect of intensified recent human exploitation of this bay such as reclamation and construction of industrial complex, that was beyond the scope of this paper.

Percent compositions showed similar results in the analysis of variances except that the site effect was marginal with p=0.03. That is, percent compositions showed seasonal differences, high values in winter and spring, and low values in summer and fall. And they were slightly higher at outer bay site than at inner bay sites. They were about 12 (winter) and 11% (spring) at Site 3, 9% (both winter and spring) at Site 2, 5% (both winter and spring) at Site 1 and 3% (winter) and <1% (spring) at Site 0.

Size and C, N contents of adult and egg

Size range of the adult female *Calanus sinicus* was 2.5～3.1 mm and the diameter of the spherical egg of this species was about 160 μm. Dry weight of adult females was 155.3±42.6 μg (mean± standard deviation). This large standard deviation was due to the large variation among the groups sampled at different time of the year. The variation within the groups sampled at the same time was much less than this. This indicates that the adult females caught at different time of the year at this bay were different subpopulations, which implied that there was seasonal variation in fecundity. Egg dry weight was not measured.

Carbon contents of the adult females also varied with the time of sampling. The mean and standard deviation were 44.4 μgC and 12.5 μgC, respectively. Carbon content was about 31.7% of the dry weight (only matching data points were included, i.e., the numbers of dry weight measurements and C, N measurements were not the same). The nitrogen content was 13.1±3.3 μgN (mean±standard deviation). The CN ratio was about 3.8. Carbon and nitrogen contents of an egg were 0.35 μgC and 0.07 μgN, respectively.

Egg production rate

Table 1 shows the results of egg production measurements. Average egg production was calculated from pooled number of adults in 5-liter incubation containers and total eggs obtained. Maximum egg production by single adult female was obtained from smaller container (1-liter beaker) with 1 to 5 females.

Two peaks in egg production, spring and fall, were found both in the first and second series of experiments (Table 1). In the first series of experiments, the peaks of average and maximum egg production appeared in September and in April~May. The average and maximum egg production rates were 7.6 and 14.0 eggs female^{-1} day^{-1}, respectively, in September. In April, they were 16.3 and 39.0 eggs female^{-1} day^{-1}. In the second series of experiment, the peak time was delayed a little. That is, the spring peak was at early June and April of the next year, and the fall peak was in October. However, the rates were more or less comparable, 39.0 versus 31.7 for maximum and 16.3 versus 11.8 for average in spring, and 14.0 versus 18.9 for maximum and 7.6 versus 11.4 for average in fall (Table 1).

In the first series of experiments, no egg was produced in winter and summer. But in the second series of experiments, the target species showed potential fecundity in winter. In summer, the target species were not caught enough for the experiment.

In the peak time of spawning, egg production of this species at the population level was 12.8% of body carbon. At an individual level, maximum potential specific egg production rate (in terms of carbon) was about 30.7%. The ratio of population egg production to the maximum potential was 41.7% (Table 2).

Sea water temperatures showed typical pattern of seasonal fluctuation in temperate zone. They were the highest in summer with up to 25.4°C, the lowest

Table 1. Summary of measurements of egg production of *Calanus sinicus* in Asan Bay, Korea [added to Table 1 of Park and Lee (1995)]

Experiment No. and Date		No. of females in the jar	Average (maximum) egg production (eggs female^{-1} day^{-1})		Sea water temperature (°C)	Particulate Organic Carbon (μgC l^{-1})
I-1	'93 Sep. 20	1~3	7.6	(14.0)	22.1	328.9
I-2	'93 Oct. 16	1~24	1.2	(7.0)	19.3	362.8
I-3	'93 Nov. 29	1~50	0.2	(2.0)	10.1	426.6
I-4	'94 Feb. 17	1~30	0	(0)	3.9	631.4
I-5	'94 Apr. 9	1~38	16.3	(39.0)	6.4	536.4
I-6	'94 May 14	1~18	12.1	(18.3)	13.6	241.6
I-7	'94 May 31	1~17	2.7	(6.6)	14.4	258.3
I-8	'94 Jul. 3	1~7	0	(0)	18.1	179.5
I-9	'94 Aug. 6	1~10	0	(0)	24.1	411.8
II-1	'95 May 24	1~19	8.2	(23.4)	13.0	
II-2	'95 Jun. 2	1~15	11.8	(31.7)	15.5	
II-3	'95 Jun. 24	1~4	5.1	(20.2)	17.9	
II-4	'95 Jul. 27	1~3	6.3	(21.6)	21.7	
II-5	'95 Aug. 23	*	*	*	25.4	
II-6	'95 Sep. 15	*	*	*	23.7	
II-7	'95 Oct. 14	1~14	11.4	(18.9)	20.0	
II-8	'95 Nov. 27	1~10	0	(0)	11.5	
II-9	'96 Jan. 11	1~29	1.0	(11.5)	3.7	
II-10	'96 Feb. 13	1~29	0.8	(6.0)	2.3	
II-11	'96 Mar. 16	1~28	5.3	(9.6)	3.3	
II-12	'96 Apr. 13	1~26	10.3	(22.6)	5.7	
II-13	'96 May 18	1~20	9.0	(22.3)	11.0	

*No target species was found in the study area

Table 2. Comparison of rates of egg production to those of Calanus species. Ratio "realized : potential" represents in situ rate relative to temperature-dependent potential rate (maximum observed or rate on abundant food) as reported in the study cited. -: not reported [added to Table 3 of Park and Landry (1993)]

Species	T(°C)	Location	Egg production rate		Realized	Source
			(eggs female^{-1} d^{-1})	(% C d^{-1})	Potential	
C. finmarchicus	0	E. Greenland	12.1	2.8	0.61	Hirche (1990)
	0	W. Spitsbergen	13.7	3.1	0.56	
	6	Emerald Basin	1.7	-	0.06	Runge (1985b)
	6-7	Browns Bank	21-30	-	0.66	
C. pacificus	7-12	Puget Sound	0-48	0.0-13.0	0.0-0.76	Runge (1985a)
	7-12	Puget Sound	0-33	-	0.0-0.7	Frost (1985)
	12-19	S. California	0-57	-	0.0-1.0	Mullin (1991)
C. marshallae	10	Oregon	2-49	0.6-14.6	0.07-1.0	Peterson (1988)
U. vulgaris	26	Hawaii	0-16	0.0-5.1	0.0-0.30	Park and Landry (1993)
C. sinicus	3.7-24.1	Asan Bay, Korea	0-16.3	0-12.8	0.0-0.42	Present study

in winter with about 2.3°C, and intermediate in spring and fall with 13~15°C. Particulate organic carbon (POC) contents, which could be used as a measure of food availability for this species, sustained relatively high levels in this bay with the annual average of about 375 μgC l^{-1} and the minimum of 179.5 μgC l^{-1}. Seasonal variation of POC with higher value in winter as shown by Moon *et al.* (1993) was also confirmed (Table 1).

Concentrations of particulate organic carbon (POC) measured as a key for food availability in the first series of experiments (Table 1) showed no significant correlation with the egg production ($p > 0.1$). As mentioned above, POC concentrations were usually higher than 200 μgC l^{-1} with annual average of 375 μgC l^{-1}, suggesting that this species were not food limited in this bay. Correlations between the egg production and seawater temperatures were not significant for both average egg production and maximum egg production ($p>0.1$, Fig. 3), either.

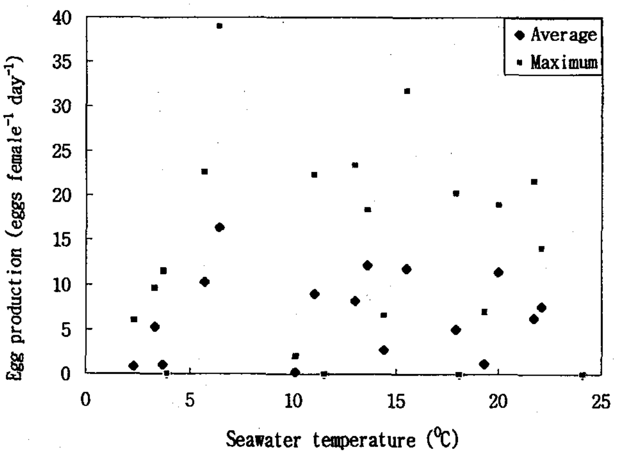

Fig. 3. Egg production rates (eggs female^{-1} day^{-1}) at different habitat temperatures.

Feeding efforts and gross efficiency of egg production

Feeding efforts of this species measured in the laboratory condition with cultured food *Stichococcus bacillaris* and expressed in terms of clearance rate (volume swept clear by an individual for an hour, F) showed exponentially decreasing trend with the increase of food concentrations (Fig. 4). That is, the ideal relationship between food concentrations and feeding efforts shown by Frost (1972) and Dagg and Walser (1987) was obtained in the present experiments, too. When F was fitted to the food concentrations (fc), the exponential equation, $F=3.17+37.629\ e^{-0.0005\ fc}$, was obtained (Fig. 4).

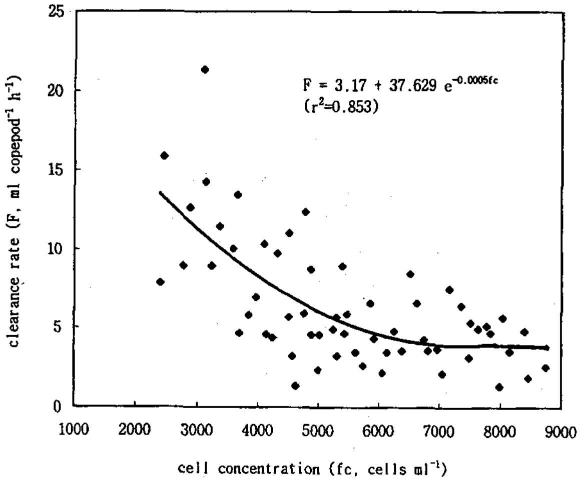

Fig. 4. Feeding effort (clearance rate, F, ml copepod^{-1} h^{-1}) by *Calanus sinicus* measured in the laboratory at different food concentrations (fc). The nonlinear curve fitting yielded an equation $F=3.17+37.629\ e^{-0.0005\ fc}$ ($r^2=0.853$).

Although the variability of F at a given food concentration was relatively big, the coefficient of determination of this nonlinear regression (r^2=0.85) was very high.

The asymptote of the regression curve, F=3.17 (ml individual^{-1} h^{-1}), was assumed to be the feeding effort of this species in nature. It was because the highest food concentration of the laboratory experiments was far less than the minimum POC in the study area when 8 pgC cell^{-1} for *Stichococcus bacillaris* was adopted from the similar sized phytoplankton (Frost, 1972; Checkley, 1980a). When this value of F was applied to the minimum value of POC, 179.5 μgC l^{-1}, daily ration of this species was calculated to be 13.7 μgC individual^{-1} d^{-1}, that was about 31% of the body carbon. Then, gross efficiency of egg production in case of maximum population egg production of 16.3 eggs female^{-1} d^{-1} was 41.6%. These calculations were based on the assumption of continuous feeding (no diurnal feeding rhythm), and the effect of temperature on feeding was not considered.

DISCUSSION

Habitat temperature and food availability have received the most attention as factors potentially affecting the growth of marine copepods (Checkley, 1980b; Park and Landry, 1993, and references therein). But in the present study, neither food nor temperature showed significant relationship with egg production, one form of growth, of the *Calanus sinicus*. Food concentrations judged by the measurement of POC were usually high in Asan Bay throughout the year (Moon *et al.*, 1993), so this species in this bay may not be food limited.

In this circumstance, influence of habitat temperature on growth may override that of food availability in nature (Huntley and Lopez, 1992; Saiz *et al.*, 1997). If temperature affects the egg production, these two variables will show certain relationship or correlation. As shown in Fig. 3, both average and maximum egg productions show no correlation with temperature at all. If there exists an optimum temperature for egg production, the rate will be highest at the optimum and will decrease for both directions of temperature changes, resulting in negative parabolic relationship. Fig. 3 did not show this pattern, either. Instead, this species in this bay showed potential for egg production for wide range of temperatures suggesting year-round potential of egg production.

On the other hand, the egg production by *Calanus sinicus* was similar to that of comparably-sized species of the genus *Calanus* and *Undinula* regardless of habitat temperatures (Table 2). Therefore, it can be said that habitat temperature also has little influence on the egg production of this species in this bay.

Chen (1964) reported three reproductive peaks of this species in the central part of the southern Yellow Sea. Lin and Li (1984, 1986) also reported that there was a remarkable seasonal fluctuation in egg production by this species in Xiamen Harbour, China (24° 26' N). Lin and Li (1984, 1986) reported three major spawning periods between December and mid May. But unfortunately, they did not sample or experiment during the other season of the year, from July to October. On the contrary, potential of year-round egg production by this species was reported by Huang *et al.* (1993). Although they did not measure the egg production directly but inferred from seasonal change in stage composition of this species in Kii Channel in Japan (33°~34° 30' N), they reported that the reproduction of this species took place throughout the year, and that this species did not seem to produce diapause eggs. Therefore, it can be concluded that this species can and do reproduce eggs year-round with some variations in the rates with the season of the year depending on the locality, and that this species has two reproductive peaks in the study area.

One other purpose of this study was to see whether the observed seasonal distribution pattern was a reflection of the life history pattern within a confined bay system or a result of long range horizontal migration. If the observed distributional pattern is a result of long range horizontal migration, the best proof would be the data on distribution obtained by covering wide areas and every month of the year. Unfortunately, these kinds of data were not obtained in this study.

There were two peaks in egg production but one peak in seasonal distribution. The growth period from eggs to adults depends on temperatures, and it is about two months if sea water temperature is around 10°C (Uye, 1988). The duration gets longer with decreasing temperatures. The sea water temperatures in Asan Bay were lower than 10°C from November till April or May. They became lower than 10°C right after the fall peak in egg production and remained at very low down to 3.7°C in January, and became to rise up to 10°C until the spring peak in egg production. In this circumstance, the growth would be retarded. Thus, the inference is possible that spring peak in abundance is a result of high egg production in previous fall so that the growth period is about 6 months.

If the same scenario is applied to the spring peak in egg production, there should be abundance peak in summer or early fall caused by fast growth in higher temperatures (less than 6 months of growth period). But summer and fall abundances were still low. Park and Lee(1995) suggested the high predation pressure by the abundant demersal fishes in this bay in summer (Whang, 1994) for this lack of summer-fall abundance peak without any direct evidence of high predation pressure such as food selectivity of the fishes. At a glance, it seemed to be plausible. However, if this is the case, the reduced abundance in summer and fall may diminish the population eventually. The peak abundance in next spring may not be expected.

The abundance of this species in summer was very low. In addition, it is hard to believe that this species produces diapause eggs in the warm seasons (Huang *et al.*, 1993; almost all the eggs spawned in spring were actually hatched in the laboratory in this study). Then where were the adults responsible for the fall peak in egg production just before they produced the eggs in this bay? Only long range horizontal migration in and out of this bay can explain the presence of adults in fall. According to Zhang (1995), population density of this species was highest in the central part of the southern Yellow Sea both in May and September. This supports the postulation that majority of this species moved from the Asan Bay to the central part of the Yellow Sea during the summer of highest habitat temperatures. In this context, both life cycle and long range horizontal migration seem to be responsible for the observed distributional pattern in this bay.

Gross efficiency of egg production, the rate of egg production to ingestion in terms of carbon content, was calculated to be 41.6% with the clearance rate of 3.17 ml individual^{-1} h^{-1}. This feeding effort was a little less than 4.3 ml individual^{-1} h^{-1} of similar sized *Calanus pacificus* (Frost, 1972). However, considering the food saturated condition in this bay and the fact that differences in food quality and quantity used in the experiments affect the resultant feeding effort, this difference may not be too big.

Diurnal feeding rhythm (Head *et al.*, 1984) might inflate the ingestion rate calculated here and application of the minimum POC might cause underestimation of ingestion rate. Then the influences of these two may offset each other, although the relative degree of influences could not be estimated easily. In spite that the effect of temperature on feeding (Kiφrboe *et al.*, 1985) was not considered, this obtained value of gross efficients of egg produc tion was similar to previous results. Checkley (1980b) reported 37% of gross efficiency of egg production for *Paracalanus parvus*, and Kiφrboe *et al.* (1985) reported 36% for *Acartia tonsa* both in the laboratory conditions.

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