Reproductive strategy of *Acartia steueri* in Sagami Bay, Japan

Yasuko ONOUE[1]*, Shinji SHIMODE[1], Tatsuki TODA[2] and Tomohiko KIKUCHI[1]

[1] Department of Environment and Natural Sciences, Graduate School of Environment and Information Sciences, Yokohama National University, 79–2, Tokiwadai, Hodogaya-ku, Kanagawa 240–8501, Japan
  *E-mail: d02ta002@ynu.ac.jp
[2] Department of Environmental Engineering for Symbiosis, Faculty of Engineering, Soka University, 1–236, Tangi-cho, Hachioji, Tokyo 192–8577, Japan

Abstract—Reproduction, hatching success and population dynamics of the dominant copepod *Acartia steueri* were studied in Sagami Bay, Japan from February 2002 to December 2003. *A. steueri* occurred through the year in the water column, and it produced physiologically different eggs, subitaneous and diapausing. Subitaneous eggs were produced through the experimental period, whereas diapausing ones were restricted from February to August in both years. Population egg production rate (EPR) increased with the abundance of adult males and females from February and reached maximum in June. However, planktonic population of *A. steueri* did not increase during summer to winter because diapausing eggs occupied a great part of their reproduction (~98%). Recruitment rates in October to December 2002 and September 2003 were higher than population EPR, implying that diapausing eggs of *A. steueri* had a key role to support the recruitment into water column when the reproductive ability of the population diminished rather than to contribute to an increase of the planktonic population rapidly in their favorable seasons.

Key words: egg production, diapausing egg, recruitment, *Acartia steueri*

Introduction

Presently, 50 marine calanoid species are known to produce resting eggs (Belmonte 1997, Mauchline 1998), and two types of resting eggs are distinguished; quiescent subitaneous and diapausing eggs (Grice and Marcus 1981, Uye 1985, Marcus 1996). Subitaneous eggs hatch within a few days, however, they can become quiescent when they are exposed to adverse environmental conditions. Diapausing eggs hatch only after the completion of a refractory phase, which may last for a few weeks to months or even several years (De Stasio 1989). After passing through the refractory phase and when environmental conditions becoming favorable, diapausing eggs hatch all together (Marcus 1996). On the other hand, some species produce diapausing eggs which hatch without any environmental cues when refractory phase finished (Grice and Gibson 1981, Ianora and Santella 1991, Belmonte 1997, Chen and Marcus 1997, Onoue et al. 2004). Among these copepods, *Labidocera scotti*, *Pontella meadi* in the Gulf of Mexico (Chen and Marcus 1997) and *Acartia steueri* in Sagami Bay (Onoue et al., 2004) are known to have diapausing eggs, some of which have relatively short length of refractory phase. Consequently, their eggs have various lengths of refractory phases, and they hatch sporadically over several weeks. These eggs were named delayed-hatching eggs by Chen and Marcus (1997). After that, they are redefined as diapausing eggs because egg physiology does not have to be identified by egg hatching pattern but by the length of refractory phase of each egg (Onoue et al. 2004).

Neritic copepods have been known to change their abundance seasonally, and some species disappear from the water column during their environmentally adverse season. These copepods have been known to have diapausing eggs with long refractory phases (Marcus 1996). Diapausing eggs with long refractory phases are accumulated in the sediment to avoid environmentally adverse season. On the other hand, diapausing eggs with various lengths of refractory phases might be a bet-hedging strategy to promote the survival of some offspring. By expanding the period over which eggs hatch, a female might extend her offspring's abilities to utilize resources (e.g., temporal differences in food quality and quantity) and reduce mortality by avoiding heavy predation over some limited period of the year (Chen and Marcus 1997). However, in the Gulf of Mexico, *L. scotii* and *P. meadi* are restricted to present in water column during a part of a year (Chen and Marcus 1997). Thus, the nauplii emerged from diapausing eggs with various lengths of refractory phases might successfully recruit into water column just before their next population increase.

A. steueri is known to produce morphologically different two types of eggs, smooth and spiny eggs (Uye 1983, Onoue et al. 2004). The spiny eggs are diapausing eggs with various lengths of refractory phases in Manazuru Port (Onoue et al.

2004). In this study site, *A. steueri* exists in water column through a year, though it decreases their abundance in summer (Onoue et al. 2004). Subsequently, *A. steueri* increase their abundance in late autumn. Similarly in Irish Sea, *Temora longicornis* has diapausing eggs and were collected from water column through a year (Castellani and Lucas 2003, Engel and Hirche 2004). Castellani and Lucas (2003) suggested that the resting eggs of *T. longicornis* have a key role to enhance the rapid spring increase of this species from the low population density during winter. Therefore, it might be expected that the population increase of *A. steueri* would be related with the hatching of diapausing eggs in the sediments. The present study aims to identify the season when the hatching of diapausing eggs of *A. steueri* contributes to the recruitment into water column and the ecological implication of the diapausing eggs for the population dynamics of this species.

Materials and Methods

Acartia steueri was collected at a fixed station of Manazuru Port (35°09′49″N, 139°10′33″E; depth, 5.5 m) located in the northwestern coast of Sagami Bay, Japan from February 2002 to December 2003 (Fig. 1).

Zooplankton abundance samples were collected once or twice a month. In particular, samplings were carried out every 2 days in the period when *A. steueri* produced diapausing eggs. Zooplankton was collected by gently towing a 180 μm mesh net (diameter: 30 cm; length: 150 cm) obliquely from the 5 m depth to the surface, and fixed in 5% buffered formalin seawater for determining abundance of adult males and females of *A. steueri*.

Live samples of *A. steueri* to estimate the egg production rate (EPR) were collected once a month from February to April 2002, every week from September 2002 to September 2003 and twice a month from October to December 2003. When *A. steueri* produced diapausing eggs, females were collected every two days to obtain detailed information. Each sample was transferred to the laboratory in an insulated container within 30 minutes. In each sampling, twenty adult females of *A. steueri* were sorted under a dissecting microscope. Under *in situ* conditions, adult females were kept individually in an incubation chamber for 24 h following Onoue et al. (2004). The incubation chamber was immersed in a 10 ml beaker, which has ca. 20 ml capacity, containing ca. 15 ml of ambient seawater pre-screened through a 70 μm mesh to avoid contamination from other eggs. After 24 h, the females were removed from their chambers and numbers of subitaneous and diapausing eggs were counted. The egg types were determined by their morphology, where subitaneous eggs had smooth surface and diapausing ones had spines on their shells (Onoue et al. 2004). Total EPR was de-
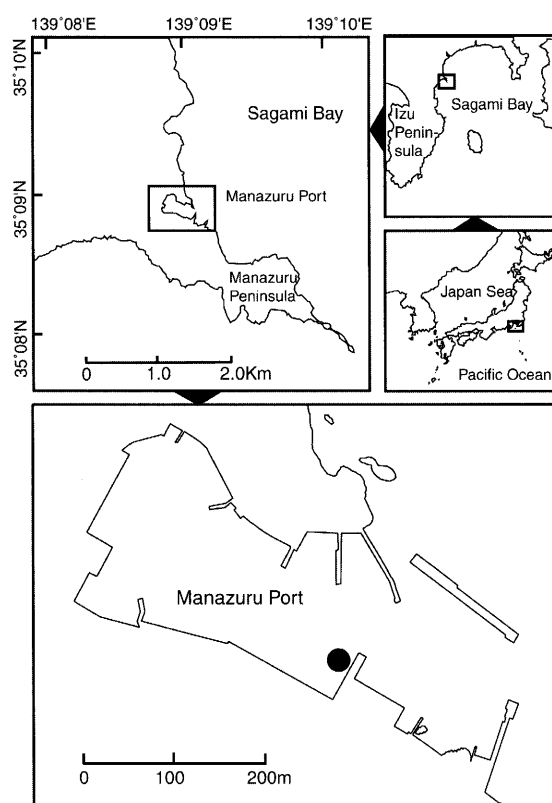

Fig. 1. Location of sampling site.

termined as sum of subitaneous and diapausing eggs. Eggs of dead females were not counted, and excluded from further analysis. Hatching success was monitored after one to three days from spawning. Some eggs that showed signs of decomposition were classified as inviable eggs.

To determine recruitment rate of nauplii, *A. steueri* was collected every month from October 2002 to September 2003, with a 3 m oblique haul using a 30 cm diameter and 35 μm mesh plankton net. Recruitment rate (R) was calculated by using the equation:

$$R = N_{II}/D_{II},$$

where N_{II} is abundance of second stage of nauplius and D_{II} is the instar duration of N_{II} stage (Uye 1982). Instar duration is determined from the relationship between development rate of *A. steueri* and temperature (Uye 1980) by using the water temperature of the sampling site.

Chlorophyll *a* concentrations were determined by filtering two replicate samples of seawater from the surface of Manazuru Port, following Holm-Hansen et al. (1965), and surface water temperatures were also measured at the same time.

Results

Environmental conditions and the abundance and repro-

Table 1. Mean monthly changes of temperature, chlorophyll a concentration (Chl. a), abundance, EPR, population EPR and hatching success of *Acartia steueri* in Sagami Bay between February 2002 and December 2003; mean±1 standard deviation.
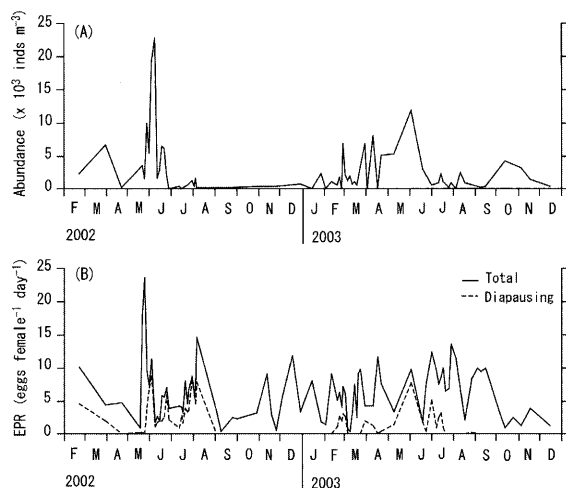
Month		Temperature (°C)	Chl. a (μg l^{-1})	Abundance (inds m^{-3})	EPR (eggs female^{-1} day^{-1})		Population EPR (eggs m^{-3})		Hatching success (%)	
					Total	Diapausing	Total	Diapausing	Total	Subitaneous
Feb	2002	13.2	2.0	2356.7	10.1	4.5	16691.3	7436.7	45.2	84.9
Mar		14.0	0.5	6680.8	4.4	2.0	10845.3	4929.7	N.D.	N.D.
Apr		16.5	0.6	148.6	4.7	0.0	198.3	0.0	91.1	91.1
May		18.7±0.8	2.6±1.2	5146.9±3552.0	11.9±9.0	2.3±3.1	28629.9± 8067.3	8221.1± 9769.4	51.7±45.2	95.9± 4.2
Jun		19.8±0.8	4.0±3.8	7658.3±8590.0	5.0±3.2	3.3±2.7	23096.6±34632.3	15475.3±26843.4	30.0±17.7	96.6± 3.8
Jul		23.1±1.8	2.4±1.9	525.4± 449.5	5.7±2.2	3.5±2.4	2509.5± 3491.7	2052.1± 3511.4	52.5	75.0
Aug		26.8±0.4	8.2±5.2	737.9± 729.3	9.3±4.7	6.1±1.7	3584.2± 3676.0	2319.7± 2267.1	N.D.	N.D.
Sept		25.1±1.9	1.5±1.4	305.7	2.1±1.6	0.0±0.0	513.1	0.0	85.6	85.6
Oct		21.2±1.1	0.5±0.1	19.0	2.8±0.6	0.0	396.1	0.0	91.7	91.7
Nov		16.2±1.7	0.5±0.4	334.0	4.6±3.7	0.0	182.8	0.0	54.8	54.8
Dec		14.5±1.2	0.2±0.1	685.1	6.8±4.5	0.0	1275.5	0.0	N. D.	N.D.
Jan	2003	13.3±0.4	0.6±0.5	2355.3	4.9±4.5	0.0	2343.2	0.0	91.8± 7.7	91.8± 7.7
Feb		12.6±1.2	1.3±1.1	2072.2±2712.5	5.5±2.7	1.4±1.3	6672.4± 8558.2	2118.6± 3564.7	61.7±11.5	83.8±15.3
Mar		13.6±0.9	0.7±0.4	2167.8±1963.8	4.8±3.5	0.5±1.0	5489.8± 6249.0	983.1± 1984.4	64.7±28.3	76.3±13.0
Apr		14.7±0.7	1.3±1.8	4455.8±4040.9	7.8±3.8	0.6±0.7	20138.4± 2395.6	2337.4± 3212.0	72.5±18.3	87.0± 3.7
May		18.1±1.9	0.8±0.4	5276.7	3.3	1.5	10266.9	2291.7	56.7	87.9
Jun		22.0±0.0	2.0±0.9	7419.7±6185.3	6.4±4.1	3.2±3.9	32207.4±39357.1	17140.5±26266.5	35.8±30.7	92.6±12.8
Jul		22.7±0.9	6.3±6.1	1002.6± 665.1	9.4±2.6	1.6±1.8	6427.3± 4647.1	1127.7± 1815.1	68.2±18.7	86.4± 8.3
Aug		24.0±1.3	1.9±0.9	1146.5±1206.6	7.2±4.0	0.1±0.1	3846.4± 5365.3	0.0	87.8± 9.0	87.8± 9.0
Sep		24.7±0.8	7.8±1.4	274.6± 156.1	9.8±0.2	0.0	1309.8± 983.2	0.0	89.8± 8.9	89.8± 8.9
Oct		20.4±1.3	0.5±0.1	4178.3	2.0±1.1	0.0	2065.6	0.0	82.2±25.2	82.2±25.2
Nov		17.8±0.4	0.7±0.2	2281.7±1273.1	2.6±1.9	0.0	2490.8± 1584.4	0.0	92.9	92.9
Dec		17.4±0.2	0.4±0.2	385.0	1.3	0.0	193.4	0.0	77.7	77.7

ductive characteristics of *Acartia steueri* from this study are summarized in Table 1. Water temperature and chlorophyll *a* concentration varied markedly during a year (Fig. 2). Water temperature increased from late February to early September and ranged annually between 12.0 and 27.2°C. The values and seasonal trend were similar in both 2002 and 2003. Chlorophyll *a* concentration varied from 0.1 to 12.5 μg l^{-1} in 2002, and from 0.3 to 18.8 μg l^{-1} in 2003. Though chlorophyll *a* concentrations were under 1.0 μg l^{-1} in most of the sampling period, phytoplankton blooms occurred between early spring and summer. Chlorophyll *a* concentration reached over 10.0 μg l^{-1} at the blooms, which was dominated by diatoms, such as *Nitzschia* spp., *Thalassiosira* spp. and *Chaetoceros* spp., and large dinoflagellates, *Ceratium furca* and *Ceratium fusus* (Aono unpublished data).

Seasonal trend of abundance of adult males and females *A. steueri* was almost similar in both years (Fig. 3A). Adult males and females *A. steueri* increased with water temperature from February to June, and then decreased sharply in July. The abundance of adults in 2002 varied from 4.2×10 to 2.3×10^4 inds m^{-3}. In 2003, the abundance was ranged from 5.6×10 to 1.2×10^4 inds m^{-3}.
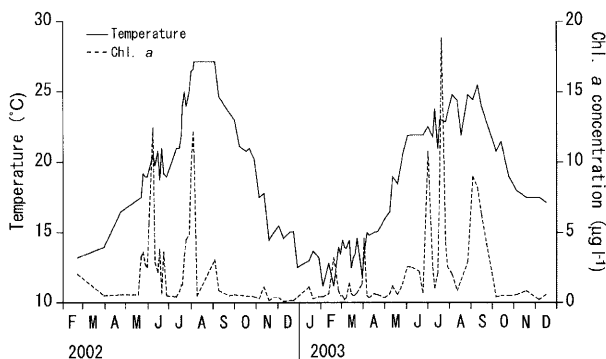
A. steueri produced two types of eggs, subitaneous and diapausing. Subitaneous eggs were produced through the two years, and diapausing eggs were produced from February to August in both 2002 and 2003 (Fig. 3B). Total EPR, which was the sum of subitaneous and diapausing eggs, fluctuated with no apparent relationships with temperature. Minimum and maximum total EPR were 0.4±0.8 eggs female^{-1} day^{-1} in September and 23.7±5.5 eggs female^{-1} day^{-1} in May, 2002, respectively. In 2003, the values ranged from 0.7±1.2 eggs female^{-1} day^{-1} in March to 13.6±3.5 eggs female^{-1} day^{-1} in July. Relative abundance of diapausing eggs varied largely during the periods when diapausing eggs were produced (Fig. 3B). In most of those periods, both subitaneous and diapausing eggs were produced at the same time. Though most of females produced only subitaneous or diapausing eggs, some females produced both subitaneous and diapausing eggs during the 24 h incubation. The maximum rates of diapausing egg production were 8.8±2.9 eggs female^{-1} day^{-1} in 2002 and 7.7±5.3 eggs female^{-1} day^{-1} in 2003, respectively.

Population EPR varied with female abundance (Fig. 4) and increased from February to June and decreased to summer. In May and June, diapausing eggs accounted for ~98% of the population EPR. Despite the high population EPR in June, the abundance of the adults was low during the summer in both 2002 and 2003 (Figs. 3A & 4). Maximum population EPR was 1.0×10^5 eggs m^{-3} day^{-1} in June 2002, and 6.0×10^4 eggs m^{-3} day^{-1} in June 2003.

Hatching success of total eggs varied with season, and was low during May and July in both 2002 and 2003 (Fig. 5). Decrease of the hatching success of total eggs started with

Fig. 2. Seasonal changes of temperature and chlorophyll *a* concentration in Manazuru Port between February 2002 and December 2003.
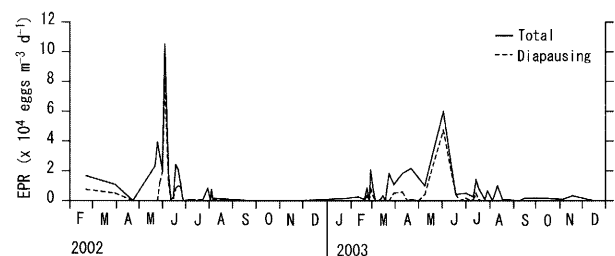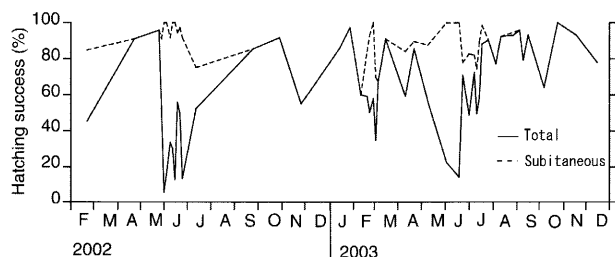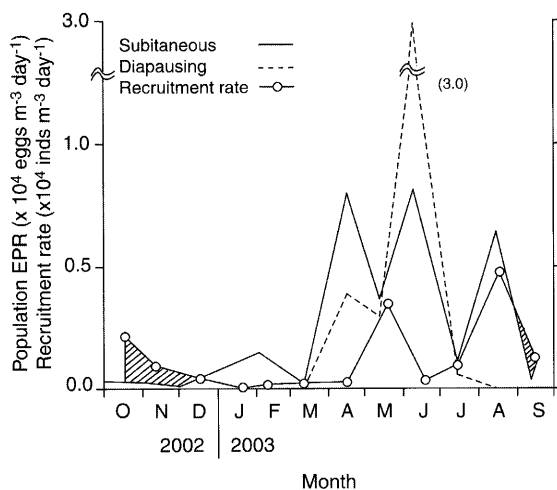

Fig. 3. Seasonal changes of abundance of adult male and female (A) and total and diapausing EPRs (B) in *Acartia steueri*.

Fig. 4. Seasonal changes of population EPR of total (Total: subitaneous plus diapausing eggs) and diapausing eggs in *A. steueri*.

Fig. 5. Seasonal changes of hatching success of total (Total: subitaneous plus diapausing) eggs and subitaneous eggs in *A. steueri*.

Fig. 6. Seasonal changes of population EPR of subitaneous and diapausing eggs and recruitment rate of *A. steueri.*

diapausing egg production (Figs. 3B & 5). On the other hand, the hatching success of subitaneous eggs was high during the experimental period (>70%). However, in autumn to winter, the hatching success of subitaneous eggs fluctuated and reached to minimum, 54.8%, in November 2002 and 59.8% in February 2003.

Relationship between the population EPR of subitaneous and diapausing eggs and recruitment rate is shown in Fig. 6. Since it takes 3 to 10 days to develop eggs to N_{III} stage at 13 to 24°C, the population EPRs before 3 to 10 days from sampling for recruitment rate were plotted. Though the recruitment rate was almost always lower than the population EPR of subitaneous eggs during the experiment, inverse relationships were observed in October and December 2002 and September 2003. Population EPR of subitaneous eggs was high during April and August, however, recruitment rate was low in April and June. Population EPR of diapausing eggs increased from April, and reached maximum in June beyond that of subitaneous ones.

Discussion

To date there are various experiment to determine the hatching of resting eggs of copepods. Relationships between environmental conditions (e.g., temperature, oxygen and sulfide concentration) and hatching of the eggs that were extracted from the sediment (Marcus 1989, Næss 1991, Katajisto et al. 1998) or spawned from females (Ban and Minoda 1991, Grice and Gibson 1977, Marcus and Lutz 1998, Katajisto 2003) were determined. Also, the hatching from the sediment samples was observed (Guerrero and Rodríguez 1998, Engel and Hirche 2004). It would be needed to determine the season when diapausing eggs hatch and recruit into the water column for understanding the ecological meaning of diapaus-

ing eggs. However, the mortality from eggs to N_{II} stage is known to be around 90% in marine copepods (Landry 1978, Uye 1982, Liang and Uye 1996), and these methods would not show the actual contribution of diapausing eggs to recruitment of population. In the present study, by measuring recruitment rate from nauplius's abundance, we would obtain more reliable evidence to confirm the recruitment from diapausing eggs. In addition, *Acartia steueri* is known to live in enclosed bays (Ueda 2001) and was collected very rarely from the outside stations near Manazuru Port (Shimode 1998). Therefore, the population of *A. steueri* in Manazuru Port would be isolated from neighboring regions, and it is well assumed that the influence of populations from outside the port, if any, would be minimal.

Diapausing eggs of *A. steueri* have various length of refractory phase in each egg (Onoue et al. 2004) and were produced in every spring to early summer during this study period. It is well known that many copepod eggs are accumulated in the bottom sediment as resting eggs (Kasahara et al. 1975, Marcus 1990, 1995, Guerrero and Rodríguez 1998). In fact, we collected the diapausing eggs of *A. steueri* from the bottom sediments of Manazuru Port (Onoue unpublished data). Engel and Hirche (2004) showed continuous hatching of eggs of *Temora longicornis* and *Centropages hamatus*, which are known to have diapausing eggs in other regions, for 12 month from sediment samples. Although it was uncertain whether number of the hatched nauplii from the diapausing eggs were seasonally changed or not, it might imply that diapausing eggs hatch sporadically throughout a year and recruit into water column as well as subitaneous ones. Our present study clearly indicates that the recruitment rate of October to December 2002 and September 2003 exceeded the population EPR. Therefore, at least during these periods, the nauplii hatched from diapausing eggs and contributed to the recruitment into the water column.

In a previous study, *A. steueri* decreased their abundance in summer (Onoue et al. 2004), which was also confirmed in the present study (Fig. 3). The EPR of *A. steueri* in both Onagawa Bay (Uye 1981) and Manazuru Port (Kondo 2004) decreased when temperature was over 23 and 22.5°C, respectively, even they were supplied enough food. Furthermore, most of the diapausing eggs were produced in early summer. Therefore, it might suggest that *A. steueri* produce diapausing eggs to avoid high temperature seasons. Although the EPR of *A. steueri* did not show a clear seasonal pattern, the population EPR varied seasonally with a marked increase from February to June (Fig. 5). However, there was no distinct peak of the adults abundance after the maximum of population EPR in each year (Fig. 3A). One of the most probable explanations of the above discrepancy is that the diapausing eggs occupied the great part of egg production during the periods (Fig. 4). Fig. 4 also indicates that the population reproductive ability of *A. steueri* is diminished from

summer to winter. During this period, the recruitment rate exceeded population EPR (Fig. 6). Therefore, rather than contributing to an increase in the species population density, the diapausing eggs of *A. steueri* seem to play a key role in supporting the recruitment when the reproductive ability of the population is diminished.

Recruitment rate of *A. steueri* was low in April and June even when population EPR of subitaneous eggs was high (Fig. 6). In this period, hatching success of subitaneous eggs was also high (77–100%), implying that the low recruitment rate was caused from high mortality of early nauplius stages or high predation pressure on eggs. The diapausing eggs that are spawned by the species that exist in water column through a year are thought to be produced for minimizing mortality from predation or preventing intraspecific competition (Engel and Hirche 2004). In Manazuru Port, *A. steueri* did not disappear from water column through a year (Table 1, Fig. 3), and the diapausing eggs were produced when the mortality of the eggs or nauplii was considered to be high. In addition, when diapausing eggs were produced, the abundance of adult *A. steueri* reached the maximum value of the year. Our result indicates that *A. steueri* might also produce diapausing eggs to reduce their intraspecific competition for food depletion caused by over crowding. *Eurytemora affinis* is known to use a chemical cue which originated from the over crowding as an indicator of the forthcoming food depletion (Ban and Minoda 1994). Therefore, the results of this study seems to support the assumption of Engel and Hirche (2004) and the diapausing egg production of *A. steueri* might be controlled by the interactions among factors that influence the population dynamics of this species.

The ecological meaning of diapausing eggs with long refractory phase has been mainly thought as a bridge to connect temporally divided populations (Marcus 1996). On the other hand, the production of diapausing eggs of various lengths of refractory phases is considered as a bet-hedging strategy through spreading hatching times to survive under high predation pressure or intraspecific competition (Chen and Marcus 1997). The result of the present study implies that diapausing eggs with various lengths of refractory phases have another ecological importance as a support of continuous recruitment during unfavorable seasons for sustaining their planktonic population. On the other hand, in case of *A. steueri*, the recruitment rate that exceeded the population EPR seemed to be very low compared with the population EPR of diapausing eggs. Diapausing eggs would be accumulated in the sediment as an egg bank to secure its planktonic population year after year.

There are fewer studies of distribution, reproductive characteristics or diapausing eggs of *Acartia* in East Asian coastal waters than Europe or North America. However, East Asian coastal waters include wide range of climate, from subarctic to tropical, and it is expected that investigating and comparing the reproductive characteristics in this regions will contribute to our understanding of the ecology and evolution of diapause. It would be interesting to accumulate further information in East Asian coastal waters.

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