Estimation of production of the copepod *Calanus sinicus* during spring in the northern East China Sea

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Abstract: We estimated the production of the copepod *Calanus sinicus*, including somatic production of copepodite stage 1 (CI) to copepodite stage 5 (CV) and egg production of adult females, to elucidate the role of *C. sinicus* during spring in the northern East China Sea, including the southern waters of Korea. To estimate the somatic production of the copepodites, an empirical equation for broadcasters (Hirst & Bunker 2003) was used. The total biomass of the *C. sinicus* population, including CI to adult males and females, ranged from 0.11 to 30.23 mg C m⁻³, with a mean of 8.69 mg C m⁻³. The egg production rate (EPR) of adult females of *C. sinicus*, measured over 24 h of shipboard incubation, ranged from 0 to 14.9 eggs female⁻¹ day⁻¹ (mean 5.8 eggs female⁻¹ day⁻¹), equivalent to mean 33.6 µg C m⁻³ day⁻¹. The weight-specific EPR (WSEPR) of adult females averaged 0.023 day⁻¹, and significantly increased with increasing water temperature at 5 m depth and surface chlorophyll *a* concentration, respectively. WSEPR decreased with increasing body mass of individual adult females. The total production of the *C. sinicus* population ranged from 0.02 to 3.67 mg C m⁻³ day⁻¹ (mean 0.91 mg C m⁻³ day⁻¹) and the depth-integrated mean total production was estimated to be 52.72 mg C m⁻² day⁻¹. CV production accounted for 54% of the total production. By contrast, EPR contributed on average only 3.7% of the total production rate. Our estimate of the production of *C. sinicus* can be applied for potential comparisons of region-specific copepod production.

Key words: *Calanus sinicus*, copepod, copepodites, egg production rate, somatic production

Introduction

Copepods are important grazers of phytoplankton and microzooplankton, as well as a trophic link in the pelagic food web between primary producers and higher trophic levels (Banse 1995, Kiørboe 1997, Calbet & Saiz 2005). Measurement of secondary production of zooplankton is essential to understanding energy flow in marine ecosystems (Kimmerer 1987, Banse 1995, Verity & Smetacek 1996). Data on secondary production of marine mesozooplankton are rare compared to data on primary production, possibly due to the lack of a simple and robust method for measuring secondary production of mesozooplankton (Hirst & Bunker 2003, Hirst et al. 2005, Kimmerer et al. 2007, Yebra et al. 2017).

Secondary production of zooplankton consists of somat-

ic production (i.e. growth of juveniles) and egg production (i.e. fecundity of adult females) (Runge & Roff 2000). In general, the egg production rate (EPR) of copepods is measured directly by incubating adult females for 24 h (Runge & Roff 2000). Somatic production can be measured by various methods, including both classical and biochemical methods (Kimmerer & McKinnon 1987, Hirst & Bunker 2003, Kimmerer et al. 2007, Yebra et al. 2017). However, because measuring the growth rate of juveniles directly is a difficult task, several empirically-based global equations have been suggested to estimate the growth rate and then predict the production of marine copepods (Hirst & Lampitt 1998, Peterson et al. 2002, Hirst & Bunker 2003). These equations may be valuable to predict growth and production of copepods when no reliable growth rate measurements are available (Peterson et al. 2002).

The northern East China Sea (ECS) has a complex current circulation system, including the Tsushima Warm Current, Taiwan Warm Current, Yellow Sea Coastal Cur-

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rent, and Changjiang Diluted Water (Chen et al. 1995, Lie et al. 2003, Chen & Sheu 2006, Lie & Cho 2016). These complicated environments provide a good spawning ground for important species in the fishery industry such as anchovies and hairtail (Chen et al. 1997, Kim et al. 2005). Many studies have examined the spatial and temporal variations in water mass, nutrients, chlorophyll *a* (Chl *a*), primary productivity, and mesozooplankton biomass and abundance in the northern ECS (Gong et al. 2006, MOF 2006, Zhang et al. 2007b, Kim et al. 2009, Choi et al. 2011, Hwang et al. 2013, Kang et al. 2015, Lie & Cho 2016).

The copepod *Calanus sinicus* Brodsky, 1962 is widely distributed in the shelf around the northern Pacific Ocean (Uye 2000), and is also one of the dominant calanoid species in the Inland Sea of Japan (Uye & Murase 1997, Uye 2000), the Yellow Sea, and the northern ECS (Kang & Hong 1998, Zhang et al. 2005, Kang et al. 2007b, Huo et al. 2008, Kang et al. 2011, Kim & Kang 2018). There have been many studies on the population dynamics (Kang & Hong 1998, Pu et al. 2004, Kang et al. 2007b, Kang 2008, Kang et al. 2013), over-summering site (Wang et al. 2003), EPR (Park 1997, Zhang et al. 2007a, Huo et al. 2008, Wang et al. 2009, Kang et al. 2011), feeding (Huo et al. 2008, Kim & Kang 2018), and somatic production (Kang 2008) of *C. sinicus* in the Yellow Sea and around the northern ECS, including the southern waters of Korea. However, little is known about secondary production of *C. sinicus* in the northern ECS.

The aims of this study were to evaluate the production of *C. sinicus* during spring in the northern ECS, including the southern waters of Korea, and to understand the controlling factors related to the fecundity of females.

Materials and Methods

Field sampling

The cruise for measuring production of the copepod *Calanus sinicus* was carried out from April 29 to May 8, 2004, at nine stations in the northern ECS, including the southern waters of Korea, on the R/V *Eardo* (Table 1, Fig. 1). Temperature and salinity were recorded with a conductivity-temperature-depth (CTD)-rosette (SBE 911, Sea-Bird Scientific, USA). To depict more detailed temperature and salinity conditions, temperature and salinity data from an additional 52 stations from the same cruise (MOF 2006) were used. To measure Chl *a* concentrations, water samples (500 mL) from various depths (0, 10, 20, 30, 50, 75 and 100 m) at the nine stations were filtered onto Whatman GF/F glass filters (47 mm) during the cruise, placed into 1.8-mL cryogenic vials (Nalgene, Thermo Fisher Scientific, USA), and stored in liquid nitrogen until the end of cruise. After the cruise, the cryovial samples were transported to the laboratory on dry ice in an insulated box. In the laboratory, the filters in the cryogenic vials were

Table 1. Water depth, mean water temperature (WT) of the water column, mean chlorophyll *a* (Chl *a*) concentration of the water column, and mean body mass of adult female.

Station	Depth (m)	WT (°C)	Chl <i>a</i> ($\mu\text{g L}^{-1}$)	Body mass of adult female ($\mu\text{g C ind.}^{-1}$)
Ieodo	50	12.0	1.93	121.4
B4	80	13.5	1.55	107.1
B9	105	16.6	0.80	93.2
D1	48	11.3	1.03	135.4
D7	104	14.8	0.52	103.5
D11	104	15.4	0.49	83.3
H6	140	15.9	1.03	93.0
H3	89	14.5	1.12	98.9
H1	26	13.7	1.03	124.4

Fig. 1. Study area and sampling stations in the northern East China Sea including the southern waters of Korea.

placed into 7 mL of 90% acetone and maintained at -20°C for 24 h. The Chl *a* concentration was measured using a fluorometer (10-AU, Turner Designs, USA) according to Parsons et al. (1984).

Abundance and biomass

Mesozooplankton were sampled using a vertical net tow from the near-bottom to the surface with a 0.5-m diameter, 200- μm mesh net fitted with a flowmeter (Model 438-110, Hydro-bios, Germany) for estimating the volume filtered by the net. The samples were preserved in neutralized formalin at a 5% final concentration for subsequent analysis and transported to the laboratory. In the laboratory, the mesozooplankton samples from each station were identified as copepodite stage 1 (CI) through copepodite stage 5 (CV) and adult males and females of *Calanus sinicus* using a stereoscopic microscope (Stemi 2000-C, Zeiss, Germany), and counted to determine abundances. Also, the prosome length of each developmental stage of *C. sinicus* was measured using the stereomicroscope with an ocular micrometer. The carbon contents of *C. sinicus* individuals

were estimated from the length-weight relationship (Uye 1988):

$$\log_{10} BW = -9.416 + 3.378 \log_{10} PL,$$

where PL is the prosome length (μm) for copepodites and BW is the body mass ($\mu\text{g C}$).

EPR

The EPR of *Calanus sinicus* was measured by the incubation method (Runge & Roff 2000, Peterson et al. 2002). To measure EPR, adult females of *C. sinicus* were collected in a vertical net tow (0.5 m in diameter, 200 μm mesh size) from the near-bottom to the surface at the nine stations. Active and healthy adult female *C. sinicus* were sorted into 2-L glass bowls containing 64 μm screened surface seawater. Two to four females of *C. sinicus* were placed in a polycarbonate bottle (1 L) containing 64 μm screened surface seawater from each sampling station (Peterson et al. 2002), with two to ten replicate bottles depending on the sampling station, and the bottles were placed in a water bath in which surface seawater was circulated. It has been known that in some copepod species [e.g. *Calanus finmarchicus* (Gunnerus, 1770) and *C. helgolandicus* (Claus, 1863)] the feeding history of females prior to capture is important for EPR in the first 24 h after capture (Runge & Roff 2000). Therefore, we assumed that EPR would not be biased by the 64 μm screened surface seawater. We also assumed that the motion of the ship would help keep the phytoplankton in the bottles in suspension during the incubation. In addition, the bottles were manually rotated three or four times a day to prevent settlement of phytoplankton. After 24 h, the contents of the bottles were filtered through a 64- μm sieve to collect eggs and nauplii and the females were checked for viability. The eggs, nauplii, and females on the screen were preserved in 5% neutralized formalin and kept in 20-mL glass vials. The numbers of eggs and nauplii were counted, and the prosome lengths of adult females were measured using a stereomicroscope with an ocular micrometer to estimate body mass of the females. Egg cannibalism was also considered by counting crumpled egg membranes left in the vials (Runge & Roff 2000) and eggshells in the fecal pellets (Kang 2012). Egg hatching success was not measured in the EPR experiment. EPR was expressed both as numbers of eggs per female per day (eggs female⁻¹ day⁻¹) and as weight-specific EPR (WSEPR, day⁻¹). The WSEPR of a female was calculated as the carbon content of total eggs spawned divided by the body weight of the adult female (Peterson et al. 2002). The carbon content of a *C. sinicus* egg (EC, $\mu\text{g C}$) was estimated from the egg diameter (ED, μm) using the equation (Liang et al. 1994):

$$EC = ED^{3.04} \times 10^{-7.27}.$$

The ED was measured in the laboratory using a stereomicroscope with an ocular micrometer.

Calculation of total production

The total production rate of *Calanus sinicus* was calculated as the sum of egg production of adult females and somatic production of juveniles from CI to CV, excluding adult males (Runge & Roff 2000). The total production rate of the *C. sinicus* population (P , $\text{mg C m}^{-3} \text{ day}^{-1}$) was calculated as follows:

$$P = \sum (B_i \times g_i) + B_f \times g_f,$$

where B_i and B_f are the biomass of juveniles and adult females, respectively; g_i is the growth rate of juveniles; and g_f is the WSEPR of adult females. In this study, we only considered CI to CV for somatic production, because a 200- μm mesh net cannot effectively collect *C. sinicus* nauplii. To calculate the somatic production, it is necessary to know the growth rate of juveniles. Although there have been growth rate measurements of *C. sinicus* in the laboratory with excess food and temperature-dependent growth equations (Uye 1988), the production rates estimated by these equations might be overestimated for *C. sinicus* in food-limited conditions such as in the northern ECS. Therefore, the growth rate (g , day⁻¹) of juvenile *C. sinicus* was estimated from an empirical equation for broadcasters (from Table 6 in Hirst & Bunker 2003) as:

$$\log_{10} g = -0.0143T - 0.363 \log_{10} BW + 0.135 \log_{10} \text{Chl } a - 0.105,$$

where T is water temperature ($^{\circ}\text{C}$), BW is individual body mass ($\mu\text{g C}$), and $\text{Chl } a$ is chlorophyll a concentration ($\mu\text{g L}^{-1}$). We used mean water temperature of the water column at each station for T , mean body mass of CI to CV from all stations for BW , and mean $\text{Chl } a$ concentration of the water column at each station for $\text{Chl } a$.

Statistics

Correlation analyses were conducted between WSEPR ($n=52$, pooled data) and the water temperature (5 m depth and mean of water column temperature, $n=6$), $\text{Chl } a$ concentration (surface and mean of water column $\text{Chl } a$ concentration, $n=6$), and mean body mass ($n=6$) at each station. The same analyses were also applied to EPR with the water temperature and $\text{Chl } a$ concentration at each station.

Results

Temperature, salinity, and $\text{Chl } a$ concentration

During the cruise, the water temperature at 5 m depth ranged from 12.2 to 19.1 $^{\circ}\text{C}$ (mean 15.2 $^{\circ}\text{C}$), and was relatively higher in the eastern part ($>15.0^{\circ}\text{C}$) and lower in the western part (Fig. 2a). The mean water temperature of the water column ranged from 11.3 to 16.6 $^{\circ}\text{C}$ (Table 1). The salinity at 5 m depth ranged from 32.17 to 34.49, and was higher in the eastern part than in the western part (Fig. 2b). The mean salinity of the water column ranged from 32.30

Fig. 2. Spatial distribution of (a) water temperature at 5 m depth, (b) salinity at 5 m depth, and (c) surface Chl *a* concentration.

to 34.52 (mean 33.88). The surface Chl *a* concentration ranged from 0.57 to 3.65 $\mu\text{g L}^{-1}$ (mean 1.7 $\mu\text{g L}^{-1}$) and was relatively higher in the southwestern part (e.g. Ieodo station and station B4) at $>3 \mu\text{g L}^{-1}$, and lower in the north-eastern part (e.g. stations H3, D7, and D11) at $<1 \mu\text{g L}^{-1}$ (Fig. 2c). The mean Chl *a* concentration of the water column ranged from 0.52 to 1.93 $\mu\text{g L}^{-1}$ (Table 1).

Abundance and biomass of *Calanus sinicus*

The total abundance of CI to adult males and females of *Calanus sinicus* varied by station, ranging from 3 to 1,117

Fig. 3. Variation of abundance of copepodite stage 1 (CI) to adult males and females of *Calanus sinicus*.

ind. m^{-3} (mean 256 ind. m^{-3}), and was highest at Ieodo station, followed by station H1, and lowest at station H6 (Fig. 3). The total biomass of CI to adult males and females varied by station, ranging from 0.11 to 30.23 mg C m^{-3} (mean 8.69 mg C m^{-3}), and was highest at station H1, followed by Ieodo station, and lowest at station H6 (Fig. 4a). However, when we only consider the biomass of CI to CV (excluding adult males and females), which contribute to the somatic production of *C. sinicus*, the biomass ranged from 0.11 to 19.81 mg C m^{-3} (mean 5.49 mg C m^{-3}), with the highest at Ieodo station, followed by station H1, and the lowest at station H6 (Fig. 4a). The biomass of adult females varied by station, ranging from 0.004 to 18.15 mg C m^{-3} (mean 2.72 mg C m^{-3}), with the highest at station H1 (Fig. 4a). The biomass of CV also varied by station, ranging from 0.08 to 10.97 mg C m^{-3} (mean 3.71 mg C m^{-3}), with the highest at Ieodo station (Fig. 4a). The percent biomass of CI to adult males and females varied by station; CV had the highest percent biomass with a mean of 42.7%, followed by adult females (31.3%) and CIV (13.5%), and the lowest was CI (Fig. 4b). The percent biomass of adult females was the highest at station H1 (60.1%), followed by station D1 (40.8%), and the lowest was station D11 (1.9%) (Fig. 4b).

Egg production rate

The mean egg diameter of *Calanus sinicus* was $162 \pm 9.5 \mu\text{m}$ ($n=93$ eggs) and egg carbon content was estimated to be $0.28 \pm 0.05 \mu\text{g C egg}^{-1}$. The EPR of *C. sinicus* ranged from 0 to 14.9 eggs $\text{female}^{-1} \text{day}^{-1}$ (mean 5.8 eggs $\text{female}^{-1} \text{day}^{-1}$) and was relatively high at stations B4 and B9. However, the females at stations D7, D11, and H6 did not spawn eggs (Fig. 5a). The body mass of an adult female varied by station, from 93.0 to 124.4 $\mu\text{g C ind.}^{-1}$ (mean 106.7 $\mu\text{g C ind.}^{-1}$) (Table 1). The WSEPR of *C. sinicus* ranged from 0.003 to 0.044 day^{-1} (mean 0.023 day^{-1}) when excluding the stations where female fecundity were zero. The population EPR of *C. sinicus*, calcu-

Fig. 4. Variations of (a) biomass and (b) percent biomass of copepodite stage 1 (CI) to adult males and females of *Calanus sinicus*.

lated from the WSEPR multiplied by the adult female biomass, ranged from 0 to $217.8 \mu\text{g C m}^{-3} \text{ day}^{-1}$ (mean $33.6 \mu\text{g C m}^{-3} \text{ day}^{-1}$), with the highest at station H1, followed by station B4 (Fig. 5b), showing a different spatial variation of population EPR compared to the female EPR as eggs per female per day.

Production of *Calanus sinicus*

Somatic production of CI to CV of *Calanus sinicus* ranged from 0.02 to $3.66 \text{ mg C m}^{-3} \text{ day}^{-1}$ (mean $0.88 \text{ mg C m}^{-3} \text{ day}^{-1}$) and was highest at leodo station, followed by station H1 ($1.26 \text{ mg C m}^{-3} \text{ day}^{-1}$), and lowest at station H6 ($0.02 \text{ mg C m}^{-3} \text{ day}^{-1}$). Total production (i.e. somatic production of CI to CV + EPR of adult females) of *C. sinicus* varied by station, ranging from 0.02 to $3.67 \text{ mg C m}^{-3} \text{ day}^{-1}$ with a mean of $0.91 \text{ mg C m}^{-3} \text{ day}^{-1}$, and was highest at leodo station, followed by the nearest coastal station (H1), and lowest at station H6 (Fig. 6a). The variation in total production of *C. sinicus* was similar to that of somatic production. Depth-integrated total production of *C. sinicus* ranged from 3.38 to

Fig. 5. Variations of egg production rate of *Calanus sinicus*: (a) number of eggs of an adult female and (b) adult female population in terms of carbon.

$183.46 \text{ mg C m}^{-2} \text{ day}^{-1}$ (mean $52.72 \text{ mg C m}^{-2} \text{ day}^{-1}$), and was highest at leodo station, followed by station B4, D11, and H3 (Fig. 6b).

The percent ratio of EPR (including zero EPR) to the total production ranged from 0 to 14.7% (mean 3.7%), indicating that the contribution of EPR to the total production was very low, and most *C. sinicus* production was dependent on somatic production from juvenile growth of CI to CV. When we excluded zero EPR stations, the ratio ranged from 0.4 to 17.7% (mean 4.1%).

Factors affecting fecundity of *Calanus sinicus*

The EPR of *Calanus sinicus* ($n=52$, pooled data excluding stations with zero spawning) at 9 stations was positively correlated with water temperature at 5 m depth ($n=6$, excluding the stations with zero spawning, $p<0.001$; Fig. 7a), mean water temperature of the water column ($n=6$, $p<0.0001$), and surface Chl *a* concentration ($n=6$, $p<0.05$; Fig. 7b), but not mean Chl *a* concentration of the water column ($n=6$, $p>0.05$). The WSEPR of *C. sinicus* ($n=52$, pooled data excluding stations with zero spawning) was also positively correlated with water temperature at 5 m depth ($n=6$, excluding the stations with zero spawning, $p<0.0001$; Fig. 8a), mean water temperature of the water column ($n=6$, $p<0.0001$), and surface Chl *a* concentration ($n=6$, $p<0.05$; Fig. 8b), but not mean Chl *a* concentration of the water column ($n=6$, $p>0.05$). However, WSEPR

Fig. 6. Variations of total production of *Calanus sinicus* (e.g. somatic production of copepodite stage 1 (C1) to copepodite stage 5 (C5) plus egg production rate): (a) mean production of water column and (b) depth-integrated production.

was negatively correlated with mean of female body mass ($n=6$, $p<0.0001$; Fig. 8c), indicating that WSEPR decreases as the body mass of an adult female increases.

Discussion

Abundance of *Calanus sinicus*

There are several studies on the variation of abundance of *Calanus sinicus* in the Yellow Sea and the northern ECS. Kim & Lim (1999) reported that the abundance of *C. sinicus* in the Yellow Sea was highest in April and June (239 ind. m⁻³ and 262 ind. m⁻³, respectively), followed by August (179 ind. m⁻³) and December (32 ind. m⁻³). Kang & Hong (1998) reported that the abundance of *C. sinicus*, including copepodites, in the southern waters of Korea was highest in April and lowest in summer. Kang (2008) reported that the mean abundance of *C. sinicus*, including copepodites, was 96 ind. m⁻³ in the northern ECS around Jeju Island in early summer, which was lower than that in our research (256 ind. m⁻³). These results indicate that seasonal variation in *C. sinicus* abundance in the Yellow Sea and the northern ECS, including the southern waters of Korea, is similar among regions, with the highest abundance in spring.

Fig. 7. Egg production rate of *Calanus sinicus* as a function of (a) water temperature at 5 m depth and (b) surface Chl *a* concentration.

Egg production rate

Our mean EPR of *Calanus sinicus* (5.8 eggs female⁻¹ day⁻¹) was lower than those observed on the Korean coast of the Yellow Sea (Kang et al. 2011), the Asan Bay in spring (Park 1997), and the Yellow Sea (Wang et al. 2009), but similar to that of the southern Yellow Sea (Zhang et al. 2005), indicating that the EPR of *C. sinicus* in spring is much higher in the bay and coastal waters than offshore or in shelf waters (see Table 2).

Adult females of *C. sinicus* at stations D7, D11, and H6 did not spawn eggs during our study. Gonad maturity or gonad state, spawning timing (e.g. no eggs or not enough eggs after spawning or between spawning events), fertilization state, and feeding history of females have been known as potential causes of variability of egg production in *Calanus* spp. (Rey-Rassat et al. 2004, Niehoff 2007, Wang et al. 2009). However, we could not determine the potential causes of fecundity of *C. sinicus*; instead we randomly selected active and healthy adult females from the sample of the *C. sinicus* population and then incubated them for EPR experiments. Therefore, it is not clear why the females did not spawn during our research. In practice, it is recommended that zero spawning data should be included in egg production data to estimate the *in situ* EPR of the population (Runge & Roff 2000).

The EPR of *C. sinicus* in this study significantly in-

Fig. 8. Weight-specific egg production rate (WSEPR) of *Calanus sinicus* as a function of (a) water temperature at 5 m depth, (b) surface Chl *a* concentration, and (c) mean body mass of adult female.

creased with increasing Chl *a* concentrations (Fig. 7b), with a range of 0.49 to 1.93 µg L⁻¹, indicating that food availability, particularly phytoplankton, is an important determinant of fecundity of *C. sinicus* in spring as well as water temperature. Wang et al. (2009) showed that the EPR of *C. sinicus* in the Yellow Sea in April was generally coincident with the food availability (e.g. phytoplankton and ciliates). Kang et al. (2011) showed that adult females of *C. sinicus* in the Korean coastal waters of the Yellow Sea had a high mean fecundity from March through May (23.4 eggs female⁻¹ day⁻¹), when Chl *a* concentrations were relatively high, ranging from 0.6 to 9.6 µg L⁻¹ (mean

5.3 µg L⁻¹). Although phytoplankton is an important factor for fecundity of *C. sinicus*, it is likely that Chl *a* concentrations in this study were not enough for maximum EPR of *C. sinicus*. Copepods, particularly adult females, suffer from food limitation in the field (Peterson 1988, Hirst & Bunker 2003). Food limitation has a greater effect on female growth (i.e. EPR of adult females) than juvenile growth (Hirst & Bunker 2003). Peterson et al. (2002) used the ratio of observed EPR to maximum EPR as a measure of the degree of limitation of growth by factors such as food and temperature. Kang et al. (2011) proposed *in situ* mean maximum EPR of *C. sinicus* in the Korean coastal waters of the Yellow Sea in spring as 50.4 eggs female⁻¹ day⁻¹. In this study, the EPR of *C. sinicus* was very low compared to the mean maximum EPR of *C. sinicus* in the coastal waters and was 12% of the maximum EPR for *C. sinicus*. This result may indicate that potential food limitation in the study region was of great impact on the fecundity of *C. sinicus* in spring.

Weight-specific egg production rate of *Calanus sinicus*

The WSEPR of *Calanus sinicus* in this study was similar to that of *C. sinicus* in the southern Yellow Sea (Zhang et al. 2005). However, our value was lower than those for *C. sinicus* along the Korean coast of the Yellow Sea (Kang et al. 2011) and in the Asan Bay from January to November (Park 1997) (see Table 2). This comparison indicates that WSEPR of *C. sinicus* in spring is higher in the coastal regions than offshore, possibly due to differences in food availability for adult females for reproduction.

The WSEPR of *C. sinicus* significantly increased with increasing water temperatures at 5 m depth (Fig. 8a), although the temperature range during our research period was rather narrow (12 to 19°C). This result is consistent with the general relationship between WSEPR and temperature in adult broadcaster copepods (Hirst & Bunker 2003). However, Kang et al. (2011) showed that the WSEPR of *C. sinicus* along the Korean coast of the Yellow Sea in spring was negatively correlated with temperature, and they suggested that the lower phytoplankton concentration at warmer surface temperatures was responsible for the result. Therefore, it is likely that water temperature can increase the WSEPR of adult females within a certain temperature range, but this effect might be influenced by food availability for females in the field.

The WSEPR of the broadcasters increased positively with surface Chl *a* concentrations (Hirst & Bunker 2003). Peterson et al. (2002) showed that the WSEPR of small and large copepods off the Oregon coast increased with Chl *a* concentration at 3 m depth during summer. In this study, the WSEPR of *C. sinicus* significantly increased with increasing surface Chl *a* concentrations (Fig. 8b), consistent with previous results (Peterson et al. 2002, Hirst & Bunker 2003), indicating that the fecundity of *C. sinicus* in spring depends on phytoplankton diet. However, the coefficient of determination of the independent variable (i.e. surface Chl

Table 2. Comparison of egg production rate (EPR) and weight-specific egg production rate (WSEPR) for *Calanus sinicus* with the season and water temperature (WT). Parentheses indicate mean value of EPR or WSEPR.

Region	Season	WT (°C)	EPR (eggs female ⁻¹ day ⁻¹)	WSEPR (day ⁻¹)	Reference
Northern East China Sea	Apr.–May 2004	11.3–16.6	0–14.9 (5.8)	0–0.044 (0.016)	This study
Korean coast of the Yellow Sea	Mar.–May 2007–2010	6.3–13.3	10.3–34.9 (23.4)	0.038–0.111 (0.082)	Kang et al. (2011)
Asan Bay, Korea	Apr.–May 1994	6.4–14.4	2.7–16.3 (10.4) ^a	N.I.	Park (1997)
Asan Bay, Korea	Mar.–May 1996	3.3–11.0	5.3–10.3 (8.2) ^a	N.I.	Park (1997)
Southern Yellow Sea	Mar.–May 2001	6.7–12.8	5.4–6.3 (5.9)	0.015–0.025 (0.020)	Zhang et al. (2005)
Yellow Sea	Apr. 2006	4.9–13.4	0–25.4	N.I.	Wang et al. (2009)

^a Recalculated from Table 1 in Park (1997); N.I.: No information.

Table 3. Total production of the copepod *Calanus sinicus*. Values given with respect to the season and water temperature (WT) at which they were collected. Parentheses indicate mean values.

Region	Season	WT (°C)	Stages	Production (mg C m ⁻³ day ⁻¹)	Reference
Northern East China Sea	Apr.–May 2004	11.3–16.6	CI–adult	0.02–3.67 (0.91)	This study
Kii Channel, Inland Sea of Japan	Apr. 1987–Mar. 1988	8.7–25.9	CI–adult	0.98 ^a	Huang et al. (1993)
Northern East China Sea	Jul. 2007	12.9–21.9	CI–CV	0.03–1.40 (0.50) ^b	Kang (2008)

^a Estimated from annual production, 358 mg C m⁻³ year⁻¹; ^b Somatic production estimated by the temperature-dependent growth equations (Uye 1988).

a concentration) was very low, at 9.4% of the variability of WSEPR of *C. sinicus*, indicating that other factors, e.g. a diet on organisms without Chl *a* (Calbet & Saiz 2005, Huo et al. 2008) may also be important for WSEPR.

In general, the WSEPR of adult broadcaster copepods is negatively correlated with increasing body size (or body mass) (Hirst & Sheader 1997, Hirst & Bunker 2003), indicating that smaller copepods have a higher WSEPR than larger copepods. The WSEPR of *C. sinicus* significantly decreased with increasing mean body mass of adult females (i.e. from 83.3 to 121.4 µg C ind.⁻¹ by station) in this study, supporting previous results.

Production of *Calanus sinicus*

Studies on the secondary production of *Calanus sinicus* have been very limited compared to the EPR of *C. sinicus* (see Tables 2, 3). Total production of *C. sinicus* in this study was similar to that in the Inland Sea of Japan (Huang et al. 1993), and higher than somatic production in the northern ECS in early summer (Kang 2008) (see Table 3). Although there are limits to the direct comparison of production rates of *C. sinicus* due to the different methodology used, it would be helpful to understand the degree of variability in the production rates of *C. sinicus*. Considering the lack of data on secondary production of *C. sinicus*, our estimate of the production of *C. sinicus* can be used to generate new information on secondary production of *C. sinicus* for comparisons of region-specific copepod production.

Considering the importance of CV in the total production of *C. sinicus*, CV dominated the population of *C. sin-*

cus in early summer in the northern ECS, contributing 46.2–84.6% of total abundance (Kang 2008). The mean population biomass of juvenile stages of *C. sinicus* was the largest for CV, followed by adult females in late spring in the northern ECS (Kim & Kang 2018). In our study, the mean biomass of CV contributed 43% of total biomass, ranging from 21 to 74% of total biomass (Fig. 4b). When we consider the contribution of CV to the production of *C. sinicus*, the mean production of CV contributed 54% of total production and 56% of somatic production, indicating CV is the most important contributor for total production of *C. sinicus* in spring in the northern ECS.

Peterson et al. (1991) showed that the EPR of copepods accounted for 25% of total copepod production, summed over all species in Skagerrak. Hirche et al. (2001) showed that the EPR of *C. finmarchicus* accounted for 27% of total production, calculated from specific egg production. Kang & Kang (2005) found that the EPR of *Acartia steueri* Smirnov, 1936 in Ilkwang Bay accounted for 13.4% of total production (recalculated from Table 1, including zero EPR). Also, Kang et al. (2007a) showed that the EPR of *Acartia omorii* Bradford, 1976 in Ilkwang Bay accounted for 14.4% of total production (recalculated from Table 1, including zero EPR). Our value for the contribution of EPR to total production of *C. sinicus* is lower (e.g. 3.7% of the total production including zero EPR) than those of other species, including *C. finmarchicus*, *A. steueri*, *A. omorii*, and the total copepod community (Peterson et al. 1991, Hirche et al. 2001, Kang & Kang 2005, Kang et al. 2007a).

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