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# Life History and Emergence Pattern of *Cloeon dipterum* (Ephemeroptera: Baetidae) in Korea

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**ABSTRACT** *Cloeon dipterum* (L.) (Ephemeroptera: Baetidae), the common wetland mayfly, emerges and oviposits every season, except winter, and has overlapping generations in the temperate region. We investigated the life history of *C. dipterum* associated with drought. Field experiments and sampling were conducted in a wetland (25 by 80 m) located in central Korea. Larvae were sampled weekly within two habitat types (a large, deep wetland and a small, shallow wetland) using a dredge sampler, and adults were sampled every 2 d with cube emergence traps, from July 2011 to September 2012 (except winter). *C. dipterum* had an extended emergence period from late April to early October with four peaks: early May, mid-June, July, and August/September. When the water depth was shallow because of drought, emergence was suppressed and delayed. The accumulated degree-days and body length of the overwintering cohort that emerged in spring 2012 were markedly larger and longer than those of other cohorts. Adults emerged intensively around sunset. *C. dipterum* has a multivoltine life cycle with four cohorts per year; its life history and population density can be changed by natural disturbances such as drought and fish predation.

**KEY WORDS** degree-day, life history variability, mayfly, natural disturbance, voltinism

*Cloeon dipterum* (L. 1761) (Ephemeroptera: Baetidae) is one of the most common and abundant mayflies, distributed throughout temperate areas of the Eurasian continent, including Europe, Siberia, Mongolia, and Northeast Asia (Sowa 1975, Bae 1997). Larvae of *C. dipterum*, often occurring in abundance, can be of great ecological importance as an essential link in freshwater food webs, particularly in lentic systems such as ponds, lakes, and wetlands (Cianciara 1980). The larvae of *C. dipterum* are tolerant to changes in environmental conditions (Cianciara 1979), and recently, *C. dipterum* has been used to estimate the influence of climate change (McKee and Atkinson 2000) and the toxic effects of contaminants (Beketov and Liess 2005).

Life history information is fundamental for most ecological studies of aquatic insects (Butler 1984). For several decades, researchers have investigated the life history of *C. dipterum*, which is generally known to have two to three generations per year in temperate areas across Europe (Bretschko 1965, Crisp and Gledhill 1970, Cianciara 1979, Cayrou and Cereghino 2005). However, in unfavorable climatic conditions, *C. dipterum* has a univoltine life cycle (Kjellberg 1973). *Cloeon simile* Eaton, an allied species of *C. dipterum*,

showed bivoltinism in Europe (Cayrou and Cereghino 2003). The North American species *Centroptilum triangulifer*, formerly placed in the genus *Cloeon* (McCafferty 1990), has at least three generations per year (Sweeney and Vannote 1984).

Mayflies molt many times during the larval stage, depending on temperature and food quality (Brittain 1982). The number of molts in *C. dipterum* is variable and may depend on the feeding conditions (Cianciara 1979). It is difficult to discriminate between instars based on body length because there is no distinct size difference. *Cloeon* species exhibit a variety of life cycle patterns, and *C. dipterum* has no uniform life cycle type; in fact, the populations appear to be quite flexible, having either univoltine or multivoltine life cycles presumably depending on environmental factors (Clifford 1982). In most areas in the temperate region, *C. dipterum* has overlapping generations with a prolonged emergence period from spring to autumn, and there is a high probability of multivoltinism. However, no precise studies have been conducted to verify its multivoltinism and how this might be influenced by the temperature regime and natural disturbances. The purpose of this study was to investigate the life history and emergence patterns of *C. dipterum* in a natural habitat in temperate Asia and how these are affected by temperature and drought.

## Materials and Methods

**Study Area.** This study was conducted in wetlands at the experimental station of Korea University located

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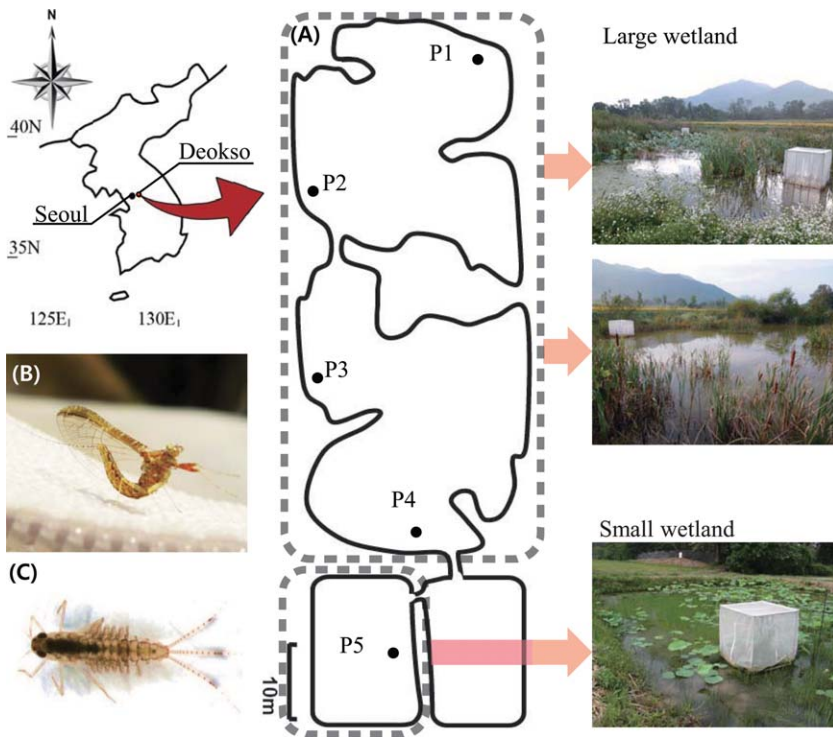


Fig. 1. (A) Sampling points and views of the study site at the experimental station of Korea University located in Deokso, Namyangju city, Gyeonggi-do, Korea ( $127^{\circ}14'16.7''\text{E}$ ,  $37^{\circ}35'02.1''\text{N}$ ); (B) female adult of *C. dipterum*; (C) larva of *C. dipterum*. (Figure in color online only.)

in Deokso, Namyangju-si, Gyeonggi-do, South Korea (Fig. 1). The wetlands were built in February 2009 and subdivided into large and small subunits (Fig. 1). The large wetland had a larger surface area ( $\approx 25$  by  $80$  m) and a deeper bed with a maximum depth of  $180$  cm and a mean depth of  $\approx 80$  cm. The large wetland did not dry up even during the dry season. Shortly after the wetlands were constructed, many aquatic plants such as *Marsilea quadrifolia* L., *Typha orientalis* Presl., and *Eichhornia crassipes* (Mart.) Solms were colonized around the edges of the large wetland, while the center of the wetland was left open. In contrast, the small wetland, located below the large wetland, had a smaller surface area ( $\approx 20$  by  $15$  m) and shallower water depth ( $\approx 20$  cm overall). It dried up during droughts, which disturbed its biota. In addition, similar aquatic plants were abundant in this small wetland with little open area. The two wetlands were connected by a small ditch ( $\approx 100$  cm in length and  $20$  cm in width), and water flowed from the large wetland toward the small wetland (only rarely during flood) because the small wetland was located  $\approx 100$  cm lower in elevation. In both the wetlands, the substrate mainly consisted of mud and the surface was covered with ice from December to early March. Approximately 60 species of aquatic insects and other benthic macroinvertebrates colonized the wetlands (Y.J.B. and C.Y.L., personal observations). One fish species, *Carassius auratus* L., was introduced to the wetlands in 2010, and

a large population of juveniles ( $10$ – $30$  mm in body length) was observed during the study period.

**Environmental Monitoring.** Environmental monitoring and sampling were conducted from July 2011, 2.5 yr after the wetlands were constructed, to September 2012. Air and water temperatures at the study area were monitored on an hourly basis using the data logger Optic StowAway Temp (Onset Computer Corporation, Bourne, MA). Water temperature was converted to degree-days using the rectangle method (Lee et al. 1999), as shown in the following equation 1:

$$\text{Rectangle DD} = (T_{\max} + T_{\min})/2 - T_b \quad [1]$$

Where DD is degree-days,  $T_{\max}$  and  $T_{\min}$  are daily maximum temperature and minimum temperature, and  $T_b$  is the base temperature for egg and larval development. For this study, we estimated the  $T_b$  value to be  $0^{\circ}\text{C}$  because *Baetis rhodani* (Baetidae) eggs can hatch even at the very low water temperature of  $3^{\circ}\text{C}$  (Elliott 1972). In addition, Nagell (1981) found that *C. dipterum* nymphs can feed (the percentage of larvae with food in the gut was almost 100%) and grow (although slowly) at  $1^{\circ}\text{C}$ . The accurate base temperature of *C. dipterum* was not investigated, and because the temperature of water does not generally drop to  $<0^{\circ}\text{C}$  (Ward 1992), we used an estimated  $T_b$  value of  $0^{\circ}\text{C}$  for this study.

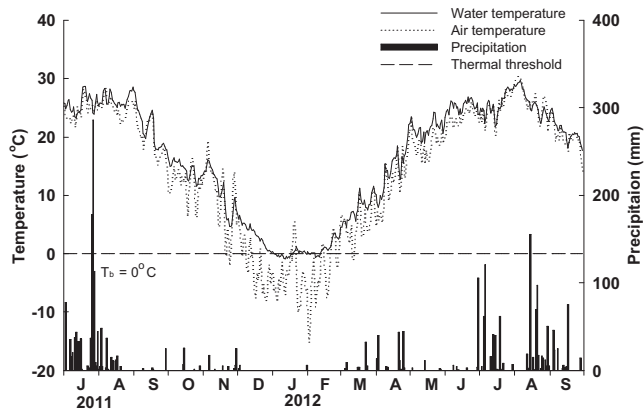


Fig. 2. Daily mean air and water temperature and precipitation values in the study area during the study period.  $T_b$ , base temperature of the thermal threshold for egg and larval development.

The precipitation data in the Deokso area were obtained from the Korean Meteorological Administration (2012). We erected measuring rulers at the wetlands near the emergence traps to monitor water level and recorded water depth on a weekly basis.

**Sampling and Processing.** During the study period, *C. dipterum* larvae were sampled almost weekly, except during winter, using a dredge sampler (40 by 25 cm; mesh, 0.25 mm) at two points in the large wetland and one point in the small wetland, for a total of 38 sampling events. Although *C. dipterum* larvae were abundant in the wetlands, care was taken to preserve the population despite the frequent sampling times. The sampled material was maintained in 500-ml bottles and fixed with 95% ethanol, and the larvae were sorted and preserved in 80% ethanol in the laboratory. Fish (*C. auratus*) inside the dredge sampler were subjectively quantified while sampling *C. dipterum*.

If the number of larvae collected was below 100, all individuals were measured, while at least 100 larvae were randomly selected to be measured if the number of larvae collected was >100. Larval body length was measured using a dissecting microscope (SteREO Discovery.V12, Carl Zeiss, Gottingen, Germany) equipped with an image analyzer (Axio Vision Rel. 4.8.2 program). The larval body length was measured from the anterior head to the terminal abdomen (excluding cerci) and separated into 0.5-mm intervals.

*C. dipterum* adults were quantitatively collected using five emergence traps (1 by 1 by 1 m; mesh, 1 mm) located at different points in the wetlands (four traps in the large wetland and one trap in the small wetland) (Fig. 1). Emerged adults were collected every 2 d from the emergence traps. In addition, the daily emergence pattern was investigated three times in June 2012 (11, 15, and 19 June) at 2-h intervals. During the investigation of daily emergence pattern, an additional three traps in the large wetland and one trap in the small wetland were used (total number of traps: 9). Collected adults were counted and sexed in the laboratory and subsequently preserved in 80% ethanol.

**Data Analysis.** The life cycle of *C. dipterum* was estimated via analysis of the size–frequency distribu-

tions using 22 size classes. The size classes were 0.5-mm intervals between 1 and 12 mm. The frequencies of each life cycle stage for each sampling date were calculated as percentages, and frequency histograms were constructed to determine the voltinism. The bias of the sex ratio (female/total) of *C. dipterum* was examined using a  $\chi^2$  test with the SAS statistical package (version 9, SAS Institute 2004).

## Results

**Environmental Conditions.** The water temperature from the beginning of July 2011 to the end of September 2012 was  $16.3 \pm 9.6^\circ\text{C}$  (mean  $\pm$  SD). The highest water temperature recorded was  $29.7^\circ\text{C}$  (7 August 2012) and the lowest was  $-0.9^\circ\text{C}$  (12 January 2012; Fig. 2). The air temperature for the same period was  $14.5 \pm 10.9^\circ\text{C}$ . The highest air temperature recorded was  $30.7^\circ\text{C}$  (4 August 2012) and the lowest was  $-15.2^\circ\text{C}$  (2 February 2012; Fig. 2). Total precipitation for that period was 2,768.3 mm.

The water depth of the large wetland during the study period was  $420.7 \pm 62.5$  mm. The highest water level recorded was 480.0 mm and the lowest was 210.0 mm when the wetland was affected by drought in June 2012. The water depth of the small wetland during the period was  $174.2 \pm 66.2$  mm. The highest water depth recorded was 260.0 mm and the lowest was 0 mm when the wetland was affected by drought in early September 2011.

**Life History.** In total, 11,877 larvae were collected from the wetlands during the study period. The number collected per quantitative sampling ( $0.1 \text{ m}^3$ ) was the largest on 30 September 2011 ( $n = 2,835$ ) and the smallest was on 16 May 2012 ( $n = 2$ ) (Fig. 3). The number of larvae sharply increased in the autumn, especially in the small wetland where the number of larvae increased in September 2011 after the water level had recovered after the drought. In contrast, the number of larvae in the large wetland did not increase to the same level as their previous abundance.

The body length of the larvae ranged between 1.1 and 11.7 mm (Fig. 4). The overwintering generation

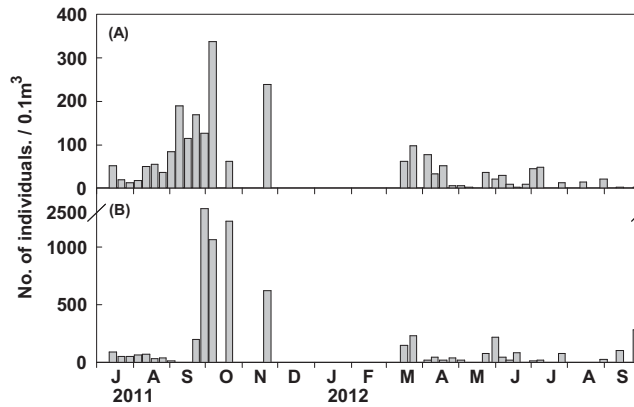


Fig. 3. The number of larvae of *C. dipterum* per 0.1 m<sup>3</sup> in the large (A) and small (B) wetlands from 2011 to 2012.

rapidly developed during spring, a period during which the first emergence occurred. The next generation also rapidly developed and emerged in June. Another generation emerged during summer, and the last generation of the year emerged during autumn (Fig. 4). The total number of final instar larvae collected during the study period was 157, with peaks in April, June, July, and September (Fig. 5).

**Emergence Pattern and Accumulated Degree-Days for Development.** In total, 1,239 adult *C. dipterum* were collected from the study wetlands during the study period, and the sex ratio was 0.5 (number of females per total adults), not significantly different from 0.5 ( $P > 0.05$ ). During 2011, 309 adults emerged in the large wetland and 38 adults emerged in the small wetland. In contrast, 218 and 652 adults emerged from each wetland during 2012. The emergence was divided into six emergence groups (E I to VI) according to the emergence peaks and number of individuals (Fig. 5). In the large wetland, as the water became shallow in June 2012, the number of adults that emerged in the summer and autumn of 2012 was less than that in 2011. In the small wetland, E V rarely emerged when the water was almost gone; however, a large number of adults emerged as E VI after the water level had recovered.

*C. dipterum* had an extended emergence period with four peaks from late April to early October. During 2012, the first emergence during spring started on 20 April (air temperature, 18.2°C) and ended on 15 May. From 7 June, the second emergence occurred and continued throughout the summer and autumn. During July and August, small emergence peaks were observed, and emergence ended on 30 September 2012. Emergence was observed within a water temperature range of 12.7–29.7°C, an air temperature range of 10.4–30.4°C, and a day length range of 11.8–14.8 h.

We classified the emerged adults into six emergence groups (Table 1) and named the cohort groups (C I to V) that were the offspring of each emergence group (Table 2). We also calculated the median number of adults in each emergence group and estimated the accumulated degree-days (ADD) for each cohort during the period between median values (Table 2). The ADD of C II, the overwintering group, was the highest (Table 2), and also the mean body length of the last instar E III, the adult group of C II, was markedly longer than those of the other groups (analysis of variance (ANOVA) with Tukey's test,  $P < 0.0001$ ) (Table 1).

As a result of the daily emergence pattern of *C. dipterum*, adults emerged intensively around sunset;

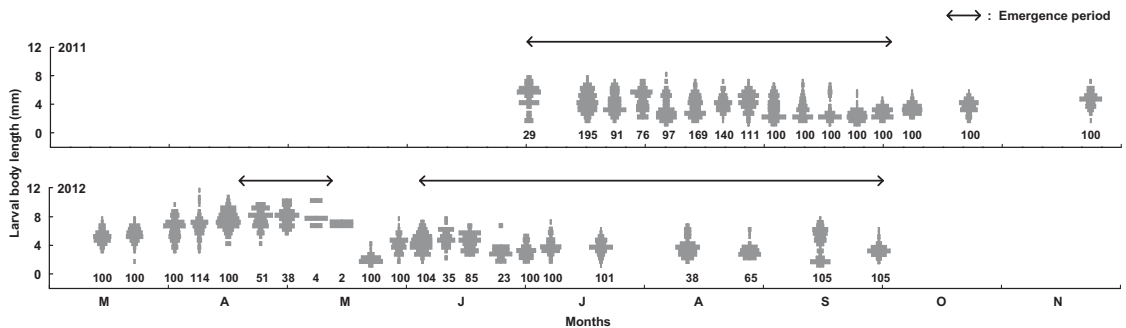


Fig. 4. The size-frequency distribution of *C. dipterum*. Width of horizontal bars shows the proportion of larvae in each body length range, and the sum of all bars on each date equals 100%. The numbers of measured individuals are displayed under the size-frequency distribution. Arrows indicate the emergence period.

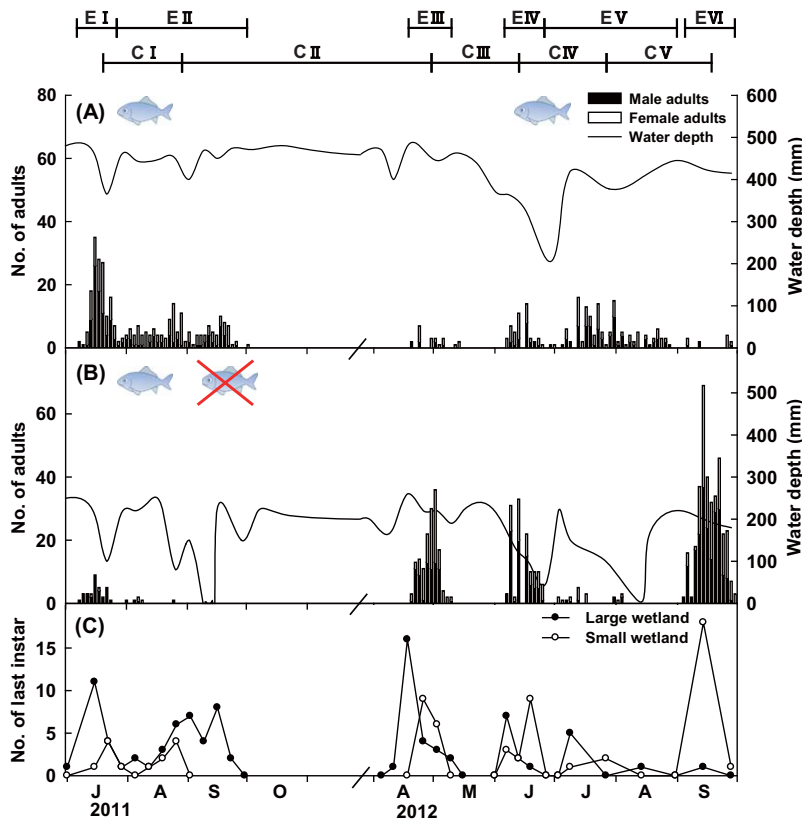


Fig. 5. Number of adults and water level at the large (A) and small (B) wetlands and fish existence; (C) the number of last instars per 0.1 m<sup>3</sup> in each wetland. (Figure in color online only.)

45.7 ± 13.1 (mean ± SE) adults emerged from 1800 to 2000 hours and 13.3 ± 4.4 adults emerged from 2000 to 2200 hours (sunset: 1950–2000 hours). No *C. dipterum* adults emerged at other times. Sex ratios were 0.4 ± 0.0 and 0.4 ± 0.1 (mean ± SE) for the two periods.

**Discussion**

**Life History.** The life history of aquatic insects is directly influenced by different thermal regimes. Multivoltine life cycles are common in Ephemeroptera,

especially in warm temperate and tropical waters (Clifford 1982, Brittain 1990). Mayflies show a remarkable variation in life history, even at the species level (Clifford 1982). The wide geographic distribution, abundance, and significant variation in life history also suggest that *C. dipterum* could be a species complex as shown by their extensive variations in abdominal markings between geographical populations (Sowa 1975). Many researchers who investigated the life history of *C. dipterum* in Europe stated that this species generally has two generations per year. In our study area, however, the combined information of the

Table 1. Number of adults, last instars, and body lengths of last instars for six emergence groups in Gyeonggi-do, Korea, from 2011 to 2012 with relative abundance of fish (*C. auratus*)

Emergence	No. adults			Last instars <sup>a</sup>		Fish <sup>b</sup>	
	Large wetland	Small wetland	Total	n	Mean ± SD (mm)	Large wetland	Small wetland
I	151	32	183	26	6.3 ± 0.6bc	++	+
II	158	6	164	43	6.1 ± 0.7bc	++	–
III	23	154	177	44	8.7 ± 1.0a	+++	–
IV	51	127	178	23	6.0 ± 0.7bc	+	–
V	140	20	160	11	5.8 ± 6.4c	++	–
VI	11	351	362	20	6.4 ± 0.5b	++	–
Mean	89	115	204	28	6.8 ± 1.4		

<sup>a</sup> The body lengths of last instars followed by the same letter are not significantly different (ANOVA; Tukey’s test; P < 0.0001).

<sup>b</sup> Relative abundance subjectively evaluated from the quantitative sampling: (+++) abundant, (++) medium, (+) rare, (–) absent.

**Table 2.** Accumulated degree-days (ADD) estimates for five cohorts of *C. dipterum* in Gyeonggi-do, Korea from 2011 to 2012

Cohort	ADD
I	1,002
II	2,400
III	987
IV	1,053
V	1,338
Mean	1,356

developmental size frequency distribution of field-collected larvae, adult emergence periods and peaks, and ADD estimates for egg and larval development applied to field temperature data has substantiated multivoltinism of *C. dipterum* with four generations per year. In the majority of previous studies, *C. dipterum* larvae were sampled monthly with 1- to 2-mm interval in body size distribution analysis, but in this study, we sampled more frequently (weekly), thus allowing for a more accurate analysis (0.5-mm interval). In European countries where winter is warmer than in Korea, such as Italy, *C. dipterum* may have a multivoltine life cycle.

Cohort spreading and overlap complicated the interpretation of the *C. dipterum* life cycle, and delineating cohorts was somewhat ambiguous. According to our previous research, *C. dipterum* eggs and larvae require  $1,221.8 \pm 116.0$  ADD for development (Lee et al. 2012). The use of development size frequencies combined with the ADD required for the development of *C. dipterum* increased our precision in interpreting the cohorts. Ephemeroptera exhibit heterogeneous growth and morphological development and an indeterminate number of instars within or among populations along environmental gradients (Brittain 1990); therefore, simple size frequency analysis or its variations can be misleading or inaccurate in determining voltinism (Taylor and Kennedy 2006). Field-derived data were useful in interpreting the areas of cohort overlap in the development frequency histograms. Because ADD is a simplification of the temperature conditions within the wetland microhabitat, it is possible that it did not include unfavorable conditions that delayed emergence for C II; this may be the reason why that cohort had a large ADD estimate.

The body lengths of C II, the overwintering larvae, were markedly longer than those of the other cohorts. In general, species with extended emergence show a gradual decrease in size throughout extended emergence periods (Clifford 1974). The winter cohort of *C. dipterum* exhibited increased larval growth periods in which greater numbers of ADD were accumulated before emergence. This supports the findings of Sweeney (1984) that a larger adult size correlates with the longer growth period experienced by overwintering generations. Temperature-induced body size differences in many ectotherms may simply be a consequence of the effect of temperature on cellular development (Van Voorhies 1996). Numerous experiments have shown that ectotherms grow larger

at lower temperatures (Van Voorhies 1996). Macan (1957) showed that species with long emergence periods and overwintering larvae show a gradual reduction in the size of emerging adults from those at the beginning of the emergence season. The largest overwintering nymphs tend to produce large early adults, and as growth speeds up during spring and early summer, nymphs reach maturity at successively smaller sizes (Langford 1975).

**Effect of Disturbance.** Lotic community structure, in particular, can be strongly influenced by physical disturbances such as floods and droughts (Resh et al. 1988); however, lentic communities can also be affected by these physical disturbances (Freeman and Freeman 1985). Our study site was affected by drought in September 2011 and August 2012, and the drought was more serious in 2012. In the large wetland, there was no significant influence in the *C. dipterum* emergence from the drought in 2011 because regular water level was preserved throughout the dry season. Owing to the serious drought in the summer of 2012, however, adults could not emerge regularly in the large wetland as well as in the small wetland.

Drought reduces the habitat size in aquatic ecosystems; therefore, competition and predator-prey interactions increase as organisms are concentrated into the diminishing habitat space (Ward 1992). We hypothesized that the *C. dipterum* population decreased and could not return to its former size because of predation pressure. *C. auratus*, the most common lentic freshwater fish in Korea, consumes insect larvae, including Baetidae larvae (Magalhaes 1993). Field data from our quantitative sampling showed that the number of *C. auratus* (body length 10–30 mm) maintained in abundance in the large wetland even during the drought season (Table 1). Stemming from this observation, it was hypothesized that the predation pressure on *C. dipterum* was higher while the water level was low as shown in the large wetland. This could be the reason behind the markedly reduced and irregular emergence pattern in 2012 compared with 2011.

In the small wetland, however, the number of emerged adults in 2012 was higher than that in 2011 despite the more serious drought in 2012. In September 2011, the small wetland was dry for a week. Following the drought, we did not observe *C. auratus* in the small wetland. After the wetland recovered from the drought, the number of adults significantly increased. Removal of fish from the wetlands led to a significant increase in the density of macroinvertebrates (Williams and Taylor 2003). In addition, resistance to drought is likely to decline with increasing body size because large individuals should have less access to physical refugia in wet benthic sediments (Lancaster and Hildrew 1993). In contrast, small, short-lived (multivoltine) taxa can quickly recruit individuals into the space liberated by the disturbance and have a lower probability of exposure than larger univoltine or semivoltine macroinvertebrates (Ledger and Hildrew 2001). Therefore, *C. dipterum*, a multi-

voltine species, was able to recruit in the small wetland when the water level was restored after the drought. For these reasons, after the drought in September 2011, the number of larvae rapidly increased in the small wetland. As a result, the number of E III and E IV adults greatly increased. During July and early August 2012, we assumed that E V could not emerge on time because the water was shallow in the large wetland and the small wetland was almost dry. After the water level of the small wetland was restored, the *C. dipterum* cohort renewed its emergence that had been delayed during the drought disturbance. Consequently, a massive emergence occurred in September 2012.

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