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PRIMARY RESEARCH PAPER

Life history of a lowland burrowing mayfly, *Ephemera orientalis* (Ephemeroptera: Ephemeridae), in a Korean stream

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Abstract Life history aspects of *Ephemera orientalis*, a common lowland burrowing mayfly that resides in temperate East Asia, were studied in terms of voltinism, secondary production, and accumulated degree days for larval development. From March 1998 to June 1999, larvae were sampled monthly (weekly or biweekly during the emergence period) from a lower reach of the Gapyeong stream in Korea, a stream typical of temperate East Asia, using a Surber sampler (0.25 m^2, mesh 0.25 mm). As a result, the mean density of *E. orientalis* was 47.21 ± 13.58 indiv. m^{-2} during the study period. Very small larvae less than 2 mm in body length were sampled on three separate occasions, and emergence was observed between late April and early October, except during late May. Based on the larval body length distribution and emergence time, two different developmental groups could be distinguished: the slow developmental group (S-group) and the fast developmental group (F-group). The F-group completed its life cycle within 4 months, whereas the S-group had a one-year life cycle. The S-group could be divided into two subgroups, dubbed the S1 and S2-groups, based on larval development. The developmental groups alternate their life cycles in the order: S1→F→S2→S1. Estimated annual production of the larvae was 68.81 mg DW m^{-2} y^{-1}; mean biomass was 8.43 mg DW m^{-2}; the annual production to mean biomass ratio was 8.16. The annual mean water temperature of the study year was 14.76 ± 6.63°C. The total accumulated degree days for larval development was 1396°C for the F-group, 2,055°C for the S1-group, and 1,975°C for the S2-group. Two different adult body size groups were distinguished ($P < 0.001$ by *t*-test): larger adults, which belonged to the S-group, were present throughout the emergence period, whereas smaller adults, which belonged to the F-group, were mainly present later in the emergence period (August–October). The difference in the accumulated degree days between the developmental groups may explain the size differences of adults.

Keywords Life history · Secondary production · Degree day · *Ephemera orientalis* · Burrowing mayfly · Temperate East Asian stream

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Introduction

The burrowing mayfly family Ephemeridae is nearly cosmopolitan in distribution and contains 96 species in seven genera (Hwang et al., 2006). The larvae are considered important freshwater benthic macro-invertebrates because of their proportionally high secondary production and individual abundance in the ecosystem, as well as their useful environmental applications, such as those used for biomonitoring and ecotoxicology (Fremling & Mauck, 1980; Edsall, 2001).

The genus *Ephemera*, which contains more than 70% (68 species) of Ephemeridae species, is widely distributed in the Holarctic, Oriental, and to a lesser degree in the Afrotropical Regions (Hwang et al., 2006). Majority of the *Ephemera* species inhabit freshwaters of East Asia. The larvae are normally found in streams containing sand/gravel substrates mixed with pebble-sized stones, but they also richly inhabit large rivers and lakes with finer substrates (McCafferty, 1975). *Ephemera orientalis* McLachlan is a common burrowing mayfly that is distributed in temperate East Asia, including Northeastern China, Mongolia, Russian Far East, Korean Peninsula, and Japanese Islands (Hwang et al., 2006). When the members of *Ephemera* occur in a stream channel, they often represent a unique pattern of altitudinal distribution. For example, in Korean streams, *E. separigata* occupies the uppermost part of the mountain stream (ca. 1000–500 m above sea level), followed by *E. strigata* in the middle stream section (ca. 500–100 m a.s.l.), and *E. orientalis* in the lowland streams and rivers (ca. 100–0 m a.s.l.) (Lee et al., 1995, 1996). Similar distributional discontinuities along gradients in ephemerid burrowing mayflies are observed in Japan (Kuroda et al., 1984; Watanabe, 1985) and North America (McCafferty, 1975). This distributional pattern is associated with phenological adaptations of the species to maximize the timing and synchrony of biological events under certain environmental conditions (Takemon, 1985; Lee et al., 1999).

Some aspects of the life histories of temperate East Asian species of *Ephemera* are known in Japan (Gose, 1970; Kuroda et al., 1984; Takemon, 1985, 1990; Ban & Kawai, 1986; Ban & KINKI Aquatic Insect Research Group, 1988; Watanabe, 1992) and in Korea (Lee et al., 1996, 1999). These studies showed that most of the Japanese and Korean species of *Ephemera* are univoltine except *E. orientalis*. Kuroda et al., (1984) presented that *E. orientalis* has three generations in a year, whereas Watanabe (1992) showed that the species is bivoltine with spring and autumn cohorts in Japanese streams. Life histories of Korean *E. orientalis* have not been studied. Despite the above studies, detailed life history phenomena such as voltinism, secondary production, and accumulated degree days for larval development have not been comprehensively studied on the temperate East Asian species of *Ephemera*. On the other hand, Dudgeon (1996) carried out a detailed life history study of *Ephemera* in a tropical Hong Kong stream in terms of secondary production and microdistribution. In that study, both *Ephemera* (*E.*) *spilosa* and *E.* (*A.*) *pictipennis* were found to be univoltine.

Due to the poikilothermic nature of aquatic insects, physiological processes and phenomena such as larval growth, adult size, and fecundity display a high degree of sensitivity to ambient temperatures (Ward & Stanford, 1982; Sweeney, 1984). In addition, secondary production estimation is a parameter that integrates survival, growth, and voltinism of aquatic insects (Benke, 1984). Therefore, analyses of accumulated degree days and secondary production are necessary to demonstrate proposed life history adaptations for given species.

In this study, life history aspects of *E. orientalis*, a widespread lowland burrowing mayfly in temperate East Asian streams, were investigated through comprehensive field sampling and analyses of voltinism, secondary production, and accumulated degree days. Particular attention was given to the phenomenon of adult body size reduction in the population during the later part of the emergence period.

Materials and methods

Study area and temperature monitoring

Field studies were conducted from a lower reach of Gapyeong stream in Gyeonggi-do, central Korean Peninsula, from March 1998 to June 1999. The stream (stream channel ca. 42 km) originated from Myeongji Mt. (1267 m a.s.l.) and emptied into the North Han River, one of the major river systems of the Korean Peninsula. The study site (37° 50′ 59″ N, 127° 31′ 25″ E) was located approximately 4 km upstream from the mouth of the stream. *Ephemera orientalis* larvae were present in abundance in a pool-run area (ca. 200 m in channel length) of the study site.

The stream at the study site was approximately 100–130 m wide and the water body varied from

73 m to 110 m in width depending on the season. Water depth (mean ± SD) at the sampling points was 0.31 ± 0.11 m and the current velocity was 0.19 ± 0.12 m s^{-1}. Although, current velocity did not exceed 0.3 m s^{-1} during most of the seasons, it increased rapidly up to 0.45 m s^{-1} in September, following the rainy season (Fig. 1). Annual precipitation in the study area in 1998 was 1707.6 mm (unpublished data of local meteorological station); more than 60% (1029.9 mm) of the precipitation was found during the rainy season (July–August) (Fig. 1). Substrate mostly consisted of sand and gravel with abundant organic detritus embedded with cobble and boulder-sized stones. *Ephemera orientalis* larvae were found within the 1–2 cm surface layer of the substrate.

Water temperature at the sampling area was monitored every 2 h using a water temperature data logger from Onset Computer Corporation (Model: Optic StowAway® Temp). The temperature recorder was installed on the surface of the bottom (ca. 30 cm in water depth), and care was taken to avoid direct sunlight at the monitoring point. Water temperature was converted to degree days using the rectangle method, as shown in the following equation (Lee et al., 1999):

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

where, DD is degree days, $T_{\max}$ is daily maximum temperature, $T_{\min}$ is daily minimum temperature, and T_b is the base temperature for larval development. There has been no information about T_b of *E. orientalis* and 0°C was often used in such a case. However, a T_b value of 8.51°C, which was derived from a laboratory experiment on egg development (Lee et al., unpublished), was used for *E. orientalis* in this study.

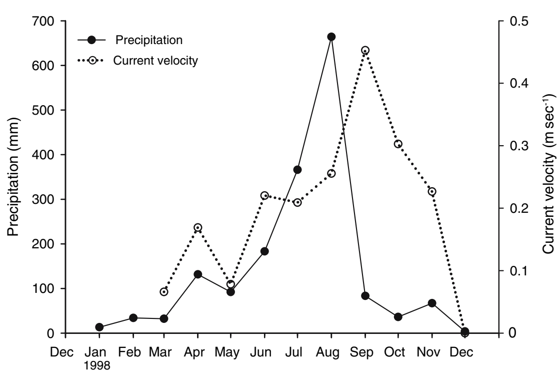

Fig. 1 Precipitation and current velocity of the study area in 1998

Sampling and laboratory procedure

Ephemera orientalis larvae were sampled every month during the period of non-emergence, but were sampled every 1 or 2 weeks during the emergence period. Four quantitative samples were taken during each sampling using a Surber sampler (50 × 50 cm, mesh 0.25 mm). Four sampling points were chosen from the side of the stream to the middle of the water channel; all of the organic material and larvae were sampled within a 10 cm depth of substrate. Sampled material was kept in a 500 ml bottle and fixed with Kahle's solution. After 2–3 days, *E. orientalis* larvae were sorted and preserved in 80% ethanol. Along with larval sampling, *E. orientalis* adults were sampled using a sweeping net. Adult emergence was additionally assessed via observing swarms or individuals attracted to lights around the sampling site. Wingpad darkening of mature larvae was also assessed to determine the time of emergence.

Larval body length and head capsule width were measured using a micrometer on a dissecting microscope (OLYPUS-SZ40). Larval body size classes were categorized in 2 mm intervals of body length and were used to analyze larval development of *E. orientalis* (Lee et al., 1999). Cohorts of *E. orientalis* were identified from the body length by Cassie's probability paper method (Cassie, 1954), which is based on statistical assumption to normality in the distribution of certain measurements, such as body length, within each cohort. Adult body size was measured by the length from anterior head to terminal abdomen excluding caudal filaments. All the statistical analysis in this study was accomplished using SAS for Windows (SAS Institute Inc., 2004).

Estimation of secondary production

Larval biomass was indirectly calculated from the head capsule width (HCW). Dudgeon (1996) showed that log dry weight (DW) and ash-free dry weight (AFDW) are strongly correlated with HCW in the case of *Ephemera spilosa*. Therefore, we randomly chose *E. orientalis* larvae ($n = 91$) and measured the HCW and DW in order to determine the relationship between HCW and DW. The log value of DW showed a significant ($r^2 = 0.810$, $P < 0.01$ by regression analysis) linear relationship with HCW, which is represented in the following equation:

$$\log\ (\mathrm{DW}) = -2.291 + 1.854\ (\mathrm{HCW}) \qquad (2)$$

HCW's were then converted to DW using Eq. 2 and the secondary production was estimated.

Actual cohort method is preferable for secondary production estimation, if all cohorts can be recognized exactly (Benke, 1993). For comparison, however, we used size frequency method because other previous studies, as in references, were also used size frequency method.

According to size frequency method, annual production estimation requires a calibration based on the cohort production interval (CPI: mean length of the aquatic stage relative to a full year); a calibration is necessary when CPI is significantly greater or less than 1 year. In this study, different CPI's were applied to different developmental groups according to their life histories. For the whole population including all the developmental groups, however, the CPI value of 12 was used as the larvae were observed throughout the study year.

Results

Quantitative sampling of *E. orientalis* larvae resulted in a mean density of 47.21 ± 13.58 indiv. m^{-2}. The density was highest on October 20 (118 ± 82.58 indiv. m^{-2}) and lowest on November 26 (2 indiv. m^{-2}). The larval body size distribution showed that the body size groups are more complicated between May and August (Fig. 2).

Based on data from the first year (1998), very small larvae (less than 2 mm in body length) were present on May 15, June 20, and December 18, but small larvae (less than 4 mm) were present almost throughout the year. Adults were found from late April to early October, except during late May. Considering that the first finding of mature larvae with dark wingpads was in late March, it appears that potential emergence lasts for over 6 months until early October. The proportion of small larvae less than 4 mm decreased between middle March and early April, but it increased again in late April (April 30). The first adults were sampled during late April.

Based on the larval body size distribution, two different developmental groups were distinguished during the study year (Fig. 3). The slow developmental group (S-group) showed a 1-year life cycle, whereas the fast developmental group (F-group) completed its life cycle within the 4 month period from May to August. Additionally, two subgroups within the S-group were recognized. The first S-group (S1-group) recruited early instar larvae in early June and developed rapidly during the summer. Mean body length of the larvae of S1-group reached 12.25 ± 1.76 mm in December, and no considerable increase in body length was observed during the winter. The second S-group (S2-group) recruited early larvae from mid-July to mid-September. Mean body length (6.28 ± 2.13 mm) of the S2-group in December was much smaller than that of the S1-group ($P < 0.01$ by *t*-test). In the spring, the S1-group matured and emerged earlier than the S2-group.

Two different adult body size groups were recognized and easily distinguished each other in the population of *E. orientalis* (Table 1). Larger adults belonging to the S-group were present throughout the emergence period, whereas smaller adults belonging to the F-group were present mainly in the later emergence period (August–October).

As shown in Table 2, estimated total annual production of *E. orientalis* was 53.61 mg DW m^{-2} y^{-1}, mean biomass was 8.44 mg DW m^{-2}, and P/B ratio was 6.36. Mean density, mean biomass, cohort production, and annual production of the S-group were much greater than those of the F-group; conversely, annual P/B ratio of the F-group was larger than that of the S-group.

Annual mean water temperature during the study period was 14.76 ± 6.63°C. The maximum water temperature (25.89°C) was recorded on July 30, 1998 (Fig. 4A). The water temperature dropped rapidly after mid-October and the minimum water temperature (3.10°C) was recorded on January 22, 1999. The daily water temperature recorded between November 18 and March 1 did not exceed the base temperature (8.51°C) for the larval development of *E. orientalis*; thus, no effective temperature was accumulated during that period. As a result, estimated sum of thermal amount, effective to larval development during the study period, was 2,340°C degree days

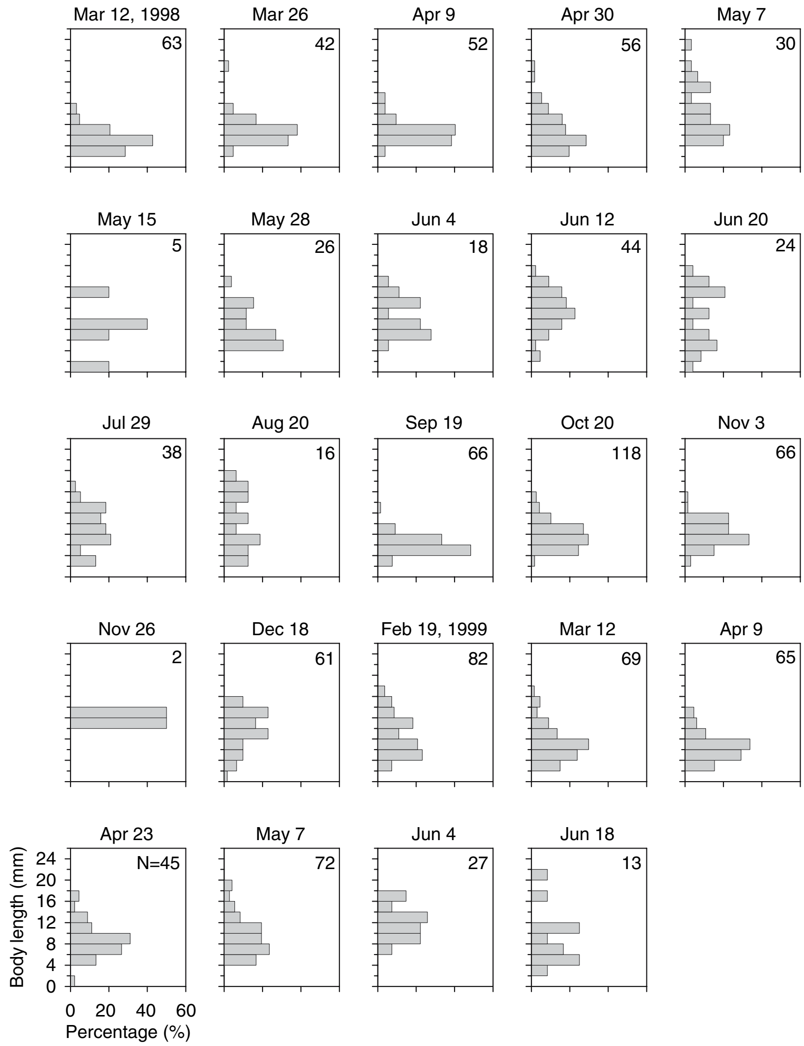

Fig. 2 Larval body size distribution of *E. orientalis* from the study area from March 1998 to June 1999

(Fig. 4B). Based on the assumption of the life cycle pattern in Fig. 3, the total accumulated degree days for larval development of the F-group from May to August was approximately 1,396°C degree days; those of the S1 and S2-groups during the developmental period were 2,055°C and 1,975°C degree days, respectively.

Discussion

Life history phenomena of aquatic insects are directly influenced by different thermal regimes. For example, cooler geographic regions at higher latitudes cause delayed development and reduced numbers of generations per year in ephemerid mayflies (Clifford, 1982; Corkum & Hanes, 1992; Newbold et al., 1994) and various other aquatic insects (Ward & Stanford, 1982; Sweeney, 1984; Brittain, 1990). Detailed studies on a riverine ephemerid mayfly, *Ephemera danica*, showed that it has a 2 or 3-year life cycle in Europe depending on its location in France (Thibault, 1971), Sweden (Svensson, 1977), Spain (Aguayo-Corraliza et al., 1991), and Britain (Wright et al., 1981; Tokeshi, 1985). A lacustrine burrowing mayfly, *Hexagenia limbata*, also showed a linear relationship between voltinism and latitudinal location in North America (Heise et al., 1987). In general, mayflies in warmer, subtropical or tropical regions are multivoltine, while those of temperate regions tend to be univoltine or semivoltine with seasonal traits (Clifford, 1982).

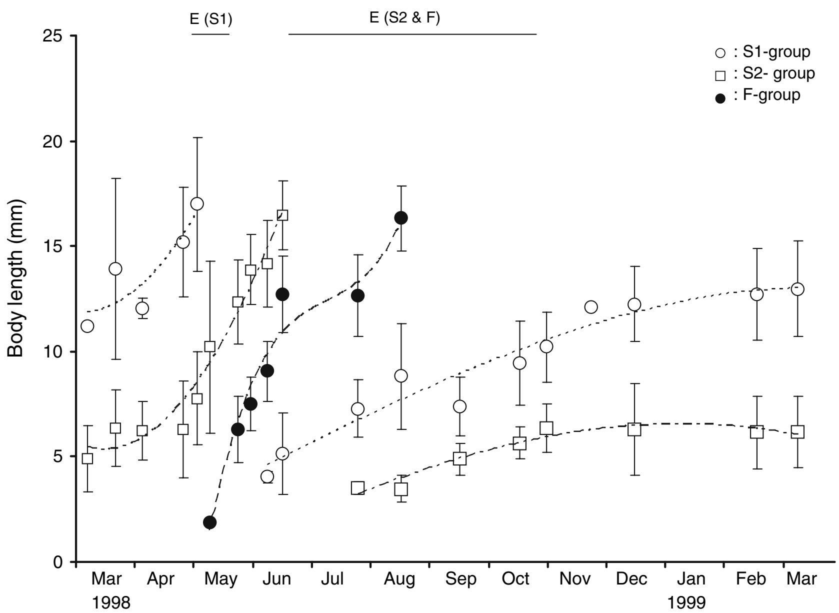

Fig. 3 Hypothetical life history pattern of *E. orientalis* proposed from the information on larval body size distribution, emergence, and developmental groups. Vertical bars mean standard deviation. E = Emergence

Table 1 Two different adult body size groups of *E. orientalis* sampled from study area

Collecting time	Mean body length ± sd (mm) (no. of examined)	
	Male	Female
May (S-group)	19.51 ± 1.06 (n = 16)	20.69 ± 0.95 (n = 13)
August–October (F-group)	15.31 ± 0.41 (n = 14)	16.07 ± 0.92 (n = 11)
p*	<0.001	<0.001

*t-test

Table 2 Secondary production information for the cohorts of *E. orientalis* in this study

Cohorts	CPI	D	B	CP	AP	P/B	
						Cohort	Annual
F-group	4	4.00	0.92	4.79	14.36	5.21	15.62
S-group	11	42.94	7.52	48.49	52.90	6.45	7.04
Whole population	12	46.94	8.44	53.61	53.61	–	6.36

Data were obtained by size frequency method using the material collected from March 1998 to February 1999. CPI = cohort production interval; D = mean density (n m^{-2}); B = mean biomass (mg DW m^{-2}); CP = cohort production (mg DW m^{-2} y^{-1}); AP = annual production (mg DW m^{-2} y^{-1}); P/B = production to mean biomass ratio

Altitude is also an important factor that determines the life history patterns of aquatic insects. Previous studies have shown that members of *Ephemera* that inhabit mountain streams in temperate East Asia are mostly univoltine and have fairly well synchronized emergence patterns, as observed in *E. japonica*, *E. separigata*, and *E. strigata* (Gose, 1970; Kuroda et al., 1984; Ban & Kawai, 1986; Takemon, 1990; Lee et al., 1996, 1999). Dudgeon (1996) also showed that ephemerid mayflies (*E. spilosa* and *E. pictipennis*) from Tai Po Kau Forest stream in Hong Kong, a mountain stream in a region of the tropics, are univoltine.

Previous studies on the life history of *E. orientalis* showed a complicated life history pattern in terms of voltinism. For example, Kuroda et al., (1984) suggested the presence of three different generations of Japanese *E. orientalis*, which were said to emerge in May, June to July, and November to December, without providing detailed cohort analysis. Watanabe (1992) recognized a bivoltine life cycle of Japanese *E. orientalis*, consisting of a slow-growing cohort and a fast-growing cohort, but did not consider a subdivision in the slow-growing cohort.

Our study provided the possibility that a burrowing mayfly species inhabiting a lowland temperate stream produces three generations within 2 years with an alternation of a fast developmental cohort (F-group) and two slow developmental cohorts (S1 and S2-groups) (Figs. 3 and 4B). The existence of larger adults in the spring (late April to early May) and the co-existence of larger and smaller adults in the late

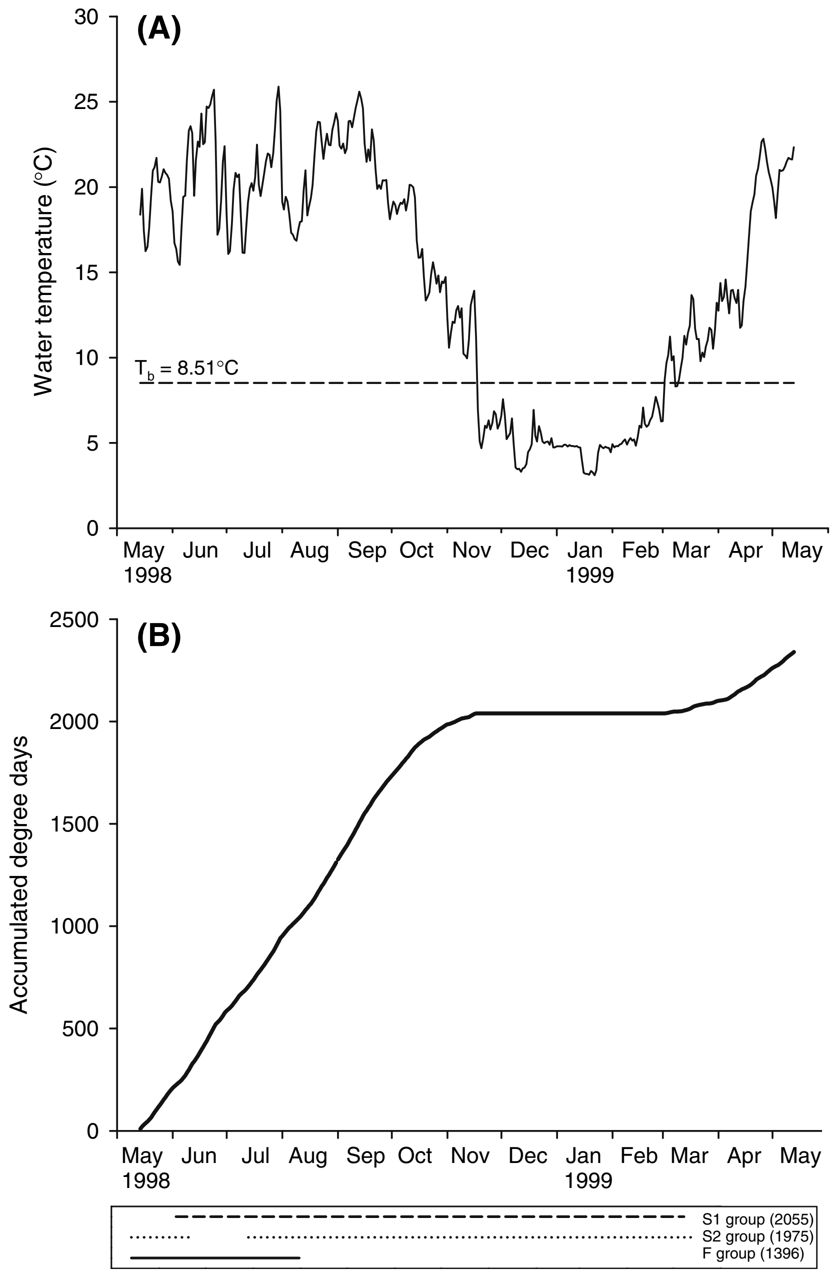

Fig. 4 Water temperature from the study area. (**A**) Water temperature profile. Tb: base temperature for larval development; (**B**) Accumulated degree days during larval development periods. Larval developmental periods of S1, S2, and F-groups with accumulated degree days are indicated in the box, below

summer (August–October) may substantiate the presence of two different developmental cohorts during that period (Table 2). The adults captured during the spring may have belonged to the S1-group, and the offspring of the S1-group in April became a new F-group generation. The F-group, actually a new generation of a previous S1-group, emerged after August, and the offspring became a new S2-group generation. The offspring of the S2-group in early June became a new S1-group generation. It could be therefore hypothesized that developmental groups alternated their life cycles in the order, S1→F→S2→S1. Thus, *E. orientalis* may complete its three generation cycles over the course of 2 years; three generation cycles include a fast-growing cohort and two slow-growing cohorts.

In addition to the analysis of voltinism, our study provided an estimated annual production of

Table 3 Estimated annual production and P/B ratio of various mayflies

Species	Estimated annual production (g DW m^{-2} y^{-1})	P/B	Sources
Multivoltine			
Baetis bicaudatus	1.40		Pearson and Kramer (1972)
B. vagans	1.80–2.5		Waters (1966)
B. rhodani	5.6	7.4–9.1	Welton et al. (1982), Tokeshi (1985)
Caenis lustuosa		15.98	Perán et al. (1999)
Ephemerella inermis		5.1–8.7	Robinson & Minshall (1998)
E. ignita	4.4	4.1	Welton et al. (1982)
E. subvaria	5.3–6.7		Waters & Crawford (1973)
Ephemera orientalis[a]	0.05	6.35	This study
Univoltine			
Cinygmula par		6.1–7.7	Robinson & Minshall (1998)
Ephemera strigata[b]	0.85	2.4	Gose (1970)
E. spilosa	0.04	3.67	Dudgeon (1996)
Ephoron leukon[c]	0.44–3.17		Snyder et al. (1991)
Hexagenia spp.		2.8–4.4	Waters (1977)
Semivoltine			
Ephemera danica	5.58	<2.1	Tokeshi (1985)

Most of estimated annual productions were derived from measurements of dry weight except those of *E. strigata*. AFDW and wet weight values were converted into DW according to Benke (1993)

[a] Estimated annual production was derived from whole population in this study (see Table 1)

[b] DW was derived from wet weight

[c] DW was derived from AFDW

E. orientalis (Table 2). Previous studies showed that estimated annual productions of mayflies in temperate streams vary depending on the species and voltinism, as shown in Table 3. Estimated annual production of *E. orientalis* (53.99 mg DW m^{-2} y^{-1}) known from this study is different from other multivoltine mayflies, univoltine burrowing mayflies, e.g., *Ephemera strigata* (Gose, 1970) and *Ephoron leukon* (Snyder et al., 1991), or semivoltine ephemerids, e.g., *Ephemera danica* (Tokeshi, 1985). In comparison, the P/B ratio of *E. orientalis* is closer to that of multivoltine mayflies, e.g., *Caenis luctuosa* (Perán et al., 1999), *Baetis rhodani* (Welton et al., 1982; Tokeshi, 1985), *Ephemerella ignita* (Welton et al., 1982), or other univoltine non-ephemerid mayflies with smaller body size, e.g., *Cinygmula par* (Robinson & Minshall, 1998) and *Ephemerella inermis* (Robinson & Minshall, 1998). These findings may substantiate that *E. orientalis* does not have a univoltine life history, but has more than one generation and probably less than two generations per year.

If a new generation started at the day of May 15, the time at which very young instar larvae were recruited (Fig. 2), estimated total accumulated degree days of the F-group (1,396°C degree days) is much lower than that of the S-group (2,055°C degree days for S1-group and 1,975°C degree days for S2-group). This could explain the reduction of the adult body size of the F-group, as shown herein. McCafferty & Pereira (1984) showed that mean maturation time of a burrowing mayfly, *Hexagenia limbata*, decreased with increasing mean water temperature at an escalating temperature regime. Therefore, the shorter maturation period of the F-group may be due to a higher and incremental temperature regime during the developmental period. On the other hand, if the degrees days had only been accumulated up to the day before the temperature declined to the base temperature (8.51°C) in November (Fig. 4A), the accumulated degree days for the S2-group (1,132°C degree days) were lower than those of the S1-group (1,324°C degree days). This difference in accumulated degree days could have also influenced the difference in the larval body length between the developmental groups of the S1 and S2-groups.

A reduction in the adult body size in the later portion of the emergence period is found in various groups of mayflies (Sweeney & Vannote, 1981; Sweeney, 1984; Takemon, 1990; Corkum & Hanes, 1992; Sweeney et al., 1995). Our study showed that the reduction in the adult size of the F-group (Table 1) is caused by smaller number of degree days. In addition, the decrease in average adult size in the later part of the emergence period, particularly from August to October, is due to an increase of the number of smaller-sized adults from the F-group cohort.

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