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Emergence patterns of the mayfly *Cloeon marginale* (Ephemeroptera: Baetidae) in a tropical monsoon forest wetland in Taiwan

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Abstract
This study presents the year-round emergence patterns of *Cloeon marginale* Hagen in relation to diel and seasonal changes in temperature, rainfall, humidity and light intensity in a tropical monsoon forest wetland LTER (Long-Term Ecological Research) site in southernmost Taiwan (22°03′N, 120°51′E). In 2000, the total precipitation was 3109 mm. About 52% of precipitation fell intensively from June to August, but there was no distinct dry season. The average daily air temperature was 22.2°C (range: 10.8 – 29.4°C). From July 1999 to 2001, emergence traps were set out for a 24-h period at least once a month, and the numbers of emerging subimagos were recorded at 10 min intervals only during emergence. *C. marginale* emerged year-round, like other tropical mayflies, but the number of emergent subimagos changed significantly with season. Emergence peaked in early summer and then declined sharply during the summer monsoon, when typhoons and heavy rain are common. The average water temperature at the start of emergence (15:00 – 16:00 h) was 23.8°C, but ranged between 14.4°C and 31.8°C. During the winter monsoon, water temperature neared a minimum (14°C) and emergence nearly stopped. The number of subimagos collected was positively correlated with water temperature ($r = 0.61$, $p < 0.001$, df = 26). Year-round, *C. marginale* emerged mainly at dusk. Emergence began as the light intensity decreased to near 80 μmol m^{-2} s^{-1}, and increased markedly when the light intensity fell below 5 μmol m^{-2} s^{-1}. Emergence ceased after darkness (0 μmol m^{-2} s^{-1}). About 62 % of the subimagos emerged at light intensities between 0 and 1 μmol m^{-2} s^{-1}. Synchronous emergence at dusk helps avoid predators and minimizes water loss.

Keywords: *Mayflies, emergence, synchrony, light intensity, temperature, monsoon, tropical forest*

Introduction

Seasonal, synchronous emergence is characteristic of all mayflies (Gibbs 1977; Sweeney & Vannote 1981, 1982; Watanabe et al. 1999). The seasonal synchronicity is determined largely by the magnitude and pattern of temperature on larval growth (Sweeney & Vannote 1981; Watanabe et al., 1999). Mayflies usually emerge when it is relatively warm and stop emerging when temperature falls below some threshold (Brown 1961; Brittain 1976; Sweeney 1978). In the field, the effect of environmental temperature on the timing of emergence is often evaluated by comparing the time of seasonal emergence between different years (Watanabe et al. 1999) or between different latitudes (Gibbs 1977). Although most tropical mayflies emerge

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year-round (Petr 1970; Wolda & Flowers 1985), and often have aseasonal life histories (Marchant 1982; Yule & Pearson 1996), they still exhibit coordinated seasonal emergence (Edmunds & Edmunds 1980). Synchronous mass emergence increases mating probability (Corbet 1964), and increases survival rate through predator satiation (Edmunds & Edmunds 1980; Sweeney & Vannote 1982).

The daily mass emergences of most mayflies occur during almost total darkness, hence, light intensity was proposed as the main factor regulating diel emergence (Edmunds & Edmunds 1980; Friesen et al. 1980). Emergence at dusk or at dawn appears to be important for avoiding predators (Friesen et al. 1980). However, low temperature can override the stimulus of light intensity (Humpesch 1971; Sweeney & Vannote 1981). Hence, in temperate regions there is a diverse range of diel emergence times, from dawn, to mid-day, to dusk (Edmunds & Edmunds 1980; Friesen et al. 1980; Harper et al. 1983; Humpesch 1971; Pinder et al. 1993). Furthermore, some temperate species of *Cloeon* living in the subtropics may exhibit emergence patterns typical of tropical species (Soldán 1987), and some tropical genera that occur in temperate regions may exhibit temperate emergence patterns (Edmunds & Edmunds 1980). Therefore, the seasonal and daily emergence patterns of mayflies in the tropics, and the environmental cues for synchronous mass emergence, are important indicators of each species ecological adaptations.

We investigated the emergence of a mayfly, *Cloeon marginale* Hagen (Ephemeroptera: Baetidae), in a protected forest wetland in Kenting National Park in southernmost Taiwan. The survey area, one of five LTER (Long-Term Ecological Research) study sites in Taiwan, is a transition zone between tropical and subtropical climates, with distinct summer and winter monsoons. *C. marginale* nymphs of all sizes were present in the wetland year-round. To investigate the relationship between environmental factors and emergence patterns, samples of emerging subimagos were collected at least once a month, continuously for 24 h, from July 1999 to 2001. To quantitatively characterize the diel emergence pattern of *C. marginale*, subimagos were collected at 10 min intervals during emergence periods. Data on year-round emergence patterns in relation to diel and seasonal changes in temperature, humidity and light intensity should further current understanding of mayfly emergence.

Study site

The study area (22°03′N, 120°51′E), is situated on the eastern side of a mountain range on the Hengchun Peninsula at the southern tip of Taiwan. The Nanjenshan Wetland is part of the Nanjenshan Nature Reserve, which is comprised of 2400 ha of virgin subtropical and tropical forests (Chen et al. 1997) in Kenting National Park. The forest extends from 200 m to 500 m a.s.l, and the study wetland is at an elevation of 330 m a.s.l. Several creeks originating in this area have dissected the landscape into gorges and ravines.

The summer monsoon, with heavy rain and typhoons, lasts mostly from May to October. The winter monsoon, usually with strong northeasterly winds but low rainfall, occurs from late October to March. In 1997 and 1998, the annual precipitation was 3134 mm and 3796 mm, respectively, with about 75% of the total falling between May and August. Nevertheless, rainy days (235 and 243) were evenly spread throughout the year, and there was no distinct dry season (Su & Su 1988; Chen et al. 1997).

The Nanjenshan Wetland, which is comprised of several connected wetlands with various sizes of areas, is about 30 ha and receives abundant detritus from the surrounding forest and shore plants. The Gufu Wetland is about 0.03 ha and locates at the southern end of the Nanjenshan Wetland. The aquatic weed *Leersia hexandra* Sw. is dominant in shallow water and shore areas, and is the primary habitat for nymphs of *C. marginale* (Perng et al. 1999).

During the summer monsoon, spates wash away much of the detritus and aquatic benthos. Aquatic insect species diversity was high. *C. marginale* nymphs are one of the most abundant detritivores in this wetland ecosystem. Very few nymphs of the other mayfly species were found during the study period.

Materials and methods

From July 1999 to 2001, we placed nine emergence cages in water 10–20 cm deep near the shore, where most *C. marginale* nymphs lived, of the Gufu Wetland. The cages, 40 cm × 40 cm × 40 cm, were covered, except on the bottom, with fine-mesh netting. The emergence cages were positioned so that the upper half was above the water and the cage was not touching the bottom substrate. This permitted nymphs and newly emerging subimagos to move freely. Mature nymphs floated up to the water surface, moulted in a matter of seconds, then the subimagos flew immediately into the nearby tree canopy. The cages were set out for a 24-h period at least once a month. Newly emerged subimagos were measured and collected at 10 min intervals only during the emergence period between approximately 16:00 and 20:00 h (light intensity 0–350 μmol m^{-2} s^{-1}). In the meantime, water temperature was measured near the shore where most the mayfly nymphs lived. Light intensity (μmol m^{-2} s^{-1}, LI-COR LI-250 Light Meter), relative humidity and air temperature were also measured about 2 m away from the water. At the condition of diffuse daylight, 1 μmol m^{-2} s^{-1} equals about to 19 lux (Larcher 1995).

To examine the effects of seasonal weather conditions (e.g. low temperature in winter and spates in summer and autumn) on the number of emerging subimagos, the seasons were defined as spring (March to May), summer (June to August), autumn (September to November), and winter (December to February). Differences among seasons in the average number of emerging subimagos collected during 24-h periods were tested with a GLM (square root transformation of raw data) followed by multiple comparisons with LSD tests (SAS Institute 1989). The significance of the relationship between number of emergent subimagos and water temperature was tested with a linear regression.

Results

In 2000, the total precipitation was 3109 mm. About 52% of precipitation fell intensively from June to August, but there was no distinct dry season (Figure 1A). The average daily air temperature was 22.2°C, and ranged from 10.8 to 29.4°C (Figure 1B). The average water temperature at the start of emergence (15:00–16:00 h) was 23.8°C, but ranged from 14.4°C to 31.8°C (Figure 1C).

Seasonal emergence

Subimagos of *Cloeon marginale* emerged year-round in the Gufu Wetland from July 1999 to January 2001, although only 0.66 % emerged during the winter (Figure 1D). Emergence peaked in July 1999 and again in July–August 2000, and declined to lower levels in November. Emergence increased gradually from April to early summer. The daily average number of emerging subimagos collected between July 1999 and May 2001 (Figure 2) differed significantly among seasons (GLM: $F(3,19) = 9.27$, $p = 0.0009$). An *a priori* LSD test showed that the number of subimagos emerging in summer was significantly higher than in the other seasons, and the number emerging in winter was significantly lower than in other seasons ($\alpha = 0.05$).

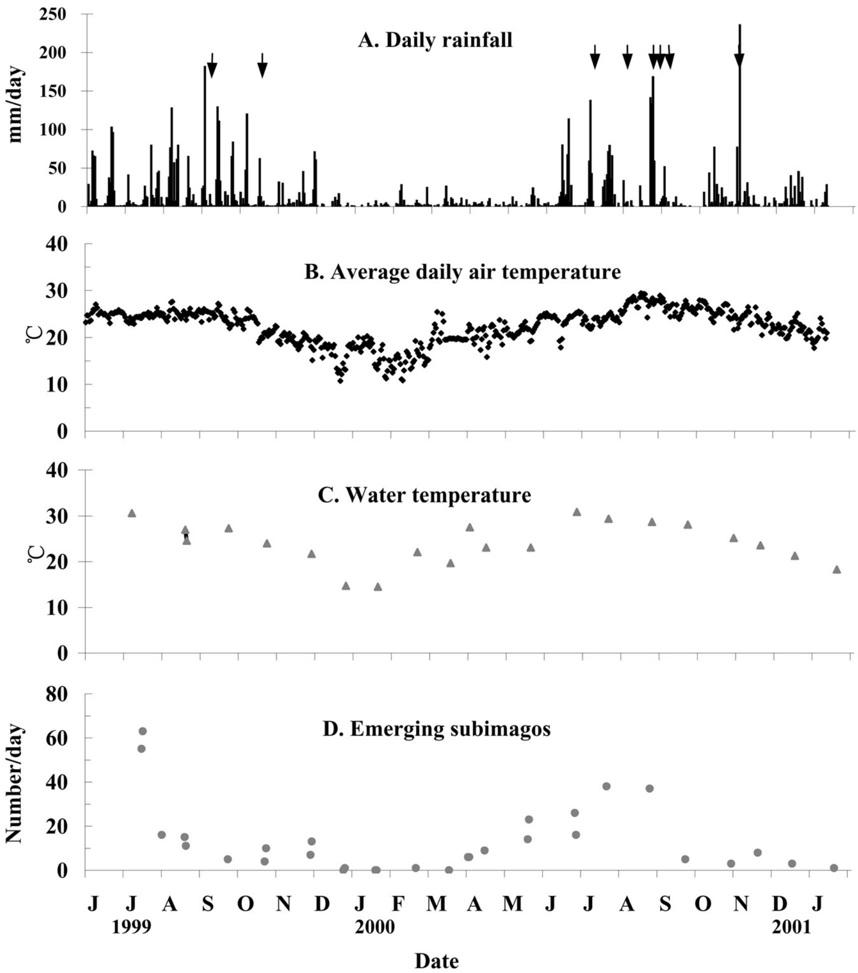

Figure 1. Microclimate and the emergence of *C. marginale* in Gufu Wetland, July 1999 to January 2001. A, daily rainfall (arrows indicate typhoons); B, average daily air temperature; C, water temperature measured at the start of emergence (15:00 – 16:00 h); D, total number of subimagos emerging into nine emergence cages per day.

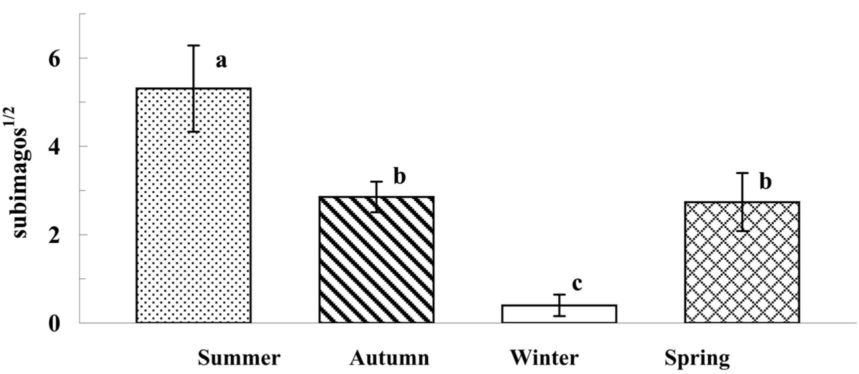

Figure 2. Average number of emerging *C. marginale* subimagos (± SE) collected in nine emergence traps per day in Gufu Wetland by season, July 1999 to May 2001. For statistical analysis, the data was transformed by square root. Means sharing the same letter are not significantly different (LSD, $\alpha = 0.05$).

The number of subimagos collected (Figure 1D) was positively correlated ($r = 0.61$, $p < 0.001$, $df = 26$) with water temperature at the start of emergence (Figure 1C). Emergence occurred almost every day when water temperature was above 20°C, but almost stopped during the winter when the water temperature was 14–20°C. Although emergence peaked in summer, it declined to distinctly lower levels after frequent and heavy rainfall produced by the summer monsoon (Figure 1A). Heavy rain created spates in the shallow Gufu Wetland. Daily rainfall was often above 100 mm, especially during typhoons. There were two typhoons in 1999 (at the end of August and in early October), and six typhoons in 2000 (July–October; arrows in Figure 1A).

Diel emergence

Emergence regularly occurred near and at dusk (Figures 3A–D), with peak emergence always occurring at extremely low light intensities. The time of the onset and peak of emergence was

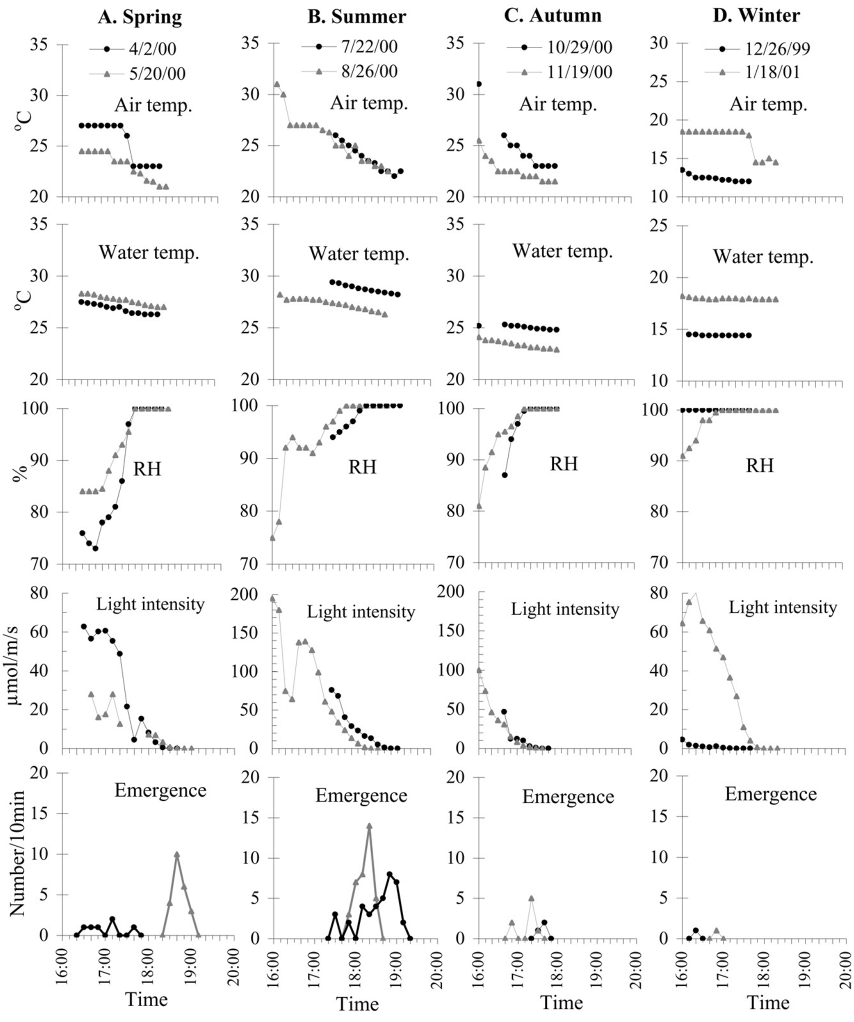

Figure 3. Emergence of *C. marginale* subimagos and changes in air and water temperature, relative humidity and light intensity at 10-min intervals between approximately 16:00 and 20:00 h for two dates in each season.

delayed as day length increased. Emergence began when light intensity had decreased to about 80 μmol m^{-2} s^{-1}. However, 88% of the subimagos emerged when light intensity was 5 μmol m^{-2} s^{-1} or less, and 62% of the subimagos emerged during a 10–20 min interval when light intensity was less than 1 μmol m^{-2} s^{-1} (Figure 4). Emergence stopped when it was dark (0 μmol m^{-2} s^{-1}).

Discussion

Seasonal emergence

In the study wetland, *Cloeon marginale* emerged year-round, like other tropical mayflies (Petr 1970; Wolda & Flowers 1985; Yule & Pearson 1996), but the number of emergent subimagos of *C. marginale* changed significantly with season. This is in contrast to the asynchronous, aseasonal emergence of mayflies on tropical Bougainvillea Island, where temperature, rainfall and humidity varied little throughout the year (Yule & Pearson 1996). At Nanjenshan, *C. marginale* emergence rates were very low during the winter. The lowest water temperature in Gufu Wetland was 14°C, which is lower than the minimum water temperature of about 19°C in tropical regions near the equator (Masteller & Buzby 1993; Yule & Pearson 1996). Temperature can significantly affect growth rates (Sweeney et al. 1986; Lauzon & Harper 1986). Low temperature increases the number of mayfly nymph instars (Brittain 1982), which depresses and delays mayfly emergence (Brittain 1976; Sweeney et al. 1986). The timing of mayfly emergence is strongly affected by the thermal conditions experienced during nymphal growth periods (Sweeney & Vannote 1981; Watanabe et al. 1999). The density of *C. marginale* nymphs increased in October and peaked in December (Perng et al. 1999). In addition, most of the ratios of older nymphs to younger nymphs in winter were at the highest level (unpublished data). Typically, these conditions should produce high emergence rates. However, *C. marginale* emergence rates were lowest during the winter, demonstrating that low temperature is the dominant factor affecting emergence in this tropical monsoon wetland. In

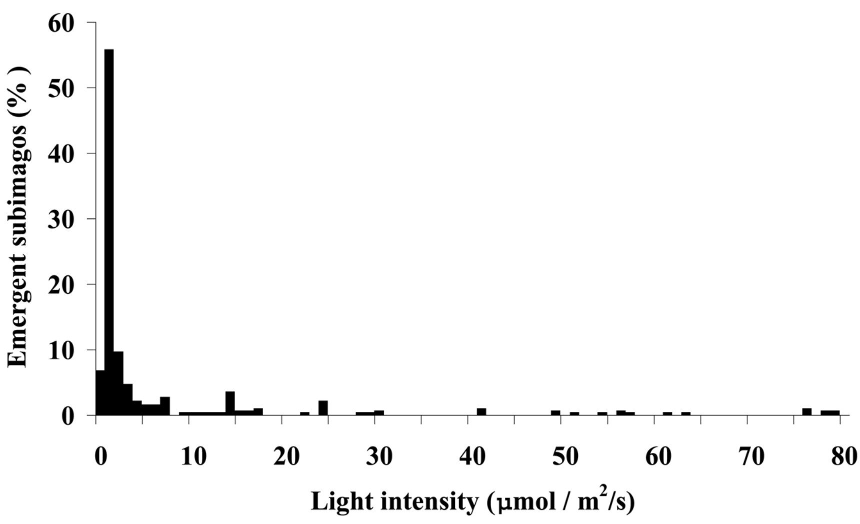

Figure 4. The percentage of *C. marginale* subimagos collected in relation to light intensity in Gufu Wetland, July 1999 to January 2001.

April, after the winter, emergence rates increased. They increased sometime after water temperature increased, suggesting low, cold season temperatures somehow delay mayfly emergence during cold season (Brittain 1976; Sweeney et al. 1986).

Although emergence peaked in early summer, it declined to a much lower level with the onset of heavy summer rains. Nymphal densities were lowest during this period (Perng et al. 1999). The frequent and unpredictable spates are thought to be the primary cause of the increase in nymphal mortality in aquatic insects (Dudgeon 1996; Yule & Pearson 1996). In Hong Kong, the synchronous emergence of univoltine *Ephemera* mayflies prior to the summer monsoon may be the product of the strong selective pressure exerted by heavy rainfall on nymph survival and adult emergence (Dudgeon 1996). Therefore, although *C. marginale* can emerge year-round, the mass emergence during early summer probably results from the constraints imposed by low winter temperatures and summer spates.

Diel emergence

Year-round, most *C. marginale* emerged synchronously just before full darkness, and seasonally, the time of emergence changed consistently with photoperiod. Thus, low light intensity (5 μmol m^{-2} s^{-1} or less) seems to be the dominant factor regulating the circadian rhythm of emergence. Because the mass activities of tropical mayfly species occur consistently near or at darkness, this may indicate an adaptation of tropical aquatic insects for escaping from heavy predation (Edmunds & Edmunds 1980; Friesen et al. 1980; Marchant 1982). Under the cover of darkness, emerging subimagos of *C. marginale* on the water surface are less likely to be preyed on by the abundant mosquito fish, wolf spiders and dragonflies etc. that actively exploit the land–water interface in our study wetland. Very few bats were found during the study period. In addition, at dusk, the air temperature usually fell 5–8°C and the relative humidity always reached 100%. Thus, emergence at this time minimized subimago water loss, especially in the summer. There are two species of *Cloeon* that emerge nearly all day long in Europe. In the desert of North Africa, these same two species have a shortened subimaginal stage and emerge at night to avoid the high temperature and low humidity of daytime (Soldán 1987).

During the winter, there was no mass emergence of *C. marginale* at low light intensities. The few subimagos that emerged did so at early dusk, as in other seasons. Thus, the constraints imposed on emergence by low temperature override the stimulus of light intensity (Humpesch 1971; Sweeney & Vannote 1981). The peak emergence of *Baetis intercalaris* is usually at dawn or dusk. However, most peak emergence shifted to mid-day at lower temperatures in June. Thus, emergence can be delayed until air temperature is high enough for emerging adults to fly (Friesen et al. 1980). The adult mayflies of *C. marginale* have only a short time (longevity: from several days to about two weeks) immediately after emergence to reproduce. Hence, although the strong north wind dominated in winter may not have a direct effect on the occurrence of emergence, it could greatly disturb adult mayfly swarming and mating.

In summary, the seasonal and diel emergence patterns of *C. marginale* in southernmost Taiwan were strongly influenced by seasonal changes in temperature, rainfall and photoperiod. Emergence can be viewed as an integral part of life history strategy (Brittain 1980). Different species of mayflies exhibit behavioral plasticity and a wide range of adaptations to a variety of environmental constraints (Brittain 1982; Soldán 1987). Thus, the mayfly emergence rate could serve as a useful indicator of changes to the environment, including those caused by global warming. The synchronous mass emergence of *C. marginale* and some other species of aquatic insects occurs at very low light intensity. In certain locations, it could be important to prevent light pollution from interfering with aquatic insect emergence.

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