

## Life history attributes of the rare mayfly *Siphonisca aerodromia* Needham (Ephemeroptera:Siphonuridae)

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**Abstract.** Over a 3-y period, we examined the biology of late-instar nymphs, adults, and eggs of the rare predaceous mayfly *S. aerodromia* at Tomah Stream, Maine, to identify life history attributes associated with the mayfly's movements between the stream channel and the bordering floodplain. Eggs were deposited in the stream channel in June and hatched in November and December. Embryonic development occurred in 47–92% of eggs from unmated females. With rising water levels following snowmelt in March or April, nymphs moved from channel to floodplain, where most nymphal growth and development took place. Sex ratios of nymphs in the floodplain were female biased (1 M:1.4 F in 1991 and 1 M:2.1 F in 1992). Nymphs molted to the final instar earlier in 1991 than in 1992 and male nymphs molted to the final instar before female nymphs in 1991 but not 1992. Time in the final instar decreased as the season advanced. Seasonal emergence was protandrous and lasted 10–11 d during late May and early June; timing of seasonal emergence in 1991, 1992, and 1993 was related to maximum air temperatures and persistence of standing water in the floodplain during May. Emergence of subimagos was female biased in 1991, but male biased in 1992. Diel emergence was from 0700 to 1700 h (EST) and occurred only when water temperature was >11°C.

**Key words:** mayfly, floodplain, emergence, sex ratio, parthenogenesis, egg development.

*Siphonisca aerodromia* Needham was originally collected from the Sacandaga River in New York early in the century, but disappeared in the 1930s following construction of the Sacandaga Reservoir (Edmunds et al. 1976). It has since been reported at only 1 location in New York (Barbara L. Peckarsky, Cornell University, personal communication to Kathryn J. Schneider, New York Natural Heritage Program); 9 locations in the Mattawamkeag, Passadumkeag, East Machias, Dead River, and St. Croix drainages in Maine (Burian and Gibbs 1991); and 3 locations in eastern Canada (Magnin and Harper 1970, Fiance 1978, Hutchinson 1989). The species is listed as a candidate for the Federal Endangered list (Category 2) (US Department of the Interior 1991).

The life history of *S. aerodromia* is complex and involves seasonal movements between the stream channel and adjacent inundated floodplain (Gibbs and Mingo 1986). At Tomah Stream, Maine, early instar nymphs feed on detritus and are found beneath the ice in the stream channel from January to March. During high water following snowmelt, in March or

April, nymphs move from the stream to the bordering, inundated, sedge-dominated floodplain. Here, nymphs are predaceous, ingesting mainly mayfly nymphs of the genus *Siphonurus*, an unusual feeding habit for mayflies. Most nymphal growth and development occurs in the floodplain, and final-instar nymphs are present in late May and early June.

The importance of lateral interactions involving movements of organisms and exchanges of nutrients and organic matter is well documented in rivers with bordering floodplains and annual seasonal flooding patterns (see reviews by Ward 1989 and Gladden and Smock 1990). More is known of lateral migrations during periods of flooding and importance of the floodplain habitat for fishes (e.g., Larimore et al. 1973, Guillory 1979, Welcomme 1979, Ross and Baker 1983, Kwak 1988) than for invertebrates. Invertebrate production and distribution (Gladden and Smock 1990) and movements between the channel and the floodplain by drift and crawling (Smock 1994) are documented for hardwood forest floodplains of headwater streams in the southeastern United States. These floodplains may be inundated for up to 9 mo. In Sweden, nymphs of the mayflies *Parameletus* spp. move into the temporary floodplain of a stream following snowmelt. Here they are preyed upon

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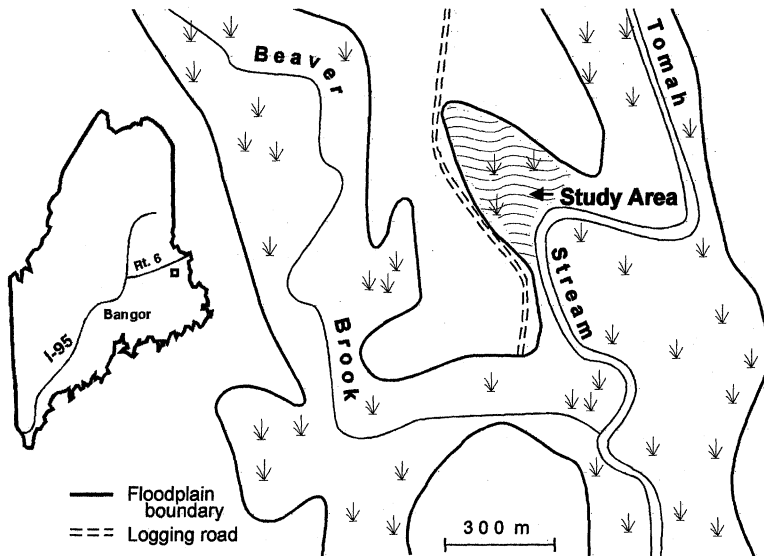


FIG. 1. Map of the study area at Tomah Stream, Maine, USA.

less (Soderstrom and Nilsson 1987), grow more rapidly, and emerge earlier (Olsson and Soderstrom 1978) than nymphs that remain in the river where temperatures are lower and food is less abundant.

Elevated temperatures of shallow water in the floodplain, abundance of food, and shelter and emergence sites provided by the flooded vegetation may result in an advantageous habitat for some invertebrates. However, the transient nature of this floodplain habitat requires that aquatic immatures complete their development and emerge before the water disappears. Animals inhabiting the floodplain must have life histories that accommodate the considerable annual variation in the time standing water remains here. Temperatures of shallow water in the floodplain are greatly influenced by air temperatures, and daily maximum air temperatures are a good indicator of temperatures in exposed shallow water (Ward 1992). High air temperatures can also affect the persistence of standing water in the floodplain by increasing evaporation. We were interested in the timing and synchronization of nymphal development and emergence of subimagos of *S. aerodromia* under floodplain conditions, and in how these life history attributes are affected by annual variations in air temperature and time standing water remained in the floodplain.

Gibbs and Mingo (1986) reported that late-

instar nymphs of *S. aerodromia* in the floodplain showed a female-biased sex ratio of 1M:1.8F. We wished to determine if the female-biased sex ratio of the late instar nymphs is a consistent feature of the life history of the species, and if there is a female bias in emerging subimagos. Although biased sex ratios are sometimes reported for aquatic insects, including mayflies (see reviews by Brittain 1982, Butler 1984), their purpose is not generally understood, nor how they are achieved and how they vary among life-cycle stages.

In addition to late nymphal developmental and emergence patterns, we report duration of the subimaginal stage, longevity of adults, mating and oviposition behavior of adults, and embryonic development of eggs from unmated females of *S. aerodromia*. These results will contribute to our understanding of how life history attributes affect the species' ability to use the stream and its associated floodplain at different times of the year.

### Study Area

Tomah Stream is a 4th-order tributary of the St. Croix River in Washington County, Maine (Fig. 1). Along a 10-km reach of the stream south of Route 6, low elevation areas form a floodplain dominated by sedges, especially the tussock sedge *Carex stricta* Land. Along some

reaches of the stream, substantial areas of this floodplain extend from both banks, while in others, the floodplain exists only in small isolated pockets. During much of the year (June–March), the stream is confined to its channel. Between December and March the stream is usually covered by ice and snow. During late March or early April, the ice melts, and runoff from the melting snowpack rapidly covers the adjacent floodplain. During April and May the inundated area gradually decreases, and the stream is usually confined to its channel by early June. In some years, heavy rains can cause the floodplain to be temporarily inundated at other times of the year.

The study site was 1.6 km south of Route 6 (45°26'42"N, and 67°34'50"W) (Fig. 1), north of the confluence of Tomah Stream and Beaver Creek. Here, the stream has a straight-walled channel and a sand-and-gravel substrate with submerged *Cardamine pennsylvanica* Muhl. (bitter cress). The study site floodplain was associated with the west bank of the stream and covered an area of about 7.6 ha.

Macroinvertebrates, especially mayflies (*Siphonurus* spp. and *Leptophlebia* spp.), are abundant in the inundated floodplain (Gibbs and Mingo 1986). In April, when substantial areas of the floodplain are inundated and the water is deep (>1 m), the fish species *Salvelinus fontinalis* (Mitchill) (brook trout), *Notropis cornutus* (Mitchill) (common shiner), *Gasterosteus aculeatus* Linnaeus (three-spine stickleback), *Esox niger* Lesueur (chain pickerel), and *Catostomus commersoni* (Lacépède) (common white sucker) are also present (Gibbs and Mingo 1986). In May, as water levels drop, fish disappear from the floodplain.

## Methods

### Nymphs

To determine sex ratios of nymphs and time of molt to the final instar, nymphs were sampled in the floodplain at about weekly intervals from the last week of April until the end of May in 1991 and 1992. Samples, consisting of 1-m sweeps through the submerged vegetation with a 30-cm-wide D-frame aquatic net (752- $\mu$ m aperture), were taken in water 0.2–0.4 m deep. Initially, 31 sweeps were taken on each sampling date at 2-m intervals along a transect at a right

angle to the stream. However, as water receded from the floodplain during late May, only 9–12 sweeps were taken on each sampling date (wherever water was deep enough) (Table 1). Samples were preserved in 95% ethyl alcohol in the field, and invertebrates were later separated from the debris and preserved in 70% ethyl alcohol. *Siphonisca aerodromia* nymphs were sexed on the basis of the presence of developing forceps on the 9th abdominal sternum of the males. Development is sufficiently advanced by late April to allow male nymphs to be distinguished from female nymphs. Nymphs in the final instar were identified by size of the wing pads.

### Subimagos

To determine seasonal and diel emergence patterns, subimagos emerging in 1991 and 1992 in the floodplain were collected with 12 floating traps. Traps were 44 cm high, covered an area 50  $\times$  50 cm, and consisted of aluminum window framing covered with plastic netting on the sides and plexiglass on top. Floats were strips of styrofoam 12 cm wide and 10 cm deep attached to the trap base. Traps were set out as soon as final instar nymphs were found in benthic samples and taken in when emergence had ceased and no nymphs could be found. Traps were initially arranged along a transect at a right angle to the stream but eventually were placed wherever pools of water remained. We moved traps frequently as water levels changed. By the time emergence had begun, only a small amount of water remained in the floodplain and we believe that a large portion of the emerging population was captured in the traps. Nymphs crawled up the sides of the traps before molting to subimagos. Exuviae of emerged subimagos on the inside and outside of the traps were counted and sexed. Subimagos inside the traps were released, except for individuals retained for further study (about 4% of the emergence associated with the traps in 1991). Depth of water below the exuviae and the distance of the exuviae above the water surface were recorded in 1991. Although traps were not set out in 1993, we regularly visited the study area and monitored emergence by checking the vegetation for subimagos and exuviae.

We used subimagos emerging on 28 and 29 May 1991 to determine duration of the sub-

maginal stage. Individual subimagos were retained in screen-topped cardboard ice-cream containers supplied with damp paper toweling. Containers were kept in the shade at the study area and checked morning and evening, and date of molt to the imago was recorded.

### *Imagos*

To determine longevity of imagos, imagos from the subimago study were retained under the same conditions and procedures as the subimagos, and longevity of the imaginal stage was determined. Imago flight, mating, and oviposition activity were monitored in the study area from early morning until dark, 26 May–1 June 1991, and from 1700 h until dark on 5, 7, 8, and 11 June 1992.

### *Influence of environmental factors on nymphs and subimagos*

We determined ranges of water temperature over which seasonal and diel emergence occurred in 1991 and 1992. Daily minimum and maximum water temperatures were recorded in late May and early June; water temperature was measured every 2 h from 0700 to 1900 during the seasonal emergence period.

We examined the relationship between date of molt to the final instar nymph, dates of first emergence, and peak emergence, and spring weather trends. We obtained records of minimum and maximum air temperatures and precipitation for May 1991, 1992, and 1993 from the Moosehorn National Wildlife Refuge at Calais, Maine, which is 42 km from our study area. To allow us to determine if early seasonal emergence was associated with years with periods of high temperature during May, we calculated mean minimum and mean maximum temperatures and accumulated degree days  $>0^{\circ}\text{C}$  and  $>20^{\circ}\text{C}$  for May 1991, 1992, and 1993 (Table 2). Also, the study area was photographed weekly during May and early June 1991, 1992 and 1993 to record the extent of inundation of the floodplain.

### *Development of unfertilized eggs*

To determine when eggs hatched in the field and the percent embryonic development in eggs from unmated females, we took unfertilized

eggs from six 24-h-old imagos reared from subimagos captured as they emerged in 1993. Eggs were dissected from the imagos and placed in 11.5-cm diameter culture dishes where they adhered to screening (153- $\mu\text{m}$  aperture silk bolting in cloth) which had replaced the bottom of the dish. The screening with the attached eggs was enclosed in a small sack of the fine screening and then in a coarse-mesh sack weighted with a stone and placed (10 and 11 June) on the substrate in the channel of Tomah Stream. The sacks were retrieved on 7 November, before the possibility of ice cover made their retrieval uncertain. Eggs were then held in the laboratory under static conditions at  $4\text{--}5^{\circ}\text{C}$ , the temperature of water in the stream channel during November and early December (Gibbs and Mingo 1986). Eggs were checked daily and hatches recorded. Final counts of eggs with and without developed embryos were made on 2 January 1994. Newly hatched nymphs were retained, under the same conditions as the eggs, and were checked daily for survival and evidence of molting. The only food available to the nymphs was the detritus, algae, and small organisms from the stream, which were attached to the egg sacs.

### *Data analysis*

Chi-square Goodness-of-fit tested departure from an expected 1:1 sex ratio in nymphs and emerging subimagos. Two-way ANOVA was used to determine if percent of male and female nymphs in the final instar differed and whether the timing of molt to final instar differed between the sexes. Kolmogorov-Smirnov 2-sample test was used to determine if duration of the subimaginal stage and longevity of males and females were different.

## Results

### *Nymphs*

Mean abundance of *S. aerodromia* nymphs in the floodplain generally increased during the sampling period in both 1991 and 1992 (Table 1), reflecting a concentration of nymphs as the water retreated from the floodplain. It is difficult to compare density of nymphs either between sampling periods or between years as even small changes in water level due to rainfall, absorption, or evaporation affected the area in-

TABLE 1. Mean ( $\pm 1$  SE) number of nymphs per sample and percent in final instar (FI) in 1991 and 1992 samples.

Date	No. of sweeps	Female		Male		Total female + male	
		No. of nymphs	% FI	No. of nymphs	% FI	No. of nymphs	% FI
1991							
25 Apr*	31	2.2 (0.4)	—	1.5 (0.3)	—	3.7 (0.6)	—
3 May*	31	6.2 (1.0)	—	4.8 (0.6)	—	10.9 (1.5)	—
11 May*	31	12.5 (1.3)	—	7.6 (1.0)	—	20.2 (2.2)	—
16 May*	12	18.3 (3.9)	5.5	13.3 (2.2)	13.8	31.5 (6.0)	9.0
22 May	9	8.0 (1.4)	66.7	7.4 (1.3)	79.1	15.4 (2.6)	72.7
1992							
24 Apr*	31	2.5 (0.5)	—	1.0 (0.3)	—	3.5 (0.7)	—
1 May*	31	2.5 (0.4)	—	0.7 (0.2)	—	3.2 (0.5)	—
7 May	31	2.4 (0.4)	—	1.9 (0.4)	—	4.3 (0.8)	—
15 May*	31	3.0 (0.5)	—	1.0 (0.2)	—	4.0 (0.6)	—
21 May*	12	6.6 (3.3)	32.9	3.5 (2.2)	30.9	10.0 (5.4)	32.3

\* Dates on which male:female ratios of nymphs were significantly different from 1:1 (Chi-square Goodness-of-fit;  $p < 0.025$  in 1991 and  $p < 0.001$  in 1992).

undated and the density of nymphs. Decrease in mean abundance between 16 and 22 May 1991 may have been due to 1.3 cm of rain recorded in the area between sampling dates, which extended the area inundated.

Significantly more female than male nymphs were collected in 1991 and 1992 on all dates except one (Table 1). Also, when data were totaled for the 5 sampling dates, significantly more female than male nymphs were collected ( $p < 0.001$ ) in both years. The sex ratio (M:F) for all nymphs collected in 1991 was 1 M:1.4 F and in 1992 1 M:2.1 F.

Final-instar nymphs were first noted in the samples earlier in 1991 (16 May) than in 1992 (21 May) (Table 1). Also in 1991, male nymphs molted to the final instar before females on both 16 and 22 May, as the proportion of males in the final instar was significantly higher than that of females ( $p < 0.007$ ) (Table 1). In 1992, there was no significant difference in the proportion of male and female nymphs in the final instar on 21 May (Table 1).

We determined time in the final instar from the date on which a known percentage of nymphs reached the final instar (Table 1) to the date on which the same percentage of subimagos had emerged (Fig. 2). In 1991, subimagos emerging early in the seasonal emergence period were in the final nymphal instar for 12 d (16–28 May), whereas those emerging later were in the final instar for 7 d (22–29 May). In 1992,

nymphs were in the final instar for 9 d (21–30 May).

#### *Subimago emergence*

Subimagos emerged in 1991 from 25 May to 2 June, peaking on 28 and 29 May, when 58% of subimagos emerged, and in 1992 from 26 May to 4 June, peaking on 30 and 31 May, when 52.7% of subimagos emerged (Fig. 2). In 1993, emergence began on 31 May, peaked between 5 and 7 June, and ended on 11 June. In 1991, 1992, and 1993, high air temperatures during May, as measured by mean maximum temperature and accumulated maximum degree-days  $>20^{\circ}\text{C}$  (Table 2) were more closely related to date of first emergence and peak of emergence than were accumulated mean degree-days  $>0^{\circ}\text{C}$  or mean minimum temperature. Also, in both 1991 and 1992, standing water had disappeared from the floodplain by the time subimagos had finished emerging. In 1993, however, a substantial area of the floodplain was still covered by standing water in mid June.

Emergence occurred at all times of the day from 0700 to 1900 h (Fig. 3). When daily emergence was totaled, peaks in emergence (35%) occurred from 1300 to 1500 h in 1991, and from 0900 to 1100 h (32.4%) in 1992. Diel emergence occurred when water temperatures were  $>12^{\circ}\text{C}$  in 1991 and  $>11^{\circ}\text{C}$  in 1992.

In 1991, mayflies emerged from water 0.5–

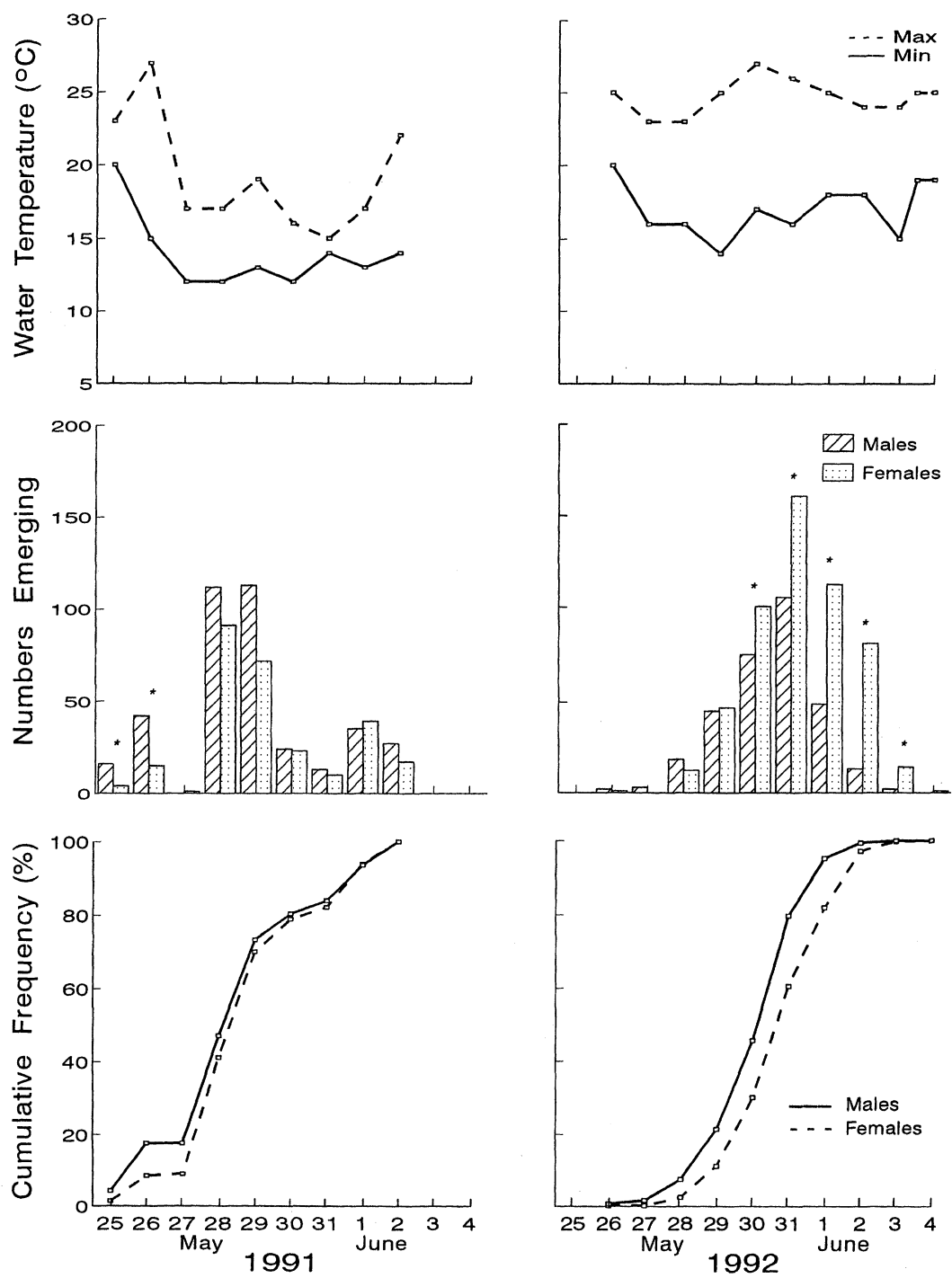


FIG. 2. Cumulative and total daily emergence of male and female *S. aerodromia* subimagos, and daily minimum and maximum water temperatures in the study area in 1991 and 1992. \* indicates a departure from a 1:1 sex ratio (Chi-square Goodness-of-fit: in 1991,  $p < 0.041$  on 25 May and  $p < 0.001$  on 26 May; in 1992,  $p < 0.05$  on 30 May,  $p < 0.001$  on 31 May and 1-2 June, and  $p = 0.001$  on 3 June).

TABLE 2. Summary of air temperature and precipitation data for May 1991, 1992, and 1993 from Moosehorn National Wildlife Refuge, Calais, Maine. Temperature (T) is recorded as accumulated degree-days of mean temperature  $> 0^{\circ}\text{C}$  and maximum temperature  $> 20^{\circ}\text{C}$ , and as mean maximum and mean minimum temperature. Precipitation is recorded as total precipitation (cm) and the number of days on which rain fell.

	1991	1992	1993
Accumulated $^{\circ}\text{C}$ days			
mean $> 0^{\circ}$	384.4	317.1	317.8
max. $> 20^{\circ}$	81.0	61.5	10.5
Mean max. T ( $^{\circ}\text{C}$ )	20.2	18.1	16.9
Mean min. T ( $^{\circ}\text{C}$ )	4.6	2.4	3.7
Precipitation (cm)	6.6	4.1	6.2
Days on which rain fell	5	4	14

44.5 cm deep, with most frequent emergence (23.3%) from water 26–28 cm deep. By the third week of May, 1991, the area of the floodplain covered with water had shrunk to only a little more than was covered by the traps. Thus, range of depths from which the mayflies emerged approximated the range of water depths occurring in the floodplain at that time. Exuviae were found 0.5–26 cm above the water surface with most (99.0%)  $< 6$  cm above the water.

Sex ratios of emerging subimagos were not consistent between study years. In 1991, signif-

icantly more male subimagos emerged than females on 25 and 26 May (Fig. 2); on other emergence dates, numbers of male and female subimagos emerging did not differ significantly. Also, significantly more males than females (1M:0.7F;  $p < 0.001$ ) emerged in 1991 when subimagos were totaled for all dates. In 1992, significantly more female subimagos emerged from 30 May to 3 June (Fig. 2); on other emergence dates, numbers of males and females emerging did not differ significantly. Also, significantly more females than males emerged (1M:1.7F;  $p < 0.001$ ) in 1992 when subimagos were totaled for all dates.

Both male and female subimagos emerged on most days during the seasonal emergence period (Fig. 2) and at most times throughout the diel emergence period (Fig. 3). When cumulative percentages of male and female subimagos emerging were compared, a higher percentage of males than females emerged at the beginning of the seasonal emergence period in both 1991 and 1992 (Fig. 2) but there was no tendency for either sex to emerge at a particular time of day.

Mean ( $\pm 1$  SE) length of the subimaginal stage of females was  $3.2 \pm 0.09$  d (range 3–4 d;  $n = 18$ ) and of males was  $3.3 \pm 0.1$  d (range 3–4;  $n = 25$ ). Length of the subimaginal stages of females and males did not differ significantly.

#### Imagos

Mean ( $\pm 1$  SE) longevity of female imagos was  $4.2 \pm 0.7$  d (range 1.5–8.5 d;  $n = 13$ ) and of male

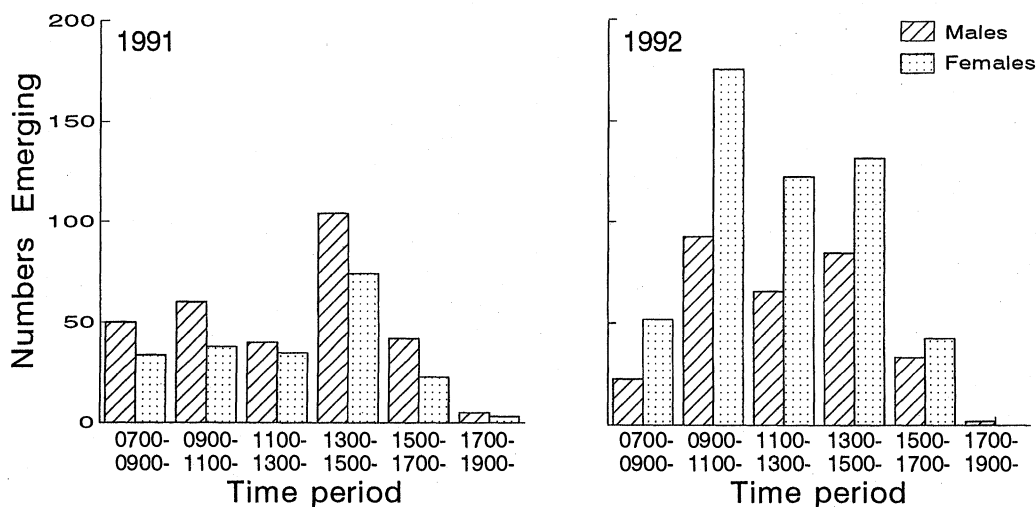


FIG. 3. Diel periodicity of pooled emergence of *S. aerodromia* subimagos in 1991 and 1992.

imagos was ( $3.5 \pm 0.4$  d) (range 1–8.5 d;  $n = 23$ ). Longevity of female and male imagos was not significantly different.

Flying adults were observed only on 7, 8, and 11 June 1992. All sightings were from 1815 to 1920 h. Male swarms were seen on 7 and 11 June; swarms were small, 6 males on 7 June, and several swarms of 3–10 males on 11 June. These swarms patrolled up and down a 15–23-m reach of the stream 3–4.5 m above the water surface.

On 11 June, mating pairs were seen from 1825 to 1920 h, after which it was too dark to continue observations. Air temperature ranged from 24 to 14°C during this time. Females flying upstream were intercepted and seized by males, and mating pairs left the swarm. One pair flew upstream 12–15 m, then away from the stream 15–20 m, then back to the stream. They completed this circuit at least 4 times, about 6 m above the water or land.

Oviposition was observed on 7 and 11 June. Ovipositing females repeatedly landed briefly on the water in the stream channel (there was no standing water in the floodplain at this time) and then resumed flight. The stream in this area was 6.9 m wide, 0.75 m deep, and had a velocity of 0.1 m/s.

No predation of flying *S. aerodromia* was observed. Predation of ovipositing females by fish was intense, however, and many were eaten as soon as they touched the water surface. Mating and oviposition of the mayfly *Siphonurus mirus* Eaton occurred at the same time as that of *S. aerodromia*.

#### *Development of unfertilized eggs*

The mean ( $\pm 1$  SE) number of eggs extracted from unmated females for incubation in the stream was  $496.7 \pm 33.6$  (range 360–559;  $n = 6$ ). Hatching of eggs in the laboratory was recorded from 10 November 1993 to 5 January 1994. The presence of a few empty chorions indicated that some eggs from all females may have hatched before eggs were retrieved from the stream (7 November). Hatching success was  $54.8 \pm 8.1\%$  (range 34.9–85.6%) and egg development (hatching success + embryonated eggs that did not hatch) was  $62.9 \pm 9.2\%$  (range 46.9–92.1%). Nymphs lived up to 50 d in the laboratory and some molted to the third instar.

## Discussion

### *Parthenogenesis and female biased sex ratios*

Thelytokous parthenogenesis, in which eggs deposited by unmated females develop into females, is known or suspected from several species of mayflies (see review by Brittain 1982). Facultative parthenogenesis is occasionally suggested when populations of known bisexual species are found with sex ratios favoring females (McCafferty and Huff 1974, Bergman and Hilsenhoff 1978) but is thought unlikely to be important in population dynamics because of the low level of hatching success reported for unfertilized eggs (Butler 1984). In only one case (Degrange 1960) have these larvae been reared to maturity. However, the high percent (up to 92%) of unfertilized eggs in *S. aerodromia* that embryonated or hatched suggests that parthenogenesis may be an important life history attribute of this species. Long adult life and evidence that mating and oviposition may not occur until at least 10 d after emergence suggest that some females may not locate mates, especially if periods of unfavorable weather occur. Reproduction by these individuals would result in a female bias in nymphs of the next generation. Regional or annual variation in proportion of the population reproducing parthenogenically would result in differing sex ratios in nymphs of the following year.

The reduction in the number of females in the population between nymphal and subimaginal stages was a consistent feature of the life history of *S. aerodromia*. It suggests a mechanism that favors survival of males over females. Different sex ratios of mayfly nymphs and subimagos occurred when female nymphs of one cohort of *Ephemera danica* Mull. showed a better ability than male nymphs to survive a sudden freeze (Svensson 1977); although males made up 60–65% of the nymphal population, males were only 45% of the total emergence. We do not know why male survival is favored in *S. aerodromia* nymphs.

### *Emergence of subimagos*

Seasonal emergence of *S. aerodromia* in 1991 and 1992 was short (9–10 d) and highly synchronous (with over 50% of individuals emerging within 2 d). Synchrony of emergence was



increased by nymphs spending less time in the final instar as the beginning of the seasonal emergence period approached. Emergence was more synchronized than early nymphal development (Gibbs and Mingo 1986) or egg hatching.

Timing of seasonal emergence is of particular importance to *S. aerodromia*; it must allow for maturation of nymphs during the inundated phase of the floodplain but ensure that emergence of subimagos is completed before the dry phase begins. Timing of emergence in 1991, 1992 and 1993 was related to maximum air temperatures in May. Early seasonal emergence was also associated with early disappearance of standing water from the floodplain. Although precipitation was not greater in 1993 than in 1991 or 1992 (Table 2), reduced evapotranspiration, associated with lower maximum temperatures and overcast skies (as indicated by the high number of days of rain in 1993) delayed the disappearance of water from the floodplain. The relationship between faster nymphal development, earlier emergence, and higher maximum air temperatures allows early emergence from the floodplain in years when the floodplain dries early and any delay in emergence would result in mortality of nymphs. In years when water remains longer in the floodplain, nymphal development may be slower and emergence later due to lower water temperatures and, possibly, reduced availability of prey due to increased dispersion.

Seasonal emergence dates in Maine are consistent with those reported at Sport Island on the Sacandaga River in New York (26 May 1914) (Clemens 1915) and in Nominique, Quebec (3 June 1941) (Hutchinson 1989), but not at Lake Melville, Labrador, where an adult was collected on 10 July 1952 (Fiance 1978), indicating later emergence at more northern latitudes. The daytime diel emergence pattern of *S. aerodromia* is characteristic of mayflies in northern latitudes where water and air temperatures fluctuate widely, and are higher during the day than at night (see review by Brittain 1982).

The tendency of *S. aerodromia* males to emerge earlier in the seasonal emergence period (protandry) than females, has been reported for other mayflies (Harper and Magnin 1971, Clifford et al. 1979, Takemon 1990). The 1991 evidence that male nymphs molted to the final instar in advance of female nymphs suggests how this

could be achieved. Why more rapid development of males occurs is not understood, unless thermal growth and developmental requirements (Sweeney and Vannote 1981) are different for male than female nymphs. Takemon (1990) reported a lower thermal development threshold and degree-day constant for male than female nymphs of *Ephemera strigata* Eaton. Protandry in the diel emergence period occurs in the mayflies *Dolania americana* Edmunds and Traver (Peters et al. 1987) and *Ephoron shigae* Takashi (Watanabe et al. 1989), but we did not observe diel protandry in *S. aerodromia*. If protandry serves to maximize male fitness (Butler 1984), diel protandry may occur only in species such as *D. americana* and *E. shigae* which mate almost immediately after emergence, and seasonal protandry in species such as *S. aerodromia* where mating is delayed until several days after emergence.

We did not observe daytime predation on emerging or flying subimagos, although mayflies are thought to be more susceptible to predation during daylight hours, and avoidance of predation may be the explanation for crepuscular and nighttime emergence of many species (Edmunds and Edmunds 1980). Intense fish predation on ovipositing female imagos in the stream channel showed that fish were abundant in the stream. Fish were also present in the floodplain in April, but they were not present in May as water in the floodplain became shallower. Thus, fish predation on later stage nymphs or emerging subimagos was avoided by movement into the floodplain. The only other predators of mayflies in the floodplain were dytiscid larvae, which were not abundant.

#### *Habitat requirements of S. aerodromia*

The life history of *S. aerodromia* allows this mayfly springtime use of the inundated floodplain, where most nymphal growth and development takes place. We suggest that the main advantages of this spring migration from the stream to the floodplain are higher water temperatures in the floodplain, abundance of prey mayfly nymphs, availability of sedge as shelter for nymphs and emergence sites for subimagos, and reduced fish predation of later stage nymphs and emerging subimagos. The main disadvantage is the temporary nature of the habitat and the possibility of nymphal mortality

in years when the floodplain dries quickly. If, as our data suggest, maximum air temperatures are related to rate of nymphal development, date of emergence of subimagos, and disappearance of water from the floodplain, then early emergence of subimagos may at least partially compensate for early drying of the floodplain.

This annual cycle of movement between the stream and the floodplain is dependent on predictable seasonal flooding of bordering floodplains following snowmelt. The alteration of this flow pattern in many of our rivers, especially by dam construction, is probably responsible for the rarity of this species.

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### Literature Cited

- BERGMAN, E. A., AND W. L. HILSENHOFF. 1978. Parthenogenesis in the mayfly genus *Baetis* (Ephemeroptera:Baetidae). *Annals of the Entomological Society of America* 71:167-168.
- BRITTAIN, J. E. 1982. The biology of mayflies. *Annual Review of Entomology* 27:119-147.
- BURIAN, S. K., AND K. E. GIBBS. 1991. Mayflies of Maine: an annotated faunal list. Maine Agricultural Experiment Station Technical Bulletin 142.
- BUTLER, M. G. 1984. Life histories of aquatic insects. Pages 24-55 in V. H. Resh and D. M. Rosenberg (editors). *The ecology of aquatic insects*. Praeger Publishers, New York.
- CLEMENS, W. A. 1915. Mayflies of the *Siphonurus* group. *Canadian Entomologist* 47:245-260.
- CLIFFORD, H. F., H. HAMILTON, AND B. A. KILLINS. 1979. Biology of the mayfly *Leptophlebia cupida* (Say) (Ephemeroptera:Leptophlebiidae). *Canadian Journal of Zoology* 57:1026-1045.
- DEGRANGE, C. 1960. Recherches sur la reproduction des Ephéméroptères. *Travaux Labatoire d'Hydrobiologie et de Pisciculture Université de Grenoble* 51:7-193.
- EDMUNDS, G. F., AND C. H. EDMUNDS. 1980. Predation, climate, and emergence and mating of mayflies. Pages 277-285 in J. F. Flannagan and K. E. Marshall (editors). *Advances in Ephemeroptera biology*. Plenum Press, New York.
- EDMUNDS, G. F., S. L. JENSEN, AND L. BERNER. 1976. *The mayflies of North and Central America*. University of Minnesota Press, Minneapolis.
- FIANCE, S. B. 1978. A new locality for *Siphonisca aerodromia* (Ephemeroptera:Siphonuridae). *Entomological News* 89:208.
- GIBBS, K. E., AND T. M. MINGO. 1986. The life history, nymphal growth rates and feeding habits of *Siphonisca aerodromia* Needham (Ephemeroptera:Siphonuridae) in Maine. *Canadian Journal of Zoology* 64:427-430.
- GLADDEN, J. E., AND L. A. SMOCK. 1990. Macroinvertebrate distribution and production on the floodplains of two lowland headwater streams. *Freshwater Biology* 24:533-545.
- GUILLORY, V. 1979. Utilization of an inundated floodplain by Mississippi River fishes. *Florida Scientist* 41:222-228.
- HARPER, F., AND E. MAGNIN. 1971. Emergence saisonnière de quelques éphéméroptères d'un ruisseau des Laurentides. *Canadian Journal of Zoology* 49:1209-1221.
- HUTCHINSON, R. 1989. Première mention de *Siphonisca aerodromia* Needham (Ephemeroptera:Siphonuridae) au Québec et répartition en Amérique du Nord. *Faberies* 14:25-27.
- KWAK, T. J. 1988. Lateral movement and use of floodplain habitat by fishes of the Kankakee River, Illinois. *American Midland Naturalist* 120:241-249.
- LARIMORE, R. W., E. C. DOYLE, AND A. R. BRIGHAM. 1973. Ecology of floodplain pools in the Kaskaskia River Basin of Illinois—an assessment of their value. University of Illinois Water Resources Center Research Report Number 754.
- MAGNIN, E., AND P. P. HARPER. 1970. La nourriture des esturgeons *Acipenser fulvescens* de la rivière Nottaway, tributaire de la Baie James. *Naturaliste Canadien* 97:73-85.
- MCCAFFERTY, W. P., AND B. L. HUFF. 1974. Parthenogenesis in the mayfly *Stenonema femoratum* (Say) (Ephemeroptera:Heptageniidae). *Entomological News* 85:76-80.
- OLSSON, T., AND O. SÖDERSTRÖM. 1978. Springtime migration and growth of *Parameletus chelifer* (Ephemeroptera) in a temporary stream in northern Sweden. *Oikos* 31:284-289.
- PETERS, J. G., W. L. PETERS, AND T. J. FINK. 1987. Seasonal synchronization of emergence in *Dolania americana* (Ephemeroptera:Behningiidae). *Canadian Journal of Zoology* 65:3177-3185.

- ROSS, S. T., AND J. A. BAKER. 1983. The response of fishes to periodic floods in a southeastern stream. *American Midland Naturalist* 109:1–14.
- SMOCK, L. A. 1994. Movements of invertebrates between stream channels and forested floodplains. *Journal of the North American Benthological Society* 13:524–531.
- SÖDERSTRÖM, O., AND A. N. NILSSON. 1987. Do nymphs of *Parameletus chelifer* and *P. minor* (Ephemeroptera) reduce mortality from predation by occupying temporary habitats? *Oecologia* 74: 39–46.
- SVENSSON, B. S. 1977. Life cycle, energy fluctuations, and sexual differentiation in *Ephemera danica* (Ephemeroptera), a stream-living mayfly. *Oikos* 29:78–86.
- SWEENEY, B. W., AND R. L. VANNOTE. 1981. *Ephemerella* mayflies of White Clay Creek: bioenergetic and ecological relationships among six coexisting species. *Ecology* 62:1353–1369.
- TAKEMON, Y. 1990. Timing and synchronicity of the emergence of *Ephemera strigata*. Pages 61–70 in I. C. Campbell (editor). *Mayflies and stoneflies: life histories and biology*. Kluwer Academic Publishers, Dordrecht.
- US DEPARTMENT OF THE INTERIOR, FISH AND WILDLIFE SERVICE. 1991. Endangered and threatened wildlife and plants; animal candidates. Review for listing as endangered or threatened species. *Federal Register* 56(225), November 21.
- WARD, J. V. 1989. The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society* 8:2–8.
- WARD, J. V. 1992. *Aquatic insect ecology: 1. Biology and habitat*. John Wiley and Sons, Inc., New York.
- WATANABE, N. C., I. YOSHITAKA, AND I. MORI. 1989. Timing of emergence of males and females of *Ephoron shigae* (Ephemeroptera:Polymitarcyidae). *Freshwater Biology* 21:473–476.
- WELCOMME, R. L. 1979. *Fisheries ecology of floodplain rivers*. Longman, New York.

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