The life history, nymphal growth rates, and feeding habits of *Siphlonisca aerodromia* Needham (Ephemeroptera: Siphlonuridae) in Maine[1]

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Siphlonisca aerodromia Needham has a univoltine life history in Maine. Adults emerge in late May or early June. Each female contains about 394 large (0.46 mm long) eggs covered with coiled fibers that anchor the eggs to the substrate. Eggs are deposited in the main channel of the stream and small nymphs appear in January. Nymphal growth rate (G_{HW}) was expressed as a percent per day increase in head width. Initially nymphs feed on detritus and grow slowly (G_{HW} = 0.28–0.79) at water temperatures near 0°C. Following snow melt, the nymphs move into the adjacent *Carex* floodplain. Here, water temperature increases, animal material, in the form of mayfly nymphs, becomes increasingly common in the diet, and growth rate increases (G_{HW} = 2.13–2.89). The sex ratio of nymphs collected in May and June was 1:1.8 (male:female).

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Dans le Maine, le cycle de *Siphlonisca aerodromia* Needham est univoltin. L'émergence des adultes se produit à la fin de mai ou au début de juin. Chaque femelle contient environ 394 gros oeufs (0,46 mm de longueur) recouverts de fibres spiralées qui en assurent la fixation au substrat. Les oeufs sont pondus dans la partie centrale du ruisseau et les petites larves apparaissent en janvier. Le taux de croissance larvaire (G_{HW}) est exprimé ici en termes d'augmentation pourcent par jour de la largeur de la capsule céphalique. Les larves se nourrissent d'abord de détritus et croissent lentement (G_{HW} = 0,28–0,79) à une température voisine de 0°C. Après la fonte des neiges, les larves migrent vers la plaine alluviale à *Carex* voisine. À cet endroit, la température de l'eau augmente et les matières d'origine animale, surtout des larves d'éphéméroptères, deviennent de plus en plus communes dans le régime alimentaire et le taux de croissance augmente (G_{HW} = 2,13–2,89). Le rapport mâles:femelles a été évalué à 1:1,8 chez les larves récoltées en mai et en juin.

[Traduit par le journal]

Introduction

Siphlonisca aerodromia Needham (Ephemeroptera: Siphlonuridae) is a rare mayfly (Edmunds et al. 1976; Fiance 1978), which was recently collected from several locations in Maine (Gibbs 1980). Little was reported about its life history and biology. In this paper we describe the life history, seasonal distribution, and nymphal feeding habits of the *S. aerodromia* in Maine during 1979 and 1980.

Study area

The study site was located 1.6 km south of Route 6 at Tomah Stream, a fourth-order stream in Washington County, Maine. Here, the stream has a straight-walled channel and a sand and gravel substrate. It is bordered by a broad floodplain consisting of meadows of *Carex vesicularia* L. and *Carex equatalis* Wahl.

During much of the year (June–March) the water level is usually low and the stream remains within its channel. Between December and March the stream is usually covered with ice and may be snow covered. During late March or early April, the spring thaw and subsequent run-off from the melting snowpack rapidly floods the adjacent *Carex* meadows. Maximum flooding occurs in April. In May, the water recedes from the floodplain and returns to the stream channel by late May or early June.

The only information available on water temperature in Tomah Stream was obtained by the authors on sampling dates. To present a more complete description of seasonal changes in Tomah Stream temperature, data from the nearby Narraguagus River United States Geological Survey recording station at Cherryfield, Maine were used (Anonymous 1979; Anonymous 1980). The Narraguagus River maximal and minimal temperatures were recorded daily. These data were used because water temperatures differed by only 0.5–1°C on those days when temperatures from both streams were available for comparison.

The stream supports a variety of macroinvertebrates and fishes. During April and May, large numbers of macroinvertebrates are found on the inundated floodplain among the clumps of living and dead sedge. Numerically, Ephemeroptera are the dominant macroinvertebrates with *S. aerodromia*, *Siphloplecton basale* (Walker), *Siphlonurus mirus* Eaton, *Siphlonurus alternatus* (Say), *Leptophlebia cupida* Say, *Leptophlebia nebulosa* (Walker), *Ephemerella temporalis* McDunnough, and *Ephemerella subvaria* McDunnough most abundant. Less abundant are *Arthroplea bipunctata* McDunnough, *Baetisca laurentina* McDunnough, *Leptophlebia johnsoni* McDunnough, and *Ephemerella septentrionalis* McDunnough. Other macroinvertebrates frequently occurring on the inundated floodplain are larval Chironomidae, Trichoptera (*Limnephilus*), Coleoptera (*Hydroporus* and *Halophorus*), Hemiptera (*Sigara*), and Amphipoda (*Hyalella azteca* (Saussure)). During this time, the fish species *Notropis cornutus* (Mitchill) (common shiner), *Gasterosteus aculeatus* Linnaeus (three-spine stickleback), *Esox niger* Lesueur (chain pickerel), and *Catostomus commersoni* (Lacepede) (common white sucker) are also numerous on the floodplain. These species, as well as *Salvelinus fontinalis* (Mitchill) (brook trout) from the stream channel, were known to feed heavily on macroinvertebrates on the floodplain, especially the Ephemeroptera (T. M. Mingo, unpublished observation).

Methods

The study area was sampled from April 1979 until June 1980 at monthly intervals between July and March and more frequently during April, May, and June. During each visit, the stream and, during April, May, and June, the inundated floodplain, were carefully sampled with an aquatic D-frame net (0.752-mm aperture). The macroinvertebrates collected were either preserved in the field in 80% ethyl alcohol or retained for laboratory observation and rearing. Specimens of *S. aerodromia* from these samples were used to determine nymphal growth, sex ratios, and feeding habits. Head width was measured to the nearest 0.01 mm using an ocular micrometer. The mean, standard deviation, and range of head widths were determined for each sampling date. Sex was determined for the larger nymphs. Nymphal growth rates, based on head capsule widths, were calculated by the method of

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Humpesch (1979) and Brittain (1983). Here, the relationship between mean head width (HW, millimetres) and time for each sampling interval within a constant growth period (t, days) was defined by the following regression equation:

$$\log_e HW_t = \log_e HW_0 + bt$$

where HW_0 is the mean head width at the start of the growth period, HW_t is the mean head width after t days, and the constant b is the relative growth in head width. Growth was then expressed as a growth rate, G_{HW} (percent per day), where $G_{HW} = 100b$.

Food habits were studied by examining the gut contents of three to five individuals on each sampling date during 1980. The gut was dissected from the nymph and placed in 80% ethyl alcohol, where it was opened and the contents dispersed. If there was extensive clumping of gut material the particles were dispersed by 10- to 15-s exposure in a sonicator. Millipore filter slides were prepared according to the technique of Cummins (1973). Each slide was examined using an 8×8 ocular grid. Five microscope fields were examined at the center of each slide, representing of a total of 5×64 grid squares on each slide. The presence of the following food categories in each grid square was recorded: detritus, animal fragments, algae, unknown. The entire slide was then scanned for animal structures that could be identified and associated with a specific organism. Although animal material was fragmented, tarsal claws and portions of caudal filaments and gills of mayfly nymphs remained sufficiently intact to be identified by comparison with organisms from the floodplain. The tarsal claws of mayflies were especially useful and the length of mayflies ingested was estimated from a regression of body length and tarsal claw length for identified prey species collected on the floodplain. Feeding behavior was also studied by observing large *S. aerodromia* nymphs in aquaria with assemblages of organisms with which they occurred in the floodplain.

Approximate adult emergence dates were estimated from the disappearance of nymphs from the floodplain. Fecundity was determined from 10 reared female subimagoes that were dissected and the eggs were counted. Length and width of 30 of these eggs were measured to the nearest 0.01 mm. Some of the eggs were placed in water to observe the egg dispersal and function of the attachment fibers.

Results

Water temperatures

The water temperatures in the Narraguagus River, which are assumed to closely approximate those in Tomah Stream, ranged between a winter low of 0°C and a summer high of 23–24°C (Fig. 1).

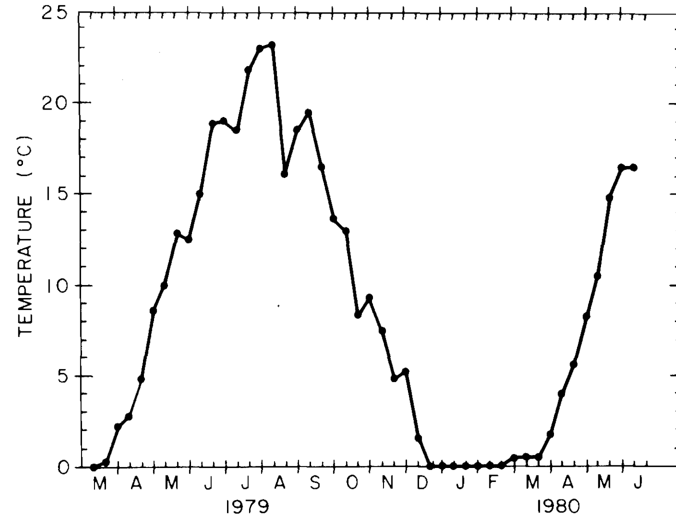

FIG. 1. Water temperatures of the Narraguagus River expressed as 10-day means.

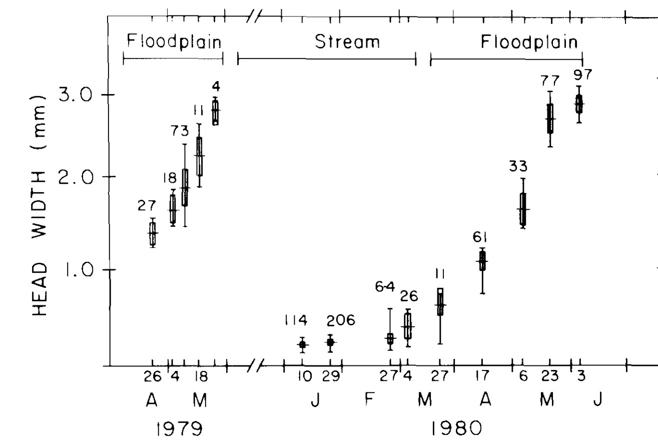

FIG. 2. Nymphal growth and seasonal distribution of *S. aerodromia*. The vertical line indicates the range, the horizontal line indicates the mean, and the box represents the standard deviation.

Nymphal development

The life cycle and seasonal distribution of *S. aerodromia* are described in Fig. 2. The species is univoltine with nymphal development occurring between January and June. From April 26 to May 24, 1979, nymphs inhabited the inundated floodplain. From January 10 to March 4, 1980, nymphs inhabited the stream channel. From March 27 until June 3, 1980, they again inhabited the inundated floodplain. Specimens collected from the stream channel on January 10 lacked gills and pigmentation and appeared to be first or near first instar nymphs. These small individuals were present in samples taken during the remainder of January, February, and March, suggesting that either hatching was prolonged over this 3-month period or that growth rates were very low. Two periods of constant exponential growth were identified for *S. aerodromia* (Table 1). During January and February 1980 nymphs grew slowly ($G_{HW} = 0.28–0.79$), but during the remainder of the nymphal stage, grew more rapidly (1979, $G_{HW} = 2.13–2.89$; 1980, $G_{HW} = 2.27–2.73$).

Feeding habits

Gut content analyses of *S. aerodromia* nymphs (Table 2) show that during early development the nymphs ingested fine detritus. Beginning in late March, however, animal material became increasingly common in the diet as indicated by both the number of individuals containing animal fragments and the mean percent of grid squares containing animal fragments. These fragments were pieces of insect cuticle, mouthparts, tarsal claws, and parts of gills and caudal filaments that were mainly from mayfly nymphs. The majority of the identifiable parts were from *Siphlonurus* nymphs, but parts from *Leptophlebia* and *Ephemerella* also occurred. The claw lengths indicated that the *Siphlonurus* nymphs in the gut were relatively small, between 3.5 and 7.5 mm in length. However, adequate numbers of *S. aerodromia* nymphs were not dissected or *Siphlonurus* claws measured to establish a relationship between the sizes of the *S. aerodromia* and the *Siphlonurus* nymphs. Chironomid larval parts were identified in two individuals. In all instances, the food material was fragmented and there was no indication that the prey were ingested whole. It was impossible to differentiate in the analyses of gut contents between material ingested directly and that ingested indirectly in association with the primary food material. The fine detrital material in the guts of the small *S. aerodromia* nymphs is presumed to have been ingested directly, but the small numbers of algal cells and the fine detrital material in the guts of the older nymphs may have

TABLE 1. Growth rates (G_{HW}, percent head width increase per day) of *S. aerodromia* during sampling periods that occurred in periods of constant exponential growth

Year and period	Days	Water temperature (°C) Mean	Water temperature (°C) Range	n^a	G_{HW}
1979, Apr. 26 to May 18					
Apr. 26				27	
	8	8.7	5.5–11		2.13
May 4				18	
	7	10.4	8–16		2.20
May 11				73	
	7	12.4	10.5–15		2.89
May 18				11	
1980, Jan. 10 to Feb. 27					
Jan. 10				114	
	19	0	—		0.79
Jan. 29				206	
	29	0.01	0–1		0.28
Feb. 27				64	
Mar. 4 to June 3					
Mar. 4				26	
	23	0.5	0.5–1		2.33
Mar. 27				11	
	21	3.9	0.5–6.5		2.27
Apr. 17				61	
	19	8.4	5.5–12.5		2.29
May 6				33	
	17	13.8	9–18		2.73
May 23				77	

[a]No. of nymphs measured.

been part of the gut content or otherwise associated with the ingested prey.

Observations on the feeding behavior of large *S. aerodromia* nymphs in aquaria with other invertebrates from the floodplain study area supported the evidence that they were feeding on mayfly nymphs. *Siphlonisca aerodromia* nymphs were agile and rapid swimmers and were observed to capture prey either by descending on the prey as it rested on the substrate or while it was swimming. Prey was held against the sternum by the mesothoracic legs. The prothoracic legs were used to manipulate the prey during feeding while the metathoracic legs were in contact with the substrate. Small nymphs of *Siphlonurus* sp., *Ephemerella* sp., and *Leptophlebia* sp. were usually completely consumed, but larger nymphs were frequently only partly consumed.

Sex ratio of nymphs

On all sampling dates on which male and female nymphs could be distinguished, the number of female nymphs exceeded that of male nymphs. (Table 3.) Chi-square analysis indicated a significant ($p < 0.01$) departure from a 1:1 ratio. Based on the total nymphs that could be sexed, the ratio of males to females was 1:1.8.

Adult emergence

Final instar nymphs approaching metamorphosis (as indicated by darkened wing pads) first appeared in 1979 in the May 18 sample and in 1980 in the June 3 sample. Adult emergence evidently occurred in 1979 during the latter part of May as only four individuals were found on May 24. In 1980, however, emergence probably occurred in June, as 97 individuals were collected on June 3.

Fecundity and egg structure

The mean number of eggs dissected from the reared subimagoes was 394 (range, 313–486). The eggs were subspherical with a mean (±SD) length of 0.46 ± 0.03 mm and a mean width of 0.34 ± 0.03 mm. Eggs were covered with coiled attachment fibers. When fragmented egg masses were placed in water and observed under a dissecting microscope, the eggs on the exterior of the mass began to swell and slowly roll off, exposing the underlying eggs. These in turn expanded and rolled off, exposing other eggs. After about 10 min the attachment coils became activated, sending out a large mass of fibers securely attaching the eggs to the substrate.

Discussion

The ecological significance of the inundated floodplain has been largely overlooked in studies of aquatic insects, although its importance as a breeding and feeding area for young fishes is well known (Hynes 1970). In this study, it was evident that on the floodplain detritus (in the form of accumulated sedge from previous years), formed a nutrient base that supported an abundant invertebrate fauna and served as a food source for other predaceous invertebrate and fish species. It appears that inundated floodplains are essential to the life cycle of *S. aerodromia*. The two other sites from which the *S. aerodromia* has been collected in Maine (Gibbs 1980) are similar to the Tomah Stream site. Information available about the type locality of *S. aerodromia* (Sacandaga River, NY) indicates that the type specimens were taken from temporary pools left after high spring water levels where "there was a great concentration of aquatic life, including several species of mayflies, with *Siphlonisca*" (Edmunds et al. 1976). The type of vegetation bordering the river was not recorded. We conclude that *S. aerodromia* may not be as rare or as limited in distribution as was originally suggested. The preferred habitat of *S. aerodromia* may usually be overlooked because collecting from

TABLE 2. Food types in the gut contents of *S. aerodromia* nymphs collected on 1980 sampling dates

Date	No. examined	No. containing animal parts	Mean % of grid squares containing: detritus	animal	algae	unknown
Jan. 10	5	0	100	0	0	0
Jan. 29	5	0	100	0	0	0
Feb. 27	5	0	100	0	0	0
Mar. 4	3	0	100	0	0	0
Mar. 27	4	1	100	1	0	0
Apr. 17	5	3	100	3	0	1
May 6	5	5	100	17	2	1
May 23	5	5	100	24	71	17
June 5[a]	3	3	100	44	0	24

[a]Two additional specimens examined for this date had empty guts.

TABLE 3. Numbers of male and female nymphs in the 1979 and 1980 collections

Date	Male	Female
1979		
Apr. 26	11	16
May 4	6	12
May 11	27	46
May 18	4	7
May 24	1	3
1980		
May 6	12	21
May 23	26	51
June 3	32	68
Total	119	224

flooded rivers is difficult and the nymphs disappear quickly from the temporary pools, which are more accessible.

Females produce an unusually small number (394) of large eggs (length, 0.46 mm). Brittain (1982) reported that most mayfly species have fecundities in the range of 500–3000, although *Dolania* has a value of less than 100. A range of 0.15–0.20 mm in length is usual, although eggs may reach up to 1 mm in the Behningiidae (Brittain 1982). The secure attachment to the substrate may facilitate the survival of the eggs over the 7-month egg stage until hatching occurs in January.

Substantially different nymphal growth rates occur at different developmental stages and appear to be related to either changes in water temperature, quality of food, or both. Initially, during January and February, the nymphs grow slowly while the water temperature is at or near 0°C (G_{HW} = 0.28–0.79). From March until emergence, as water temperatures increase, the growth rate also increases (1979, G_{HW} = 2.13–2.89; 1980, G_{HW} = 2.33–2.73). However, at the same time, animal material begins to appear in the diet. Both increasing water temperature (Humpesch 1979; Brittain 1983) and a change in quality of food ingested (Anderson 1976; Fuller and Mackay 1981) have been positively correlated with an increase in growth rate in aquatic insects. Experimental work would be required to separate the effects of these two factors.

The occurrence of predaceous nymphs in the predominately herbivorous order Ephemeroptera is of considerable interest and was reviewed by Brittain (1982). Evidence of carnivory has come mainly from analyses of gut contents or has been implied from the structure of the mouthparts. In some instances, it is not evident whether the animal material in the gut represents a primary food source or if it was ingested incidently with other food material as with the Ephemerellidae (Corkum 1980). Only rarely have the feeding habits of a carnivorous mayfly been examined throughout nymphal development as in *Dolania americana* Edmunds and Traver (Tsui and Hubbard 1979). The shift from feeding on detritus or algae to predation shown for *S. aerodromia* has also been demonstrated for several stoneflies and caddisflies (Siegfried and Knight 1976; Fuller and Stewart 1977; Winterbourn 1971).

Chironomid larvae are the most common prey of carnivorous mayflies, as reported for *Spinadis wallacei* Edmunds and Jensen (Edmunds and Jensen 1974; Flowers and Hilsenhoff 1975), *Analetris eximia* Edmunds (Edmunds and Koss 1972), and *D. americana* (Tsui and Hubbard 1979) and these are usually reported as being ingested whole. The habit of *S. aerodromia* of feeding primarily on mayfly nymphs, which it chews and fragments before ingesting, is unusual and is probably related to its ability to hold the prey securely with its legs. The manner in which *S. aerodromia* captures and ingests prey is successful in the negligible flow of the floodplain, but if attempted in an area of high flow, would probably result in the insect being displaced downstream.

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