

# Life History and Ecology of *Siphonurus mirus* Eaton (Ephemeroptera: Siphonuridae) in an Intermittent Pond<sup>1</sup>

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*Abstract.* A study of the life history of the mayfly *Siphonurus mirus* in relation to its development in an intermittent pond was conducted from April 1978 to May 1979 in Southwestern Virginia. The life cycle of *S. mirus* was univoltine with the peak emergence occurring about mid-May. Early nymphal instars did not appear in the pond until January. It appeared that *S. mirus* oviposited in the stream above the pond, and the next generation remained in the stream during the dry season, probably diapausing in the egg stage. After the pond filled again in the autumn, *S. mirus* moved downstream as an early nymphal instar. Most development occurred from March to May. Nymphs were commonly found in soft sediment at the base of loose assemblages of decaying grasses or aquatic vascular plants. The diet consisted almost entirely of fine detritus. An intermittent pond with a consistent annual cycle provides an optimal habitat for the growth and development of species which have their life cycles synchronized with the rich food resources provided by the terrestrial vegetation that has undergone aerobic decomposition during the dry season.

The relevance of life history information to the major areas of contemporary benthic research was documented in the Plenary Session of the 26th Annual Meeting of the North American Benthological Society (Rosenberg 1979). Investigations of temporary habitats provide an excellent opportunity to increase our understanding of the factors affecting the life histories of aquatic insects, because life histories in temporary habitats are often highly synchronized with environmental changes. Wiggins, Mackay, and Smith (1980) have recently reviewed the strategies of animals that inhabit temporary pools. The purpose of this study was to elucidate the life history of the mayfly *Siphonurus mirus* Eaton in relation to its development in an intermittent pond. Prior reports on the biology of *S. mirus* consist of brief notes on habitat (Clemens 1915), egg morphology (Koss 1968; Smith 1935), duration of subimago stage (Traver 1932), and seasonal occurrence (Traver 1932). There have been a few papers that discussed the biology of the genus *Siphonurus* in general or other species in the genus (Burks 1953; Clemens 1915; Clifford & Boerger 1974; Edmunds, Jensen, & Berner 1976; Morgan 1913; Needham, Traver, & Hsu 1935).

## MATERIALS AND METHODS

The study was conducted from 1977 to 1979 in a small abandoned beaver pond in Southwestern Virginia (37° 15' N, 80° 27' W). The pond was located on the headwaters of Craig Creek at an elevation of 640 m in the Ridge and Valley Physiographic Province. The pond contained water from November to May and reached a maximum area of about 900 m<sup>2</sup> with a maximum depth of 0.7 m (Fig. 1). The pond was dry from June to October, although there was some flow in Craig Creek above the pond. Water from Craig Creek probably seeped beneath the bottom of the pond during the dry season. During that time there was considerable growth of vegetation in the basin, including *Typha latifolia* Linnaeus (common cat-tail), *Scirpus* (rush), *Juncus* (rush), and *Leersia* (cutgrass). Decaying vegetation persisted on much of the bottom during the period of inundation.

<sup>1</sup>The following persons assisted in the field and laboratory: Mark Hudy, Boris Kondratieff, Elizabeth Umberger, and Trisha Voshell.

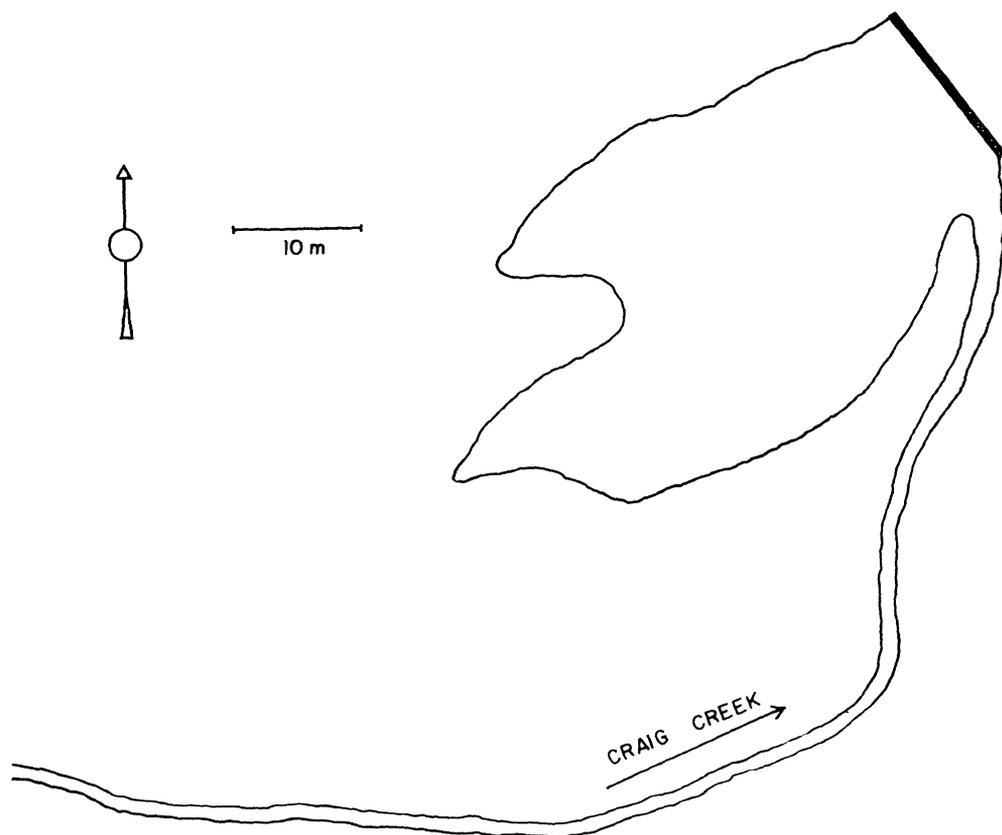


Fig. 1. Map of abandoned beaver pond on Craig Creek in Southwestern Virginia.

The dominant riparian vegetation included *Alnus serrulata* (Aiton) Willdenow (alder), *Salix nigra* Marshall (black willow), *Tsuga canadensis* (Linnaeus) Carriere (eastern hemlock), *Quercus* spp. (oak), *Rhododendron maximum* Linnaeus (rosebay rhododendron), *Pinus virginiana* Miller (Virginia pine), *Cornus florida* Linnaeus (flowering dogwood), and *Rubis* spp. (blackberry).

Samples were collected with a D-frame dip net with a mesh size of 0.9 x 0.8 mm. I attempted to make the samples quantitative by taking four alternating sweeps of the net at normal arms' length for each sample while walking forward so the sweeps did not overlap each other (average area = 1.9 m<sup>2</sup>). When the pond was covered with ice (January and February), I made a 1.0 m<sup>2</sup> hole in the ice through which I took the samples.

Benthic samples were collected at regular intervals from April - May 1978 (twice monthly) and from January - May 1979 (monthly January - March; twice monthly April - May). Three to six samples were collected from the pond, depending on available microhabitats for each time period. In addition, one or two samples were usually collected in Craig Creek. The depth was measured for each sample, the composition of the bottom described, and the relative abundance of aquatic vascular plants, filamentous algae, and decaying terrestrial vegetation noted. In addition to the benthic samples, I made qualitative observations of nymphs (presence or absence) throughout the study. Live nymphs were also taken back to the laboratory and reared in aquaria in order to observe the habits of the nymphs and to obtain specimens of subimagos and imagos.

On two occasions (17 April 1978 & 21 March 1979), additional nymphs were collected for feeding habit analyses. Nymphs were anesthetized in a saturated solution of CO<sub>2</sub> and

then preserved in 8% formalin. Gut contents were placed on microscope slides (one nymph/slide) according to the methods of Shapas and Hilsenhoff (1976). To determine feeding habits, three fields on each slide were examined at 100x magnification. The material in each field was categorized as animal matter, diatoms, other algae, vascular plant detritus, or fine detritus. The area occupied by each category was estimated by the areal standard-unit method (Welch 1948). The areas occupied by each category in the three fields were totalled for each slide and results were reported as the percent of the total area occupied by each category.

## RESULTS

### *Subimago*

Subimagoes emerged between mid-morning and mid-afternoon. It had been previously reported that members of this genus crawl entirely out of the water to emerge (Burks 1953; Clemens 1915; Edmunds et al. 1976). However, I observed nymphal exuviae on both solid objects out of the water and on the surface of the water in tangles of vegetation. In an aquarium which contained tangles of vegetation in the center and wire screen at the edge, nymphs emerged by both methods. Those that left the water climbed up until the tip of the abdomen was at the surface of the water. Those that remained in the water always supported themselves on vegetation just below the surface.

On one occasion in the field (17 May 1978), I noticed a nymph on the surface searching for a place to emerge. It climbed on vegetation and then swam away four times in 14 min covering a distance of 5 m from where I first observed it. At that point it came to rest on submerged vegetation and remained there. After 4 min the head and thorax began to emerge through the cuticle. After three more minutes the legs and wings sprung out simultaneously with all legs coming to rest on the surface film while the posterior of the abdomen remained in the exuvium still supported on the vegetation. It took 5 min more to free the caudal filaments from the exuvium, and then the organism floated free on the surface of the water for another 3 min before it flew to a height of about 5 m in nearby trees. The total time required from the nymph coming to rest until the subimago took flight was 15 min. This was in general agreement with the times recorded in the laboratory.

In order to estimate the duration of the subimago stage, specimens emerging in the laboratory were placed in ventilated plastic jars lined with wire screen to molt. The subimagoes were kept in seclusion at room temperature (ca. 21° C). The average duration of the subimago stage was 44 h (n = 9) with a range of 33-56 h. Traver (1932) reported that the duration of the subimago stage for *S. mirus* was 36-53.5 h.

### *Imago*

Of 62 subimagoes that emerged in the laboratory, 29 successfully molted to the imago stage for a survival rate of 47%. The average body length was 13.0 mm for males and 16.0 mm for females (n = 4 for each sex). In order to estimate the duration of the imago stage, some reared imagoes were kept in the plastic jars until they died. The average duration of the imago stage was 59 h (n = 9) with a range of 41-70 h.

Considerable effort was expended trying to determine the time and location of mating swarms and oviposition. Several persons made visual inspections at the pond and upstream reaches during all hours between dawn and dark. We walked up tributary streams and looked in clearings as far as 0.5 km from Craig Creek. Both white and ultraviolet light were used to try to attract organisms at night. Two sticky traps (1.2 x 0.6 m each) were placed in the pond and two traps were placed in the upstream reaches. Unfortunately, none of these methods produced much information on either the mating flights or oviposition of *S. mirus*. No specimens were attracted to the lights. It does not seem likely that there would be much nocturnal activity, because spring nights are normally very cool in the Southern Appalachians. For example, on May 17, 1978, I

attempted to collect with an ultraviolet light, but the temperature dropped to 10.0° C by dusk (8:45 PM). I hoped the sticky traps would indicate where the females deposited their eggs. However, no specimens of *S. mirus* were collected on any of the traps, even though the traps were effective at collecting other insects.

Several female imagoes were found in spider webs over the surface of Craig Creek in the section from just above the pond to about 200 m upstream. One female had an egg mass extruded from her abdomen. Two live females were collected in this section of Craig Creek about 8:00 PM, one floating on the surface and the other flying about 0.5 m above the water. No females were found in the immediate proximity of the pond. In the Appomattox River, a larger stream in the Piedmont Province, Kondratieff (pers. com.) observed females of *S. mirus* descending straight to the water's surface from an altitude that was beyond view at 5:30 - 6:30 PM. From this sketchy information it appears that mating flights of *S. mirus* occurred from late afternoon to early evening followed by oviposition in Craig Creek upstream from the pond. Edmunds et al. (1976) reported that other species of *Siphonurus* have been observed swarming from mid-morning to just at dark. They stated that "*Siphonurus* has a long ascending and descending flight with no swaying from side to side" and that "females of some species hover a few feet above the water when ovipositing, occasionally dropping to the water surface for as long as thirty seconds, then rising and repeating the performance."

#### Egg

The average fecundity of three females that emerged in the laboratory was 7907 eggs with a range of 7706-8256. The fecundity of *S. mirus* was considerably higher than Clifford and Boerger (1974) reported for *S. alternatus* (884-2023), *S. lacustris* (1712-2499), and *S. aestivalis* (933-2678). The average fecundity of *S. mirus* was higher than any species studied by Clifford and Boerger (1974), and the maximum fecundity of *S. mirus* was exceeded only by *Hexagenia bilineata* (8936).

The eggs had a general oval shape, but with irregular flat areas because they were packed so tightly in the abdomen (Fig. 2). They measured 0.20 x 0.15 mm. These measurements were made on eggs from a female that had been preserved in alcohol and then soaked in water for three days. Koss (1968) reported that *Siphonurus* spp. have the entire surface of the egg covered with accessory attachment structures that consist of threads arranged in coils. The coiled threads uncoil or spring out upon contact with water and become entangled with submerged objects or caught in small cracks or crevices. In this study, the accessory attachment structures were not apparent by SEM, but it is possible that the preparation for SEM destroyed or obscured them. The convolutions shown in Figure 2 are probably chorionic sculpturing. The areas marked with arrows in Figure 2 appear to be sites where coiled threads may have been located.

Smith (1935) observed *S. quebecensis* females carrying spherical green egg masses extruded from their abdomens. The egg mass consisted of green eggs imbedded in a green gelatinous material. The egg mass was deposited as a unit, after which it sank to the bottom, flattened out, and stuck to the substrate. Koss (1968) reported that eggs of *S. mirus* were held together by a thick gelatinous mass consisting of a very dense network of threads but that the eggs did not exist as a single mass, and he doubted that the eggs remained together in the water. In this study, I observed several brownish-orange egg masses extruded from the abdomens of females reared in the laboratory and from one female found dead in a spider web. The eggs were stuck tightly together and the mass remained intact when placed in the water.

#### Nymph

Total body length (excluding caudal filaments) and head width (at widest point across the compound eyes) of the smallest nymphs collected were 2.65 mm and 0.40 mm, respectively. Male nymphs were recognized by their developing genitalia when the head

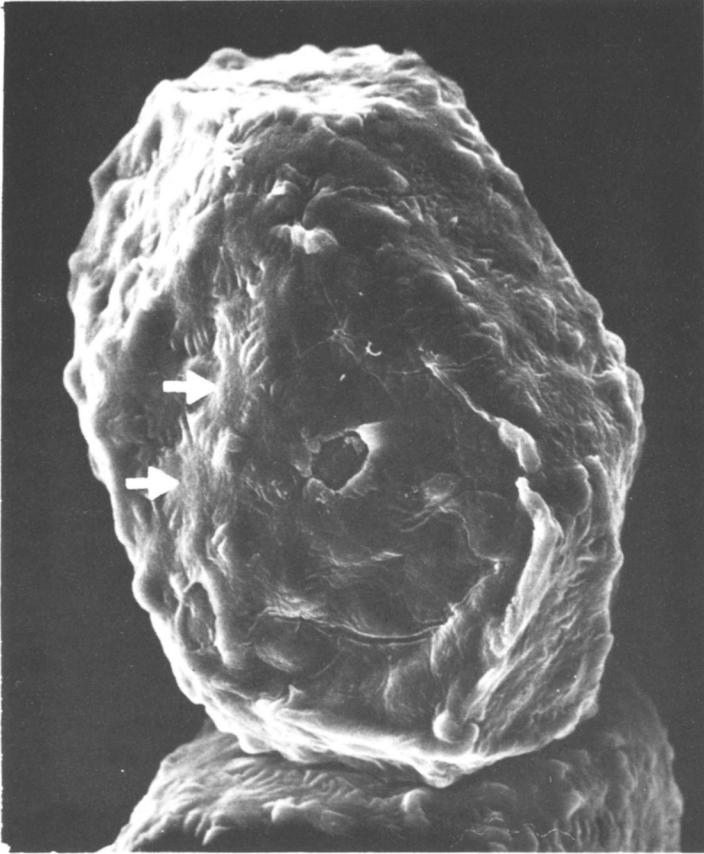


Fig. 2. Egg of *Siphonurus mirus* (500x). Arrows indicate sites where coiled attachment threads may have been located.

width reached about 1.20 mm. There was considerable difference in the size of male and female nymphs. Mature female nymphs (dark wing pads) averaged 18.0 mm total body length, but mature male nymphs were only 14.0 mm long ( $n = 10$  for each sex). The sex ratio of 1,058 nymphs was 1 male : 1.62 females. A chi square test indicated a highly significant departure from a 1 : 1 sex ratio in favor of females ( $P < 0.005$ ).

The density of nymphs averaged  $14/m^2$  (Fig. 3). On most sampling dates there were considerable ranges in density among the samples. The differences in density on a given date could be accounted for by the different habitats within the pond. The highest densities were encountered on silty bottom in loose assemblages of decaying grasses ( $37/m^2$ ). The most abundant aquatic plant was *Ludwigia palustris* (Linnaeus) Elliott. The nymphs occurred on the bottom rather than climbing on the plants. Nymphs were less abundant in dense assemblages of decaying grasses and on bare sediment ( $12/m^2$  for each). On bare sediment the nymphs could be observed swimming rapidly for short distances by means of their heavily fringed caudal filaments. Two habitats were avoided by the nymphs--mats of the filamentous alga *Spirogyra*, ( $3/m^2$ ) and areas of the bottom covered with leaves ( $1/m^2$ ).

Studies of other members of this genus reported that the nymphs were omnivorous, feeding upon diatoms, filamentous algae, fragments of plant tissue (stems, decayed leaves, epidermis, roots) and insects (mayflies, chironomids) (Edmunds et al. 1976; Morgan

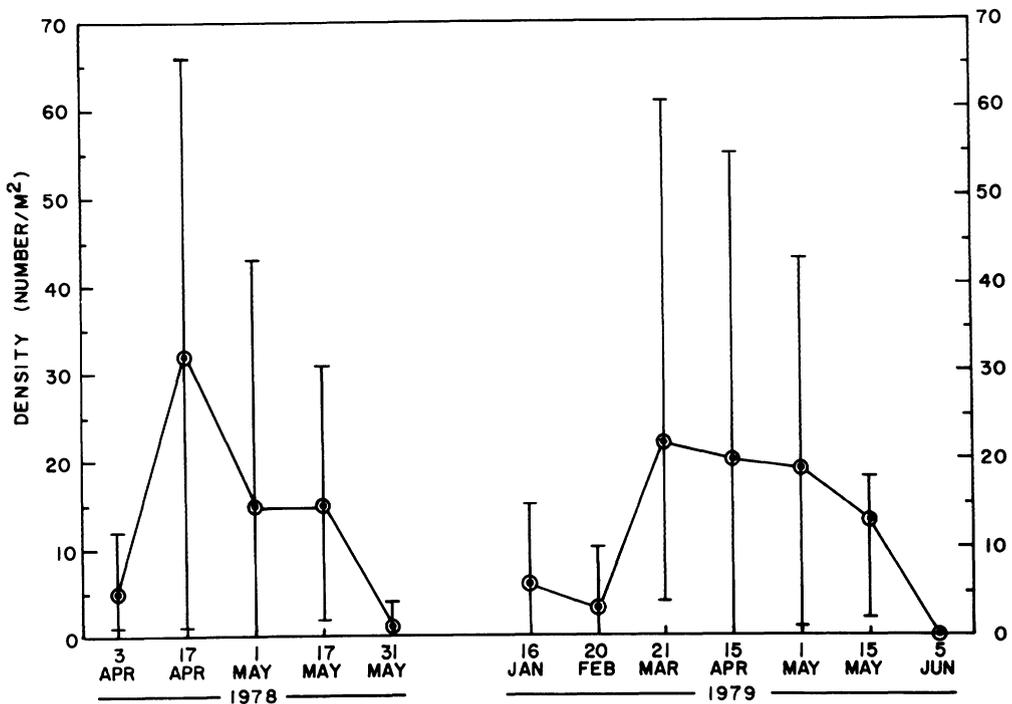


Fig. 3. Density of *Siphonurus mirus* nymphs. Circles indicate means and vertical bars indicate ranges for each date.

1913). The robust chewing mouthparts of *S. mirus* appear to be well suited for tearing apart coarse particulate organic matter or engulfing prey organisms, but in this study the diet was found to consist almost entirely of fine materials (< 1 mm). The nymphs appear to be collector-gatherers (Merritt & Cummins 1979) that ingest the organic matter residing on the sediment. There was no indication that the nymphs directly ingested the most abundant sources of food in the pond -- grasses, leaves, and filamentous algae. The guts included mostly fine detritus with some diatoms and other algae (Table 1). Guts of larger nymphs included slightly more vascular plant detritus, but because this material was in an advanced state of decay, it was probably not shredded from intact plants. Smaller nymphs ingested slightly more diatoms. No animal matter was found in the guts of nymphs.

#### Seasonal Cycle

Analysis of the life cycle by the size frequency distribution of the nymphs indicated that *S. mirus* was univoltine with the peak of emergence in mid-May (Fig. 4). Subimagos were observed emerging from the pond as early as April 22, 1978, and as late as May 31, 1978. Traver (1932) reported subimagos of *S. mirus* emerging in mid-April in North Carolina. All nymphs completed their development and emerged from the beaver pond on Craig Creek by the first week of June. During the summer and autumn of 1978, I sporadically examined puddles in the pond basin and flowing water in Craig Creek, but I did not find any nymphs. I began regular sampling again in January 1979 and found few, very small nymphs in the pond, and none in Craig Creek. The nymphs did not begin to develop until March. From March through May the nymphs developed in a smooth growth pattern. They emerged about the same time as in 1978. The development of the nymphs in the pond appeared to be directly related to temperature. They began to significantly increase in size in March (Fig. 4) when the water temperature rose sharply (Fig. 5). They grew rapidly from March to May and all nymphs emerged before the pond dried up in June. Traver (1932) found nymphs in a lake near Liberty, North Carolina, from February 18 to April 23.

TABLE 1

Feeding habits of *Siphonurus mirus* nymphs.

Sex	Head Width (mm)	Date Collected	Diatoms	Other Algae	Vascular Plant Detritus	Fine Detritus
3 ?	0.90-1.15	21 Mar. 1979	3.0	1.0	0.0	95.9
2 ♂	2.35-2.45	17 Apr. 1978	0.4	2.1	3.9	93.6
2 ♀	3.00-3.05					

There are two possible explanations for the annual occurrences of *S. mirus* in the beaver pond. First, the individuals may have entered the pond basin just before the dry season and then aestivated in a desiccation resistant stage. Burks (1953) reported that the genus *Siphonurus* inhabited breeding sites in Illinois that dried up during summer and autumn. He speculated that the eggs deposited in the spring did not hatch until the following February or March and that the eggs withstood desiccation. Wiggins et al. (1980) reported *Siphonurus* nymphs in a temporary autumnal pool lacking inlets and outlets. They placed these *Siphonurus* spp. in their group 2: "spring recruits which must oviposit on water but subsequently aestivate and overwinter in the dry basin." In order to test the hypothesis that *S. mirus* aestivated in the dry pond basin, I collected sediments from the basin when it dried completely during the summer of 1977 and placed the material in an aquarium with water. No insects were ever observed in the aquarium. In August 1978 the basin contained a little water in the middle portion of the channel and a small pool near the dam, but there were no *S. mirus* in either. A few *Chloeon* and *Paraleptophlebia* were found in the puddles. The most likely stage for *S. mirus* aestivation in the pond basin was the egg, which could have been overlooked by my methods.

A second explanation which seems more likely is that *S. mirus* passed the dry season in the upstream reaches of Craig Creek outside the pond basin. The only female imagoes collected near the water were in the 200 m of Craig Creek immediately above the pond. The eggs of *S. mirus* have accessory attachment structures (Koss 1968). Therefore, the eggs probably remained in Craig Creek near where they were deposited and in diapause until early winter. After eclosion in early winter, young instars probably migrated into the beaver pond during increased flow in Craig Creek.

## DISCUSSION

The life history pattern of *S. mirus* reported in this study does not show an exact fit with any of the classification types proposed by Landa (1968). It comes closest to his Type A2 - one generation per year, eggs in diapause until spring or summer, growth of nymphs short and rapid. But in the case of *S. mirus*, the eggs came out of diapause in early winter, and a rapid growth phase occurred in the spring.

*S. mirus* appears to require both lotic and lentic habitats to successfully complete its life cycle, similar to some *Leptophlebia* spp. Small temporary pools left by the overflow of streams in the spring are probably the typical habitat where *S. mirus* completes its development (Clemens 1915). A larger intermittent pond with a consistent annual cycle, such as the beaver pond on Craig Creek, provides an optimal habitat for the growth and development of *S. mirus*. Wiggins et al. (1980) discussed the advantages of developing in temporary pools rather than permanent water. Although Wiggins et al. (1980) restricted their definition of a pool to "an accumulation of surface water in an isolated basin that at no time during the year has either an inlet or an outlet", some of their results are probably applicable to the situation in the beaver pond on Craig Creek. The growth of terrestrial vegetation in the dry period followed by at least some aerobic decomposition before it is

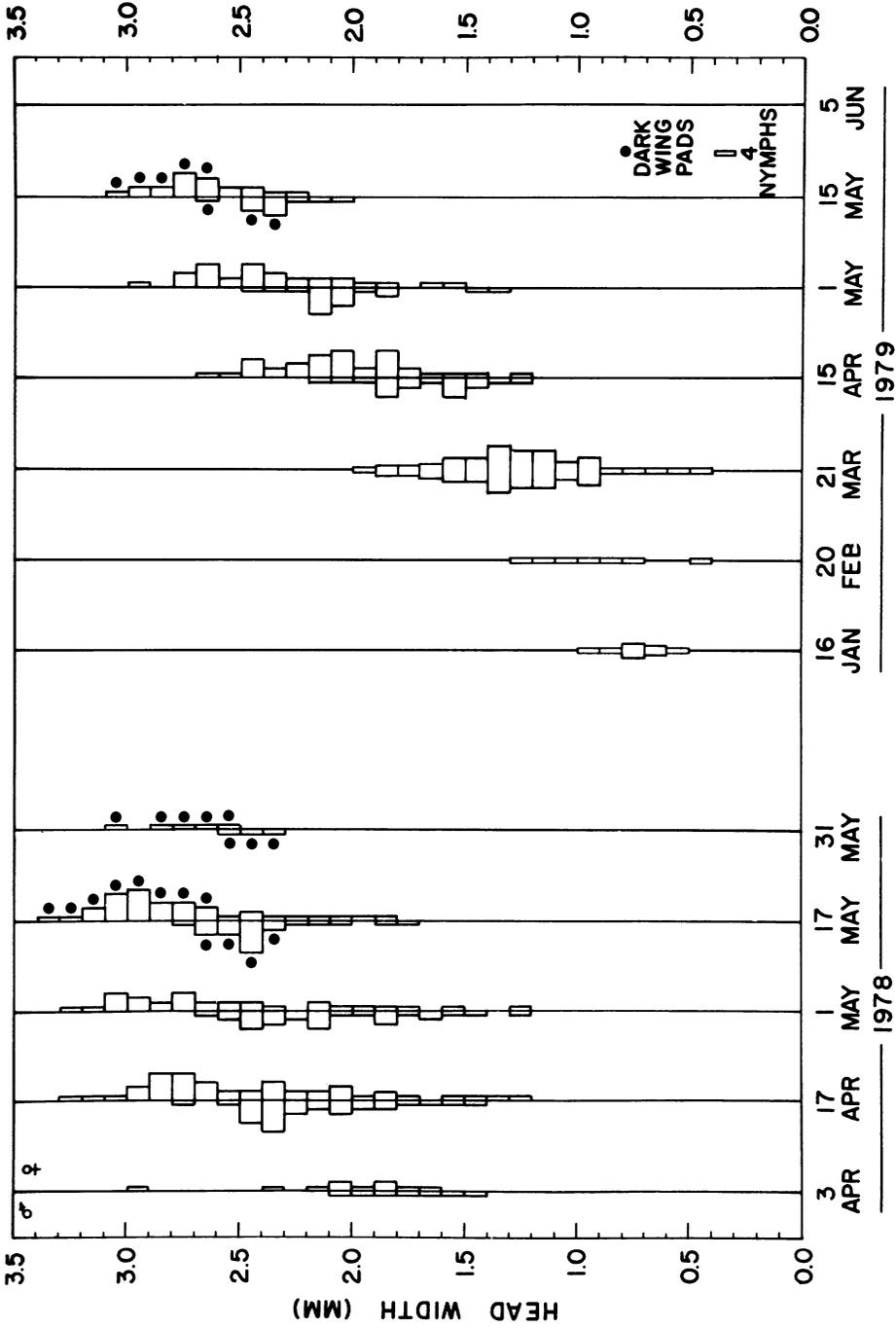


Fig. 4. Size frequency distribution of *Siphonurus mirus* nymphs based on measurement of head width. Sexes could not be separated until male head widths reached 1.20 mm.

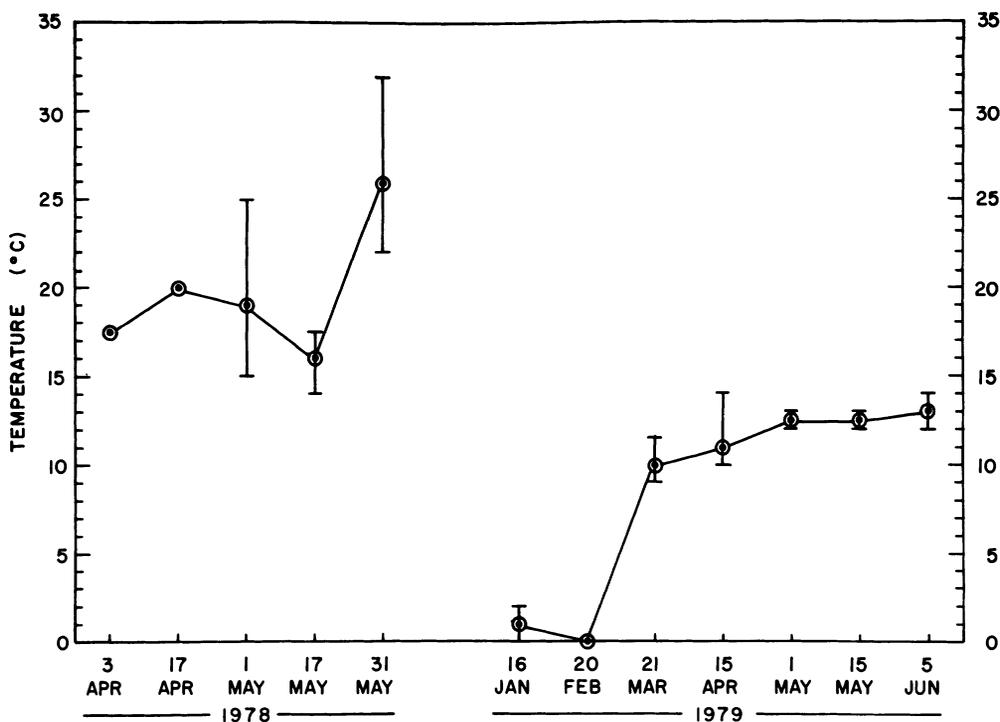


Fig. 5. Water temperature in pond. Circles indicate means and vertical bars indicate ranges for each date.

inundated provides a very rich food resource. When this occurs on an annual cycle, it keeps the ecosystem in an early stage of succession and organisms with r-selected traits (Pianka 1970) are favored as colonizers. *S. mirus* exhibits several r-selected traits. Within a watershed it has adequate capabilities of dispersal, because the early instar nymphs can use the energy of the flowing water to locate a suitable habitat. The fecundity of *S. mirus* is very high, and there are significantly more females than males. Both factors help assure the success of the species by virtue of large numbers of individuals. Lastly, the growth and development of *S. mirus* is fairly rapid, enabling it to exploit the resources before adverse conditions set in.

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