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LIFE HISTORY ASPECTS OF *ANTHOPOTAMUS VERTICIS*
(EPHEMEROPTERA: POTAMANTHIDAE)W. P. McCafferty¹ and Y. J. Bae²

ABSTRACT

The study of the larval development and life cycle of a population of the mayfly *Anthopotamus verticis* from the Tippecanoe River, Indiana was based on monthly and weekly sampling in 1990 and 1991. Larval head width and tusk length were directly correlated with body size; whereas wingpad development represented an exponential relationship with body size. Relative maturation of larvae was efficiently assessed, however, by using wingpad development. The morphology of eggs is described. Larval growth and development took place mainly from March to August. Although emergence is protracted from mid-July to mid-August, the major recruitment of new larvae occurred in August. Only one cohort was ascertained. The species overwinters as mostly young larvae. The simple univoltine life cycle appears to be related to seasonal temperature.

Larvae of *Anthopotamus verticis* (Say), and presumably the other three species of this eastern North American genus (see Bae and McCafferty 1991), are essentially hyporheic benthos inhabiting mixed gravel, pebble, and cobble substrates in streams and rivers (Bae and McCafferty 1994) and feeding largely by actively filtering small particles of detritus (McCafferty and Bae 1992). Previous studies on life history aspects of *Anthopotamus* have been fragmentary and restricted to *A. myops* (Walsh): Ide (1935) described eggs and early instar larvae; McCafferty (1975) gave some preliminary life history; and Bartholomae and Meier (1977) and Munn and King (1987) studied certain life history aspects. No studies have provided definitive life cycle information. Studies of other genera of Potamanthidae, e.g., *Potamanthus luteus* (Linn.) from Europe (Landa 1968) and *Potamanthus formosus* Eaton from Japan (Watanabe 1988) also have not been conclusive with regard to voltinism.

Although *A. verticis* is relatively common in midwestern rivers, its life history has not been previously investigated. Some 20 years of observing its protracted summer emergence from the Wabash and Tippecanoe Rivers near Lafayette, Indiana gave rise to speculation about possible life history strategies of this species. Essentially, was the prolonged emergence period indicative of a complex life cycle? Such observations and the lack of definitive life history information for the family Potamanthidae as a whole led us to study the larval development and life cycle of *A. verticis*.

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METHODS

Field investigations were conducted in 1990 and 1991 in the Tippecanoe River, White County, Indiana (in the Upper Wabash Drainage System). The study area comprises ca. 100m² of river, where *A. verticis* larvae occur in abundance, and which was described in detail by McCafferty and Bae (1992) and Bae and McCafferty (1994). Diel maximum water temperature in 1990 and 1991 ranged from 0–30°C (see Fig. 6), water level was highest (50–60cm) from November through February and lowest (10–20cm) from June through August; pH was 8.0–8.6 throughout the study period.

Weekly field samples were taken on 6/20, 6/28, 7/6, 7/11, 7/20, 7/27, 8/5, 8/10, 8/16, 8/23, 8/31, 9/7, 9/14, and 9/21 in 1990, and 5/24, 6/14, 6/23, 6/28, 7/5, 7/12, 7/20, 7/26, 8/8, 8/14, 8/24, 8/30, 9/6, 9/13, 9/19, and 10/21 in 1991. For the purposes of plotting monthly trends (e.g., Fig. 7), the last sampling dates of the respective months were used.

Larvae were sampled on all sampling dates with a 1 × 1m kick screen (0.5mm mesh) from gravel and pebble substrates in riffles and from cobble embedded in sand and gravel in somewhat slower current (see Bae and McCafferty 1994). A trowel was used to dislodge larvae into the downstream screen because larvae could be found up to 40cm deep in the substrate. Sampling continued until at least 100 larvae were secured. Larvae were carried in large buckets to the laboratory, where they were preserved in 80% ethanol. One hundred larvae were randomly selected, for structural measurements and statistical analysis. Mature larvae were sexed.

Attempts to sample subimagos and adults were made on all sampling dates at the study area from March through October by using white and black fluorescent lantern lights against a white sheet from dusk to ca. one hour after nightfall. (Observations of alate forms of this species at store lights in Lafayette over the years indicated that this was the primary flight time and that they were attracted to lights.) Only mere presence or absence of alate forms, however, could be sampled in this way. Some female adults were dissected for their eggs previous to preservation; all were preserved in 70% ethanol.

Relationships between larval body length and head width, body length and tusk length, and body length with wingpad length were demonstrated by regression analysis. Ranges, means, and standard deviations of body length were also calculated. Body length was measured from the anterior margin of the clypeus to the posterior margin of abdominal segment 10. Head width was measured as the maximal distance between the genae anterior to the compound eyes. Tusk length is the straight line distance between the base of the medial margin and the apex of the mandibular tusk (see Fig. 2). Wingpad length was measured along the mid-dorsal longitudinal line of the thorax from the medial margin to the apex of the forewingpad.

Both body length (given in 1 mm increments) and developmental stages were used in analyzing population dynamics. Wingpad development was used, as shown in Table 1, for categorizing larvae into developmental stages.

The study of egg ultrastructure and scanning electron micrographs were accomplished using a SEM as described by McCafferty and Bae (1992) and Bae and McCafferty (1994).

RESULTS

Eggs. Eggs dissected from live female adults were pale yellow and oval with two white, conical polar caps, a tageniform micropyle, and 8–10 knob terminated coiled threads on a finely tuberculate chorion (Fig. 1). The long

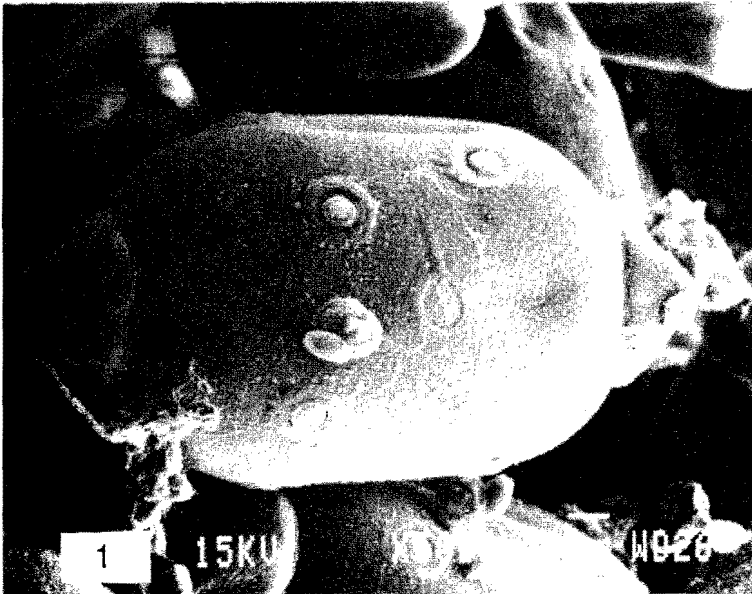
Table 1. Characteristics of larval developmental stages of *Anthopotamus verticis*.

Stage	Wingpad development	Forewingpad length (mm)	Body length (mm)	Color
I	Not developed	0	1.0-4.0	Pale
II	Forewingpads not covering hindwingpads	0.01-0.30	4.0-7.0	Faint markings
III	Forewingpads cover hindwingpads	0.31-0.50	7.0-10.0	Distinct markings
IV	All wingpads fully developed	1.00-1.50	8.0-11.0	Uniformly dark

axis of the egg was ca. 123 μ , the short axis was ca. 92 μ , and the height of the polar cap was ca. 33 μ .

When eggs were placed in an aquarium they became attached to the bottom via one of the polar caps. Fertilized eggs held in an aquarium at room temperature (22-24°C) in June, 1991 eclosed in 14 days. Mortality of first instars hatched in the laboratory was 100% within a week of eclosion.

Larval Development. The relationships of four larval developmental stages, body size and coloration, and wingpad size and development are presented in Table 1. Head width was strongly correlated ($r^2 = 0.9681$) with body length, expressed as $y = 0.1318x + 0.2150$, where y is the dependent variable of head width and x is the independent variable of body length (Fig. 3). Tusks

Figure 1. Egg of *A. verticis*, bar = 10 μ .

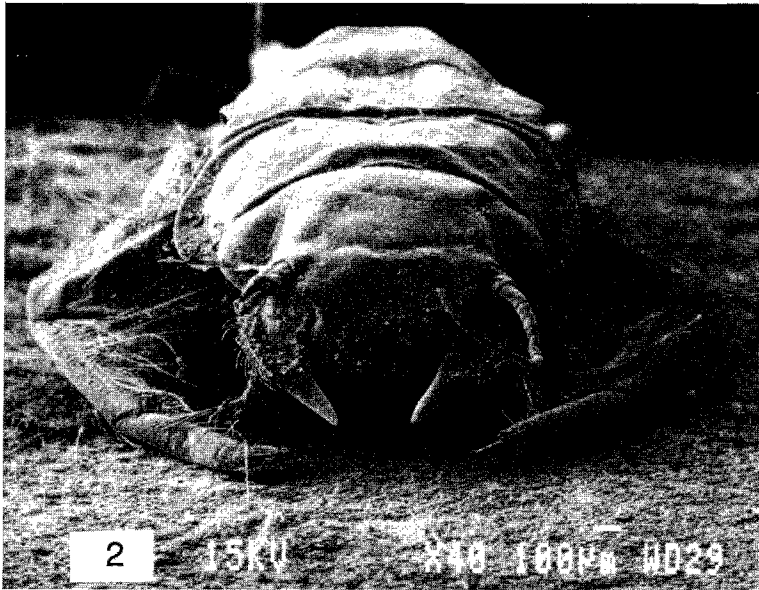


Figure 2. Larva of *A. verticis*, anterior, bar = 100 μ .

did not appear until larvae reached ca. 2.0mm in length. They then grew gradually (tusks of a Stage III larva are shown in Figure 2), being strongly correlated ($r^2 = 0.9446$) with body length, expressed as $y = 0.1674x - 0.4802$, where y is the dependent variable of tusk length and x is the independent variable of body length (Fig. 4). The development of forewingpads showed an exponential relationship ($r^2 = 0.9029$) with increasing body length, expressed as $y = 10^{(0.2937x - 2.6432)}$, where y is the dependent variable of forewingpad length and x is the independent variable of body length (Fig. 5).

Population Dynamics. Well-developed larvae (see Table 1, stages III and IV) were more abundant from March to July (Fig. 6). Diel maximum water temperatures gradually increased from 12 to 29°C during this period. The population maintained a mean body length of 4.5–5.4mm from September to March (Fig. 6). Stage I to Stage III larvae were found throughout the year, but Stage IV larvae occurred only from May to August (Fig. 8), during which time emergence was continuous.

Detailed weekly sampling data are summarized in Figures 7 and 8. The population rapidly matured from early May to mid-July (greatest increase in body size was apparent from early July to mid-July). Mature (Stage IV) larvae remained abundant until early August. Although subimagos and adults were sampled from late May to late August, the greatest emergence occurred from mid-July to mid-August, as evidenced by both increased numbers of alate forms at lights and from data on the temporal distribution of Stage IV larvae. Newly hatched larvae were recruited mainly after late July, and Stage I and II larvae became remarkably abundant in late August (Fig. 8). Most larvae overwinter as Stage I and II larvae, with smaller numbers of Stage III larvae also overwintering.

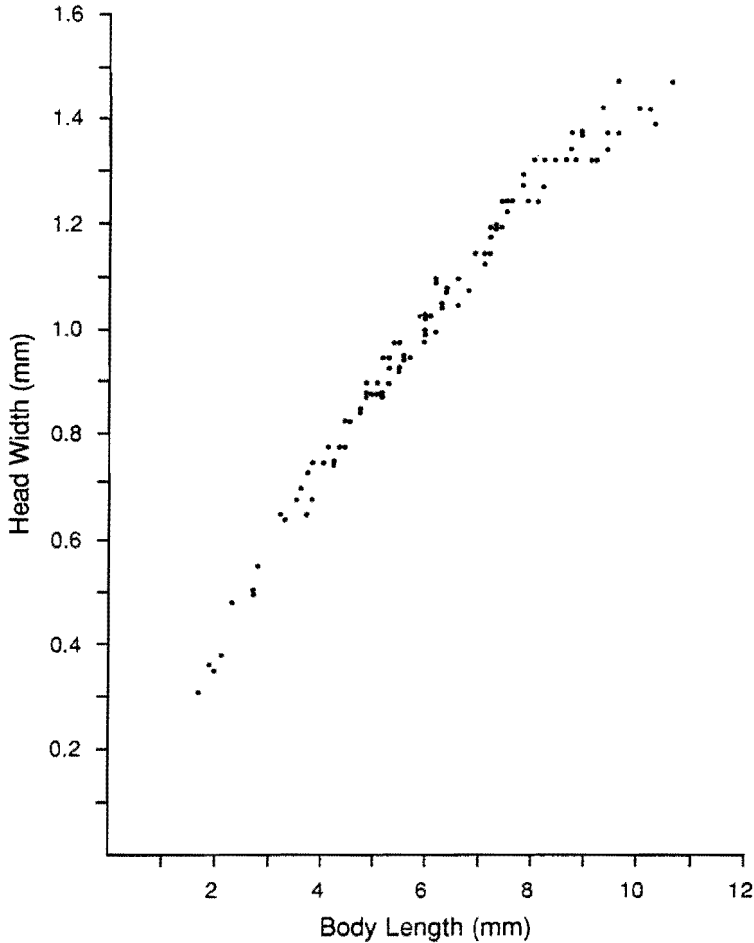


Figure 3. Relationship of body length and head width of *A. verticis* larvae [$y = 0.1318x + 0.2150$; $r^2 = 0.9681$].

Sex ratio of males to females was 1:1.3, based on larval data. Subimagos and adults were more attracted to white light than black light, and when present, were most prevalent from 2030 to 2130 hours. Males tended to be much rarer at lights, and there was no indication of whether one sex preceded the other in emergence.

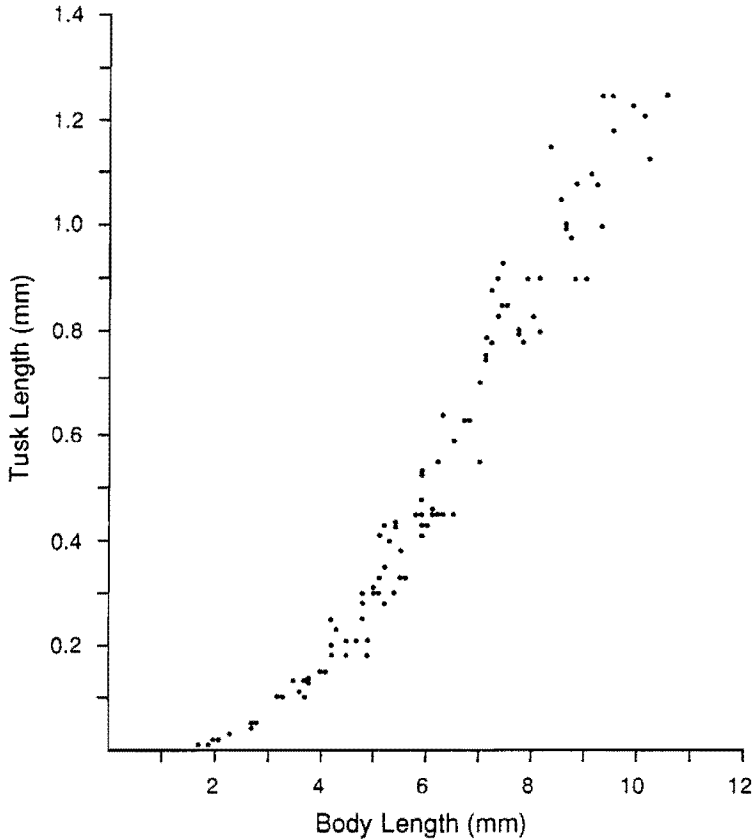


Figure 4. Relationship of body length and tusk length of *A. verticis* larvae [$y = 0.1674x - 0.4802$; $r^2 = 0.9446$].

DISCUSSION

The morphology of the eggs of *A. verticis* appears to be quite consistent with others known in the family Potamanthidae. Koss (1968), for example, described the similar eggs of *A. myops* and *A. neglectus* (Traver), and DeGrange (1960) described the eggs of *P. luteus* in Europe. See also Bae and McCafferty (1991).

The strong correlation between head width and body length in *A. verticis* indicates no allometry present with respect to head development. It also suggests that head width may be an adequate index of size development in other related mayflies.

Based on rather scant literature, most burrowing mayflies (Ephemeroidea, Polymitarcyidae, and Potamanthidae) lack tusks as early instars. *Anthopotamus myops* lacks tusks in the first instar (Ide 1935), and *Ephoron album* (Say)

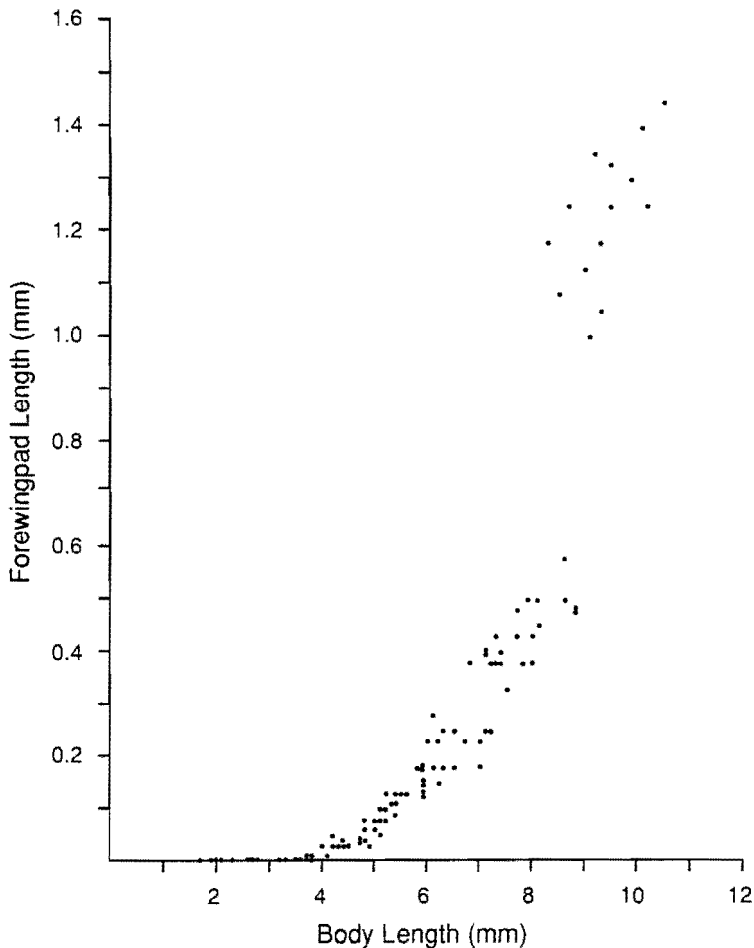


Figure 5. Relation between body length and forewingpad length of *A. verticis* larvae [$y = 10^{(0.2937x - 2.6432)}$].

(Polymitarciidae) lacks tusks in the first and second instars (Ide 1935), as does *Ephemera strigata* Eaton (Ephemeridae) (Ando and Kawana 1965). Our data on *A. verticis* would agree with these observations, although we do not know the exact number of instars involved up to the time that tusks appear in *A. verticis* (ca. 2.0mm body length). *Tortopus incertus* (Traver) (Polymitarciidae) is the only burrowing mayfly presently known to possess tusks as first instar larvae (Tsui and Peters 1974).

The growth of forewingpads in *A. verticis* showed an exponential pattern in general, with the greatest deviance in the mature larvae. This agrees with other data from mayflies in general. Among burrowing mayflies, Aguayo-

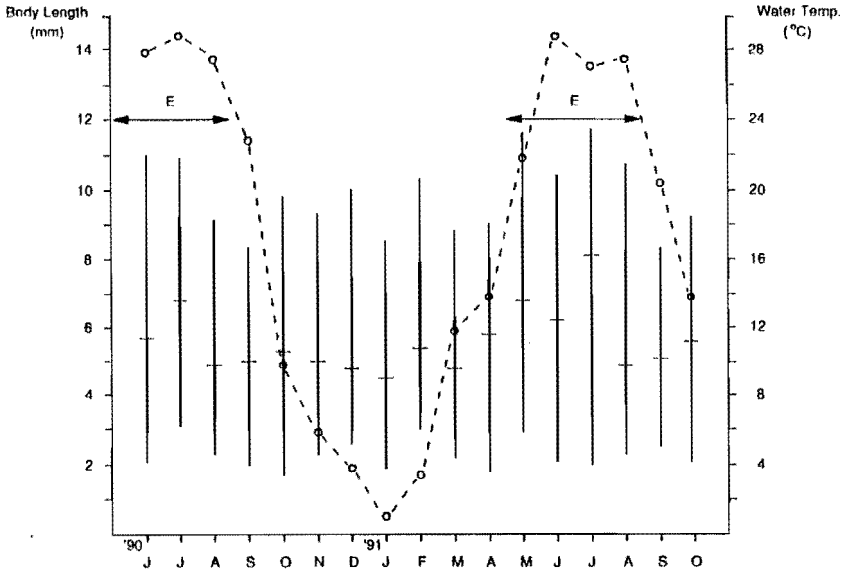


Figure 6. Ranges, standard deviations, and means of body lengths of *A. verticis* larvae, with water temperature (circles) and emergence period (E) from monthly samples (June, 1990–October, 1991).

Corraliza et al. (1981) found that wingpads of *Ephemera danica* Müller (Ephemeraidae) showed an allometric growth pattern with respect to other body parts, such as head length and width, prothorax width, and metafemur length. Takemon (1990) found that the rate of wingpad size increase in last instar larvae of *E. strigata* showed a strong deviance from the rate of head length increase.

McCafferty and Huff (1978) first used wingpad development as indicators of larval development in a heptageniid mayfly. The technique has hence been adopted in several mayfly life history studies, and for burrowing mayflies in studies of *Hexagenia limbata* (Serville) (Ephemeraidae) by McCafferty and Pereira (1984) and *H. limbata* and *Ephemera simulans* Walker by Heise et al. (1987). Our study indicated that identifying relative developmental stages of larvae by wingpad development is an easy-to-use technique in the analysis of mayfly population dynamics.

Interpreted life cycles of potamanthid mayflies have been questionable with respect to voltinism: *A. myops* from Michigan and Indiana was considered either univoltine (McCafferty 1975, Munn and King 1987) or semivoltine (Bartholomae and Meier 1977); *P. luteus* from central Europe was considered univoltine (Landa 1968), and *P. formosus* from Japan was considered multivoltine (Watanabe 1988). These studies were based on analysis of body length classes from monthly sampling or from general field observations. Analysis of larval development stage distribution was not used.

Although previous observations of the prolonged summer emergence period of *A. verticis* may have suggested a complex life cycle, our data indicate only a simple univoltine pattern. We have not found any indication of two or more independent cohorts throughout the years. The only considerable co-

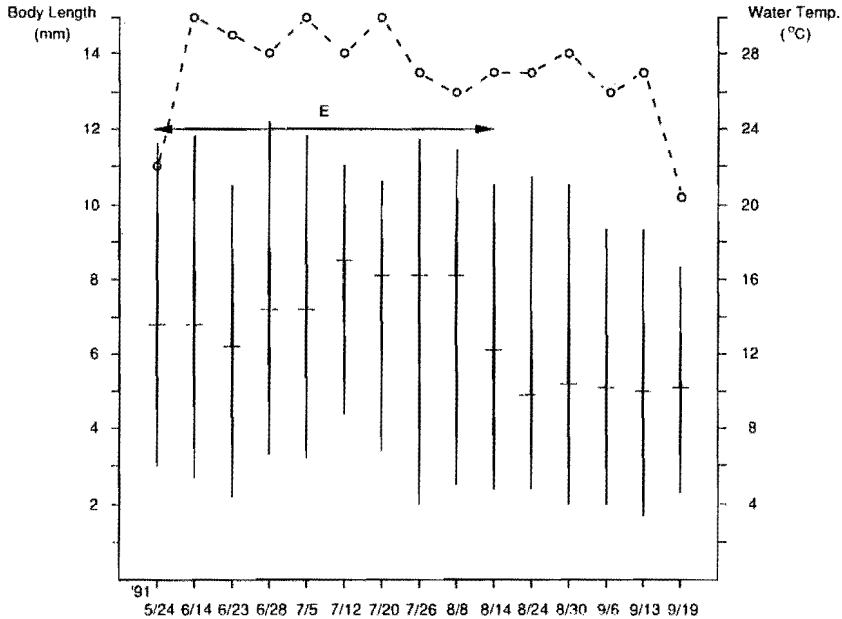


Figure 7. Ranges, standard deviations, and means of body lengths of *A. verticis* larvae, with water temperatures (circles) and emergence period (E) from weekly samples (late May-mid-September, 1991).

occurrence of young and old larvae was during the short, late summer period when the first of the new generation was heavily recruited. Some adults emerged from late May to early July, but relatively few early instar larvae were sampled during that period. Based on the laboratory temperatures (22–24°C) that allowed egg eclosion in two weeks, adequate temperatures for egg eclosion were present in the field from mid-May through late September.

The life cycle of *A. verticis* appears to be the univoltine pattern common in many temperate mayfly species and represented by rapid larval growth in the warm season (Clifford 1982). Temperature may be the major factor determining development. Other potamanthids from tropical and subtropical regions, e.g., *Rhoenanthus speciosus* Eaton from Southeast Asia and *P. formosus* from Taiwan (see Bae and McCafferty 1991), emerge throughout the year. Thus, the local life cycle phenomena found in potamanthid mayflies appear to indicate relatively flexible life history strategies sensitive to temperature, at least in part, and common to mayflies in general (Brittain 1990).

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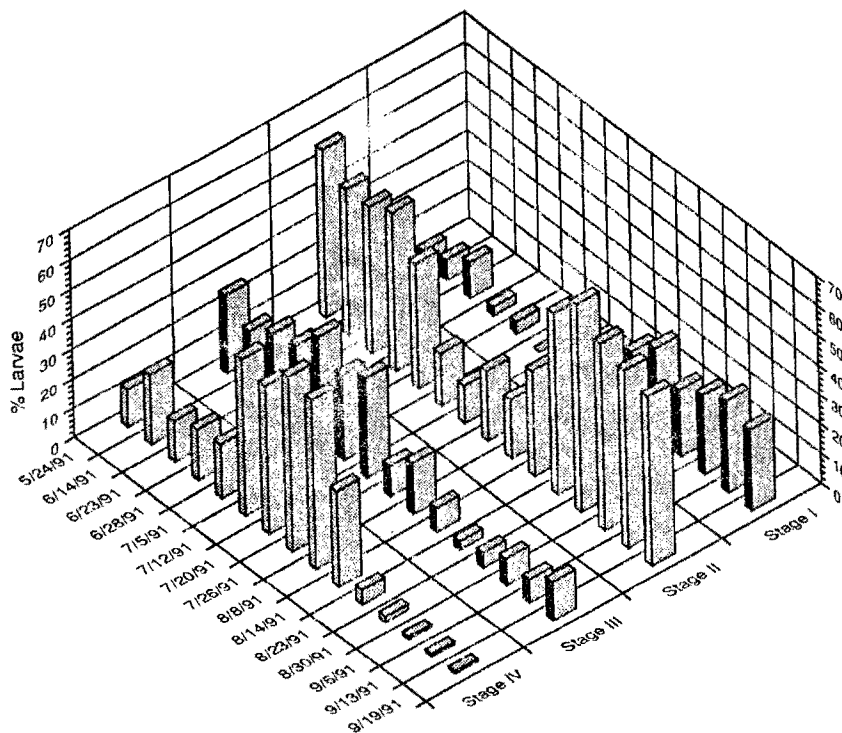


Figure 8. Three dimensional diagram of weekly population dynamics of *A. verticis* larvae from late May to mid-September, 1991, based on larval developmental stages (see Table 1).

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