

**Ecological Association of the Mayfly *Ephemerella needhami*
(Ephemeroptera: Ephemerellidae) and the Green Alga
Cladophora (Chlorophyta: Cladophoraceae)^a**

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Abstract

The behavioral feeding ecology of *Ephemerella needhami* McDunnough (Ephemeroptera: Ephemerellidae) larvae was studied using field observations, gut content analysis, scanning electron microscopy (SEM), and videomacroscopy. These techniques allowed correlation of behavior, microhabitat, and diet. Field studies showed that the mayfly larvae were intimately associated with the filamentous green alga *Cladophora*. Development of middle and late instar larvae always coincided with the early season development of *Cladophora* mats. Behavioral observation and gut analysis indicated that detritus and epiphytic diatoms associated with *Cladophora* filaments, as well as the filaments themselves, constituted the primary diet of *E. needhami*. The mayfly is primarily a collector-gatherer detritivore but also qualifies as a herbivore and a carnivore. The larvae possess several morphological and behavioral traits that are apparent adaptations for living with *Cladophora*. Life cycle synchronization, spination, coloration, and feeding behavior allow *E. needhami* to use *Cladophora* as a substrate, refuge, food, and food-gathering device.

INTRODUCTION

Larvae of the mayfly *Ephemerella needhami* McDunnough (family Ephemerellidae, or spiny crawlers as they are sometimes known) are extremely common each spring in the Tippecanoe River in north central Indiana and throughout much of eastern and central North America. Minimal information about the feeding ecology of *Ephemerella* species in general is available, and almost nothing has been reported for *E. needhami*. Shapas and Hilsenhoff (1976) reported that *E. needhami* fed on detritus, diatoms, and filamentous algae, and that other *Ephemerella* species had similar diets. Cummins et al. (1984) list the genus as belonging to the collector-gatherer and scraper functional feeding groups (FFGs). Hawkins (1985) described a western North American congener, *E. infrequens*, as a diatom scraper, detritus shredder, and collector-gatherer. Other species studied by Hawkins (1985) fed on a variety of materials including diatoms, detritus, animals, and moss; Gilpin and Brusven (1970) reported similar diets for western North American ephemerellids. Hawkins (1984) found ephemerellids in a variety of habitats, including moss. Sweeney & Vannote (1981) studied six species of ephemerellids, two of which belonged to *Ephemerella* and fed on diatoms and detritus. Gray & Ward (1978) found *E. inermis* feeding primarily on detritus; a similar diet was reported by Hamilton & Clifford (1983).

Association of *Ephemerella* with vegetation, including filamentous algae, appears to be common, particularly in the European species. Percival & Whitehead (1929) and Hynes (1961) found *Ephemerella ignita* in England associated with vegetation including *Cladophora* and moss; according to Percival & Whitehead (1929), the two plants were also common in the diet of *E. ignita*. Jones (1950) found *E. notata* in the River Rheidol associated with filamentous algae

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and reported that its diet consisted of filamentous green algae, diatoms, and detritus. Jones (1949) also found that *E. notata* prefers *Ulothrix*, but would eat moss (*Fontinalis antipyretica*) when *Ulothrix* was scarce.

The present study describes the feeding ecology of *E. needhami* and its association with the filamentous alga *Cladophora*. It is the first study to combine conventional gut content analysis with modern techniques such as scanning electron microscopy (SEM) and videomacroscopy to investigate the feeding ecology of the Ephemerellidae. A detailed account of the feeding behavior and functional morphology of *E. needhami* is given in McShaffrey and McCafferty (1990).

METHODS AND MATERIALS

Ephemerella needhami was collected at the Tippecanoe River in north central Indiana, U.S.A. At the collection site, the river is a sixth order stream, about 50 m wide, with an open canopy and cobble-gravel substrate. The greatest current velocity was 1 m s^{-1} at a water depth of 0.4 m. Field work at this site was conducted over four successive years: 1985-1988. In 1985 weekly presence/absence surveys were conducted and similar sampling on a less regular basis was conducted in 1986. One collection of larvae was also made on 21 April 1989.

A total of 35 organisms collected on 1 May 1987 and 8 May 1987 were used for detailed videomacroscopic behavioral analysis and subsequent gut content analysis. An additional 50 larvae collected in groups of 25 on 8 May 1987 and 24 May 1988, were used only for gut content analysis. Additional specimens collected on various dates were used for morphological examinations by light microscope and SEM, as well as less detailed videomacroscopic behavioral observation. Throughout the study, only mature larvae, as judged by relative wingpad development (McCafferty & Huff 1978) and head capsule width (1.1-1.6 mm), were used. To insure correct species identification, only larvae bearing the prominent dorsal stripe that is most typical of this species were used.

Cladophora was collected on 24 May 1988 and 31 May 1988. Five clumps of *Cladophora* were collected, placed in 90% ethanol, and returned to the laboratory. The number of *E. needhami* per clump was determined, as well as damp weight (excess ethanol removed) and volume.

Cladophora filament widths and epiphyte cover were evaluated by cutting the filaments into 0.5 cm segments and mounting a random subsample from each clump in euparal on a glass slide. The widths of 50 randomly chosen filaments and 50 randomly chosen terminal filaments were measured at 200x using a Whipple disk ocular grid. The number of epiphytes per 0.0147 mm^2 of surface area was determined at 200x using the same grid. Similar measurements were made for *Cladophora* filaments among the gut contents of *E. needhami*; however, only 40 filaments and 40 terminal filaments were examined from the gut contents of specimens collected on 24 May 1988.

Gut contents of *E. needhami* larvae were analyzed by removing the gut and macerating the contents in euparal on a glass microscope slide. Gut contents were classified as: animal remains (other than midges), midge remains, plant remains, *Cladophora*, diatoms, unicellular algae, filamentous algae (other than *Cladophora*), and detritus. Slides were examined at 400x with proportions of each type of food determined by measuring the area covered by each type. Area was measured by using a 10 x 10 ocular grid measuring 0.175 mm on a side. Ten randomly selected fields were evaluated for each slide.

Larvae used for videomacroscopic behavioral analyses and some gut content analyses were maintained in the laboratory in an artificial stream with current speeds varying between 0 and 1.5 m s⁻¹, depending on the configuration of substrate in the channel. Water in the channel varied between 0 and 7 cm over the substrate, which had been taken from the collection site and included rocks with attached *Cladophora*. Aeration was provided by airstones; light was provided by a 45 cm, 15 watt fluorescent light placed 15 cm over the channel bottom and operated 24 hours/day. Water temperature varied with that of the room (20-25°C).

Equipment and methodology for our underwater videomacroscopic observations were described in detail elsewhere (Keltner & McCafferty 1986, McShaffrey & McCafferty 1986, 1987, 1988, 1990). For this study, three observational arenas were used: a shallow observation flow cell (McShaffrey and McCafferty 1986, 1988), the artificial stream described above, and a small enclosure with no flow (McShaffrey and McCafferty, 1990). After videotaping, the organisms were sacrificed to obtain gut contents, and slide mounts were made of the mouthparts. Videotaped feeding behavior of nine larvae was analyzed in detail, and the resulting descriptions were then checked against the remaining videotape. Stereotypic feeding behavior and mouthpart morphology were determined as per McShaffrey & McCafferty (1986, 1988, 1990).

RESULTS

Ephemerella needhami larvae (Fig. 1a) were intimately associated with the filamentous green alga *Cladophora* (Figs. 1a, 2a), and the life cycle was timed so that most of its larval development corresponded to maximum *Cladophora* growth. The alga served as a substrate, refuge, food, and food-gathering system for the mayfly; it is also possible that the mayfly provided symbiotic benefits to the alga.

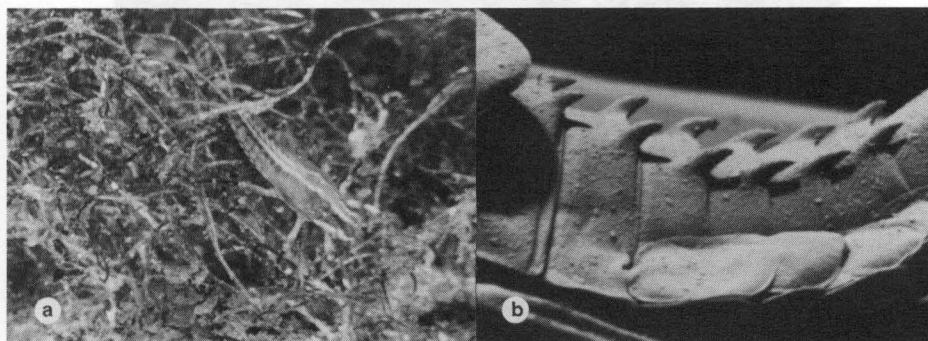


Figure 1. (a) *Ephemerella needhami* larva on *Cladophora*. (b) Dorsal abdominal spines of *E. needhami*.

Field Observations

Ephemerella needhami larvae with head capsule widths greater than 1mm were collected from mid-April to late May in 1985-1988. *Cladophora* first became noticeable in late April and formed extensive mats that began to break up by late May when the water temperature exceeded 20°C, although some smaller *Cladophora* clumps did persist throughout each summer. Almost all *E. needhami* larvae were collected in association with *Cladophora* (Fig. 1); only a very few individuals were taken on or under stones away from *Cladophora*. Very young larvae with head capsule widths less than 1mm were found only early in the season

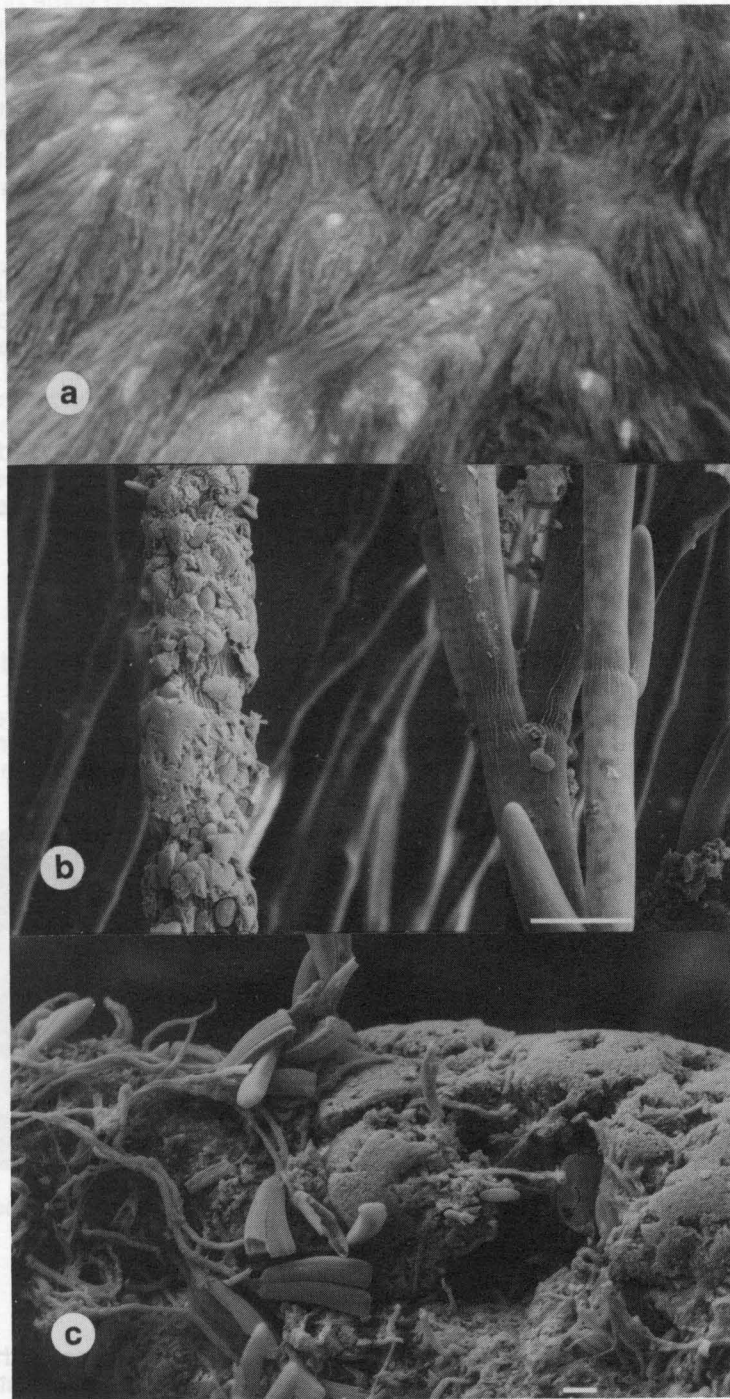


Figure 2. (a) *Cladophora* mat in natural habitat. (b) *Cladophora* filaments with and without epiphytes. Scale bar = 100 microns. (c) Epiphyte community on *Cladophora*. Scale bar = 10 microns.

in 1989, prior to any significant growth of *Cladophora* and in association with a dense growth of benthic diatoms on the substrate where *Cladophora* eventually developed. Emergence of *E. needhami* took place in late May. Quantitative samples of *E. needhami* taken on 24 May 1988 showed an average of 5.8 *E. needhami* per cubic centimeter of *Cladophora* and 8.2 *E. needhami* per gram of *Cladophora*.

Food Availability and Diet

Cladophora in the Tippecanoe River provided *E. needhami* with several potential food items. An extensive epiphyte community was often present on the *Cladophora*, and the filaments also collected detritus (Fig. 2b, 2c). *Cocconeis* sp. was by far the most abundant epiphyte, with *Achnanthes* sp., *Navicula* sp., *Gomphonema* sp., *Fragilaria* sp., and *Melosira* sp. present in smaller percentages. The epiphyte community increased as the season progressed (Fig. 3). Visual observations revealed that detritus also accumulated on the *Cladophora* as the season progressed. Quantitative measurements of the detritus were not possible because of the difficulty in removing the *Cladophora* without losing the unsecured detritus. A progressive increase in loading of detritus on *Cladophora* was noted in the artificial stream, the other two observational arenas, and the field. Larvae observed in the laboratory in early May were thus actually exposed to a higher level of detritus than was present in the field at the time. *Cladophora* growth, as measured by filament width (Fig. 4) showed an increase between 28 April 1988 and 24 May 1988, but remained the same between 24 May 1988 and 31 May 1988.

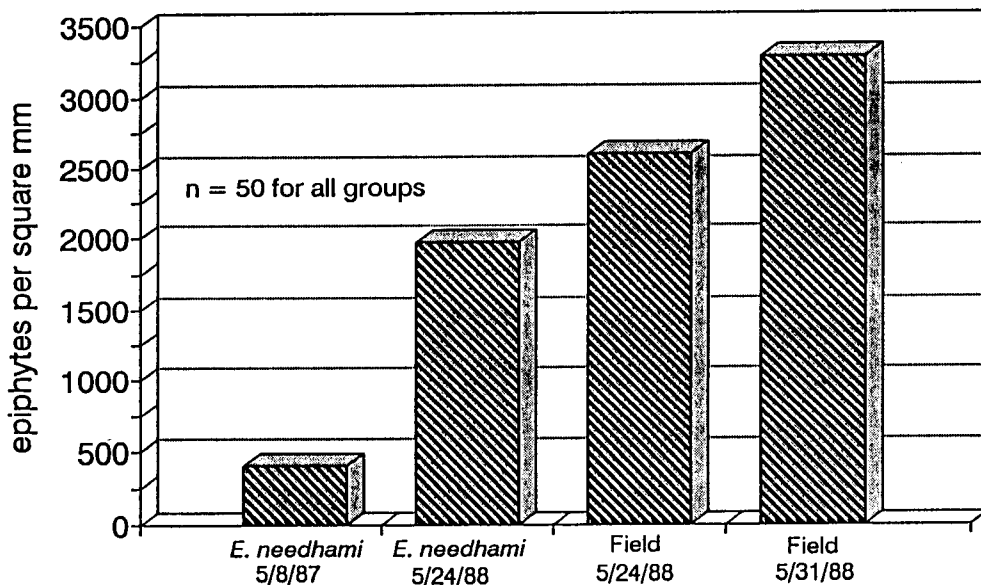


Figure 3. Number of epiphytes found per mm^2 of *Cladophora* filament. Filaments were collected from both *E. needhami* guts and directly from the field. All four values are significantly different (Student's T-Test, 95% confidence level).

In addition to the *Cladophora*, diatoms, and detritus, a number of potential prey animals were found among the *Cladophora* filaments including individuals of Chironomidae, Simuliidae, Hydropsychidae, and other mayflies from families such as Baetidae and Caenidae. Two species of Plecoptera were also present; their gut contents indicated that one was a detritivore and the other a predator feeding mainly on midges and baetid mayflies.

Ephemerella needhami in the field and in the laboratory primarily consumed *Cladophora*, diatoms and detritus (Fig. 5). Three major study groups of *Ephemerella needhami* (Laboratory, Field 1987, Field 1988) contained the same percentage of diatoms in their guts, but differed significantly (Student's T-test, 95% confidence level) in the relative amounts of *Cladophora* and detritus consumed. Animal parts, midge remains, filamentous algae other than *Cladophora*, and unicellular algae accounted for less than 1% of the gut contents in all cases. The average width of *Cladophora* filaments in the gut was less than that found in the field, and only slightly larger than the average width of terminal filaments (Fig. 6).

Feeding Observations

Larvae used two distinct methods of feeding on *Cladophora*. One method involved using the maxillae to remove detritus and other material from the *Cladophora* filaments; the second method employed the mandibles to bite off portions of *Cladophora* filaments. Thus, the two methods differed in both the type of material ingested and the mouthpart used as the primary food gathering tool. Filaments and diatoms in the gut were often relatively intact.

We observed and photographed one larva as it attacked and fed on a midge (Chironomidae: Orthoclaadiinae: *Cricotopus*) that had been feeding on *Cladophora* and associated material. Soft tissues and internal materials, including the gut and its contents, were ingested beginning at the posterior end, but the cuticle of the midge was not eaten. A little over half of the midge's abdomen was eaten. When the gut contents remaining in the midge and those of the mayfly were analyzed afterwards, we found that the gut contents of both organisms were similar, containing *Cladophora*, detritus, and diatoms. The only recognizable midge body part in the gut of the mayfly was a small section of trachea.

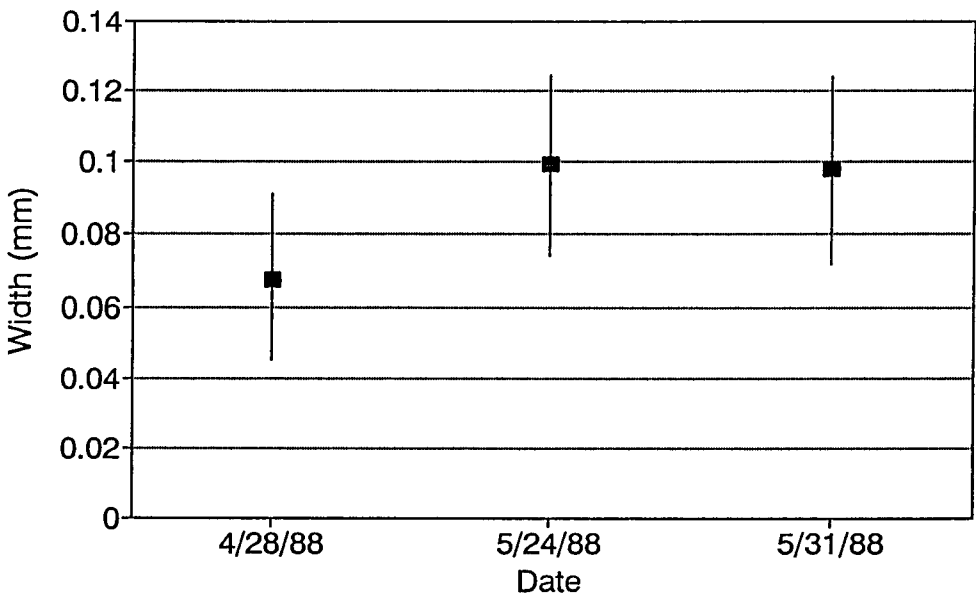


Figure 4. Mean width of 50 randomly selected *Cladophora* filaments. The bars cover the range of values. There was a significant difference between the average width on 4/28/88 and the two other dates (Student's T-Test, 95% confidence level).

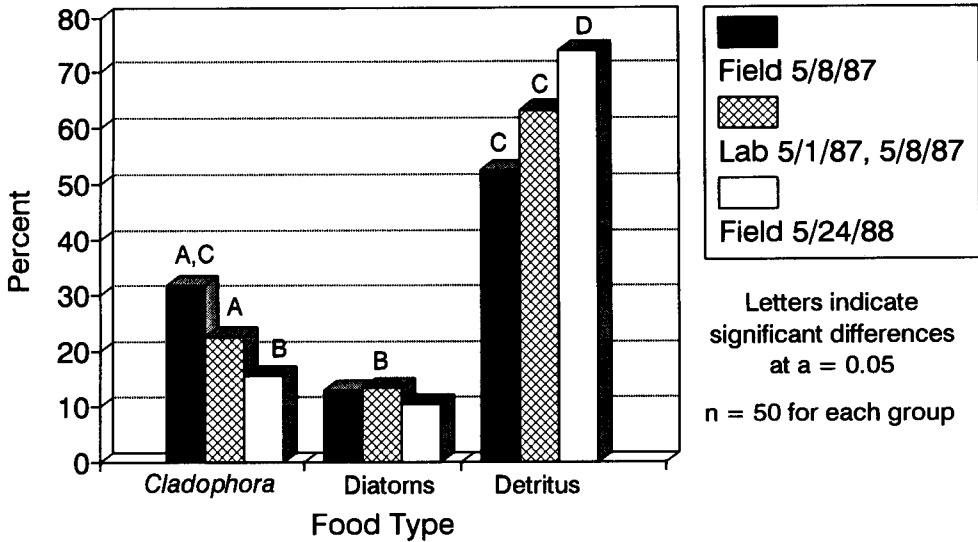


Figure 5. Gut contents of *Ephemera needhami* larvae collected in the field or raised in the laboratory.

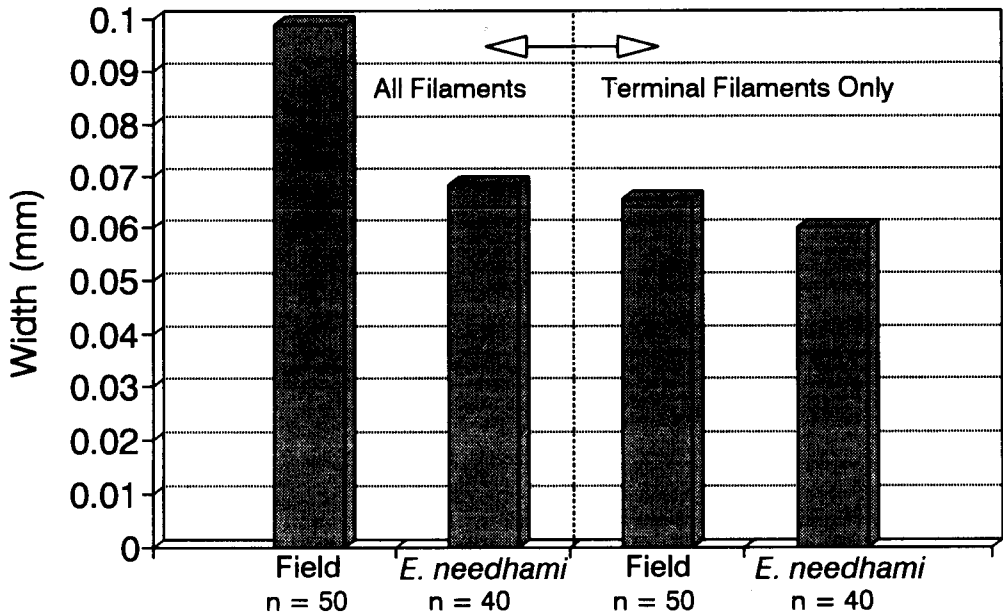


Figure 6. Mean width of *Cladophora* filaments collected from the field and from gut samples of *E. needhami*. The two bars to the right represent averages of terminal filaments (as determined by branching) only. The field sample of all filaments was significantly different from the other three samples (Student's T-Test, 95% confidence level).

DISCUSSION

Ephemerella needhami appears to be specialized for living with *Cladophora* in a number of ways. For one, the life history of the mayfly is well-coordinated with that of the associated *Cladophora*. Data collected over four years show that the seasonal presence of middle to late instar larvae was always correlated with presence of *Cladophora*. We assume that the very small percentage of larvae found on rocks without *Cladophora* were due to recent drift. Leonard & Leonard (1962) also found the larvae associated with vegetation, and their emergence data are consistent with ours in revealing a univoltine life cycle with emergence occurring when *Cladophora* mats begin to break up in late spring.

Features of *E. needhami* larvae that appear to suit them to life in the *Cladophora* microhabitat include the well-developed dorsal spines (Fig. 1b) on the abdomen and a distinct dorsal color pattern. The paired dorsal spines that occur on abdominal segments 2-8 curve posteriorly and serve as hooks to moor the larvae among the *Cladophora* filaments and would appear to easily catch on the filaments if the larva became dislodged. Similar morphology and function has been observed for other aquatic insects, including *Ephemerella ignita*, a European species found among vegetation (Hynes 1970).

Color patterns among the larvae at the Tippecanoe River range from a dark brown to dull green, with a very large proportion of the larvae being black with a highly contrasting yellowish green dorsal stripe. The dark brown color is typical of old, epiphyte and detritus encrusted *Cladophora*, while the green is typical of newer growth. These colors may help the larvae avoid visual predators. The combination of a dark larva with a green dorsal stripe may be an adaptation to disguise body outlines, or a compromise between coloration matching old or new *Cladophora* growth. Research on the population genetics and ecological significance of these color morphs is needed.

The diet of *E. needhami* also demonstrated the close ties of the mayfly to *Cladophora*. Based on gut content data and feeding observations, *E. needhami* is best described as a collector-gatherer according to the FFG categories of Cummins & Merritt (1984), and our classification of this species is thus consistent with the placement of the genus by Cummins et al. (1984). Such a classification would also be consistent with the diet of this species as reported by Shapas and Hilsenhoff (1976); their observations on diet are very similar to ours. This species is opportunistic and is able to function to some extent as a herbivore feeding on *Cladophora* (shredder FFG) or as a predator (predator - engulfer FFG). Because it does not use setae to gather its food, we do not consider *E. needhami* to be able to function as a brusher (McShaffrey & McCaffrey 1986, 1988).

Ephemerella needhami larvae do appear to be selective in ingesting food. The proportion of epiphytic diatoms ingested was the same for all larvae (three major study groups) tested, but the number of these epiphytic diatoms available to each of the three study groups was significantly different. In particular, the data for 24 May 1988 show that the larvae consumed filaments with significantly fewer epiphytes than were present on filaments in the field. In addition, individuals in situations where more detritus was available, namely the late season and the laboratory, consumed relatively more detritus and less *Cladophora*.

The apparent preference of detritus over other food items has several possible explanations. The observed response could be a simple response to increased detritus availability with no selection involved. Also, the detritus was the easiest food to ingest. Observations of feeding revealed the relative difficulty of biting off *Cladophora* filaments as compared to detritus feeding (as measured by handling time). There was an upper size limit of filament width that could be ingested. The largest filaments ingested were only about 0.1mm wide; the size of

the average filament ingested was smaller than those available in the field. The average filament width of *Cladophora* in the gut samples was comparable to the width of terminal filaments in the field, suggesting some preference for the terminal filaments, which were smaller. Epiphytes, particularly *Cocconeis* sp., were also difficult to remove and ingest. We did not observe any direct removal of *Cocconeis*, although some frustules not associated with filaments were found in the gut. The smaller number of epiphytes on *Cladophora* in the gut samples compared to the field samples was probably due to the ingestion of a higher proportion of terminal filaments, which, being younger, bore fewer epiphytes.

Another possible explanation of the preference of detritus could be related to the nutritive values of the food materials. However, whereas all three types of food have similar caloric values, the epiphytes and *Cladophora* normally have higher carbon to nitrogen ratios (Cummins & Klug 1979) and are thus more nutritionally complete. Anderson & Cummins (1979) rated detritus as the least nutritious and living algae, particularly diatoms, as being more nutritious. Shapas and Hilsenhoff (1976) documented *Ephemerebella* spp. that shifted their diets seasonally by varying the amount of detritus ingested.

Feeding on *Cladophora* by aquatic insects is apparently rare (Hutchinson 1981), perhaps because *Cladophora* contains poisonous fatty acids (Lalonde et al. 1979). Brown (1960) did find that the mayfly *Cloeon dipterum* Linnaeus would feed on *Cladophora*, but *Cladophora* was not ingested as frequently as other filamentous algae unless it was chopped up. Mechanically cutting the filaments would decrease the mechanical feeding problems discussed above, and it might release potential toxins before they are ingested by the larvae.

Overall, *E. needhami*'s diet appeared opportunistic and seemed to balance the relative advantages and disadvantages well. Early in the *Cladophora* season, when detritus was rare on the algae, relatively more *Cladophora* was consumed. Later in the season, when detritus was abundant, detritus was taken in greater proportions than *Cladophora*, and any potential problems with toxins were thus reduced. The relatively constant ingestion of epiphytes may reflect a need for some portion of high-quality food. Whether this shift in feeding reflects actual food preference or a passive response to changing environmental conditions (detritus availability, filament width) was not apparent and requires further study. Observations of small larvae collected in 1989 suggest that their diet is similar to mature larvae, although they may opportunistically exploit the bloom of benthic diatoms that precedes *Cladophora* mat development in the Tippecanoe River. Even at this stage, however, young larvae were associated with the sparse *Cladophora* already present, and some algal filaments were in their guts. It is probable that even earlier instars are detritivores, given the habits of the later instars and the detritivorous habits of other early instar mayfly larvae, even those which later specialize on other foods (Edmunds 1984). A single laboratory observation that these very early instars are interstitial in habitat would also suggest they are detritivores.

It is not clear what effect the feeding of *E. needhami* larvae has on the *Cladophora*. Generally, removal of detritus and epiphytes, which block out sunlight and nutrients, may be beneficial to the *Cladophora* (Whitton 1970). Since it appears that *E. needhami* larvae feed primarily on terminal filaments, the removal of these filaments may stimulate growth and branching of the *Cladophora*, but this has not been demonstrated. If the effect of *E. needhami* larvae feeding on the *Cladophora* is negative, then perhaps the epiphytes and detritus are beneficial to the *Cladophora* by either shielding it mechanically from ingestion, or serving as an alternate food source.

The reduction of *Cladophora* in the Tippecanoe River in late May is probably not the result of *E. needhami* feeding. For example, *E. needhami* apparently feeds only on the terminal filaments, and it is evidently not able to ingest the wider basal filaments. In any case, *Cladophora* shows seasonal growth patterns (Brown 1908, Whitton 1970), for unclear reasons (Whitton 1970). Possible explanations for the decline of *Cladophora* include temperature increases, accumulation of epiphytes and detritus reducing light and nutrient availability, and changing nutrient levels (Whitton 1970). Recently, Creed (1988) suggested a situation where crayfish could be responsible for reduction of *Cladophora* mats.

The observation of a predatory encounter was important because it illustrated the opportunistic nature of *E. needhami*. The degree of importance of carnivory in the life cycle of *E. needhami* is not clear, and we were not able to document other instances of predation. The fact that the mayfly consumed the midge without ingesting any recognizable hard body parts of the midge is disturbing because it exemplifies the danger of assessing feeding habits based only on gut contents; in this case the gut contents of the predaceous mayfly deceptively appeared similar to both those of the midge and other *E. needhami* that had fed only on detritus, *Cladophora*, and diatoms.

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