

Feeding Behavior and Related Functional Morphology of the Mayfly *Ephemerella needhami* (Ephemeroptera: Ephemerellidae)

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The feeding behavior and functional morphology associated with feeding in Ephemerella needhami McDunnough larvae were studied using videomacroscopic techniques, gut content analysis, and scanning electron microscopy. Two stereotypic feeding cycles were employed by the larvae. In the maxillary brushing cycle, the maxillae are the primary food-gathering organs, with the main food being detritus deposited on the filamentous alga Cladophora. In the mandibular biting cycle, the mandibles are the primary food-gathering organs used to bite Cladophora filaments. Epiphytic diatoms on Cladophora were another important part of the diet. Behavioral similarities are apparent in the choreography and synchronization of mouthpart movements among mayflies from several families. Functional morphological comparisons are drawn with hypognathous E. needhami, Cloeon dipterum, Baetis rhodani, and Siphonurus aestivalis, as well as the prognathous Heptageniidae. Differences in mouthpart usage and structure are related to the relative development of setal fields and combs and the feeding microhabitat.

KEY WORDS: feeding behavior; morphology; Ephemerellidae; videomacroscopy.

INTRODUCTION

Studies of behavior and functional morphology associated with feeding in aquatic insects are important tools in understanding ecological and evolutionary relationships. Historically, most of such work has been either anecdotal or spec-

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ulative, with casual observations of feeding behavior in one species often applied to any organisms with similar morphology. More recent work has emphasized rigorous observational methodology such as videomacroscopy, combined with the detailed morphological descriptions made possible by scanning electron microscopy (SEM).

Our previous studies (McShaffrey and McCafferty, 1986, 1988) of functional morphology in mayflies have centered on Heptageniidae, a group with modified, prognathous mouthparts. For the present study, we examined the functional morphology and behavior associated with feeding in *Ephemerella needhami*, a member of the family Ephemerellidae. These mayflies have more generalized, hypognathous mouthparts which resemble those of such primitive mayfly lineages as the Siphonuridae. Since several other mayfly families, including the primitive Siphonuridae, have many hypognathous species, an understanding of the general functionality of hypognathous mouthparts is critical for ecological interpretations. For similar reasons, comparative studies of mouthpart morphology and feeding behavior among these groups is important in understanding evolutionary relationships. Unfortunately, little research has been completed on this subject. Published research on the Heptageniidae includes that by Strenger (1953), Froehlich (1964), Soldan (1979), and McShaffrey and McCafferty (1986, 1988). Studies on feeding behavior and functional morphology of mouthparts among hypognathous mayflies were conducted by Brown (1960, 1961) on *Cloeon dipterum* L. and *Baetis rhodani* Pictet (Baetidae) and by Schonmann (1975, 1981) on *Siphonurus aestivalis* Eaton (Siphonuridae).

Little ecological information on *E. needhami* has been published. Ecological studies concerning the diet of organisms may give clues to the function of their mouthparts. Whereas some work on the diet of some ephemerellids has been conducted, nothing has been published regarding the diet of *E. needhami*. According to Cummins *et al.* (1984) the *Ephemerella* belong to the collector-gatherer and scraper functional feeding groups (FFGs). Hawkins (1985) described a western species, *E. infrequens*, as a diatom scraper, detritus shredder, and collector-gatherer. Sweeney and Vannote (1981) studied six species of ephemerellids, two of which belong to the genus *Ephemerella*; all of the ephemerellids in their study fed on diatoms and detritus.

The present study is the first to combine modern techniques such as scanning electron microscopy (SEM) and videomacroscopy to investigate the feeding habits of the Ephemerellidae. During the course of the study, additional data regarding the diet of *E. needhami* and its ecological association with the filamentous alga *Cladophora* were gathered, details of which are being published elsewhere.

METHODS

We collected *Ephemerella needhami* in the Tippecanoe River, a sixth-order stream in north central Indiana. At the collection site, the river was 50 m wide and had a cobble-gravel substrate and an open canopy. Fieldwork was conducted over 4 successive years: 1985, 1986, 1987, and 1988. In 1985 weekly presence/absence surveys were conducted, and similar sampling on a less regular basis was conducted in 1986. A total of 35 organisms collected on 1 May 1987 and 8 May 1987 was used for detailed videomacroscopic behavioral analysis and subsequent gut content analysis. Additional larvae were collected for less detailed videomacroscopic behavioral observation, gut content analysis, and morphological examinations by light microscope and SEM. Throughout the study, only mature larvae, as judged by relative wing-pad development (McCafferty and Huff 1978) and head capsule width (1.1–1.6 mm), were used. To ensure correct species identification, only larvae with a yellowish-green dorsal stripe, which is typical of *E. needhami*, were used in this study.

Larvae used in videomacroscopic behavioral analyses were maintained in the laboratory in an artificial stream consisting of two reservoirs constructed of clear acrylic measuring $30 \times 30 \times 30$ cm with a mean depth in operation of 20 cm. The reservoirs were connected by a channel, also made of clear acrylic, measuring 15 cm deep \times 11.5 cm wide \times 1.2 m long. Water was pumped from the downstream reservoir to the upstream reservoir through a 1.25-cm-diameter nalgene hose by a submerged pump provided with a silicon-controlled rectifier (SCR). The SCR allowed current speed in the channel to be regulated between 0 and 1.5 m s^{-1} , depending on the configuration of substrate in the channel and depth of water in the reservoirs. Water in the channel varied between 0 and 7 cm over the substrate.

The channel was filled with substrate from the collection site, including rocks with attached filamentous green alga *Cladophora*. Aeration was provided by airstones in the downstream reservoir; light was provided by a 45-cm, 15-W fluorescent light placed 15 cm over the channel bottom and operated 24 h/day. Water temperature was equal to room temperature, 20–25°C.

The videomacroscopic techniques used have been described in detail elsewhere (Keltner and McCafferty, 1986; McShaffrey and McCafferty, 1986, 1987, 1988). For this study, the observational methodology developed for the study of heptageniid mayflies was adapted to ephemerellids. Because of *E. needhami*'s strong affiliation with *Cladophora* as both substrate and food source, the alga was always included in the observational arenas. Three configurations of observational arenas and appropriate videomacroscopic equipment were used. These were (a) a shallow observation flow cell (McShaffrey and McCafferty,

1986, 1988) filled with *Cladophora* and operating at "high" current speeds (5–10 cm⁻¹); (b) the artificial stream described above, observed by means of the videocamera coupled to a 50-mm lens by a bellows unit; and (c) a 9 × 7.5 × 2-cm enclosure with 1.5-cm-deep water into which the *Cladophora* and *E. needhami* were placed and observed by means of the videocamera attached to a stereoscope. No flow or aeration was used in the latter configuration. Since *E. needhami* larvae in the field were observed to feed actively during daylight hours, visible light supplied by a fiber-optic illuminator was used in all video-macroscopic observations.

In all cases, food for the experiments was *Cladophora* and associated detritus, periphyton, and animals. After videotaping, the organisms were sacrificed to obtain gut contents and mouthparts. Both gut contents and mouthparts were then mounted on separate microscope slides for examination. Gut contents were classified as being *Cladophora*, epiphytes, detritus, or animal parts and quantified to determine the percentage composition of the diet using a Whipple ocular disk.

Several hundred complete feeding sessions were observed. Of these, 11 feeding sessions, each composed of multiple (> 10) feeding cycles, were analyzed in detail. The 11 sessions analyzed in detail were performed by nine different individuals and included seven sessions of detritus feeding, three sessions of *Cladophora* feeding, and one predatory encounter. All of the sessions chosen for detailed study were observed using configuration a or c; the observations made in the artificial stream were not at a great enough magnification for detailed study. The descriptions generated by these analyses were then checked against the remaining sessions, including those made in the artificial stream, as recorded on videotape. Feeding behavior was described as stereotypic feeding cycles composed of definite stages, using the same methodology as employed by McShaffrey and McCafferty (1986, 1988); this methodology is adapted from that used by Trueman (1968) and Keltner and McCafferty (1986). Each stage is delineated by specific movements of either the maxillae or the mandibles.

Mouthpart structures were examined using light microscopy and SEM. Specimens were prepared for SEM by dehydration in increasing concentrations of ethanol from 75 to 100%, then transferred to 50% ethanol, 50% xylene and allowed to stand for 12 h. The specimens were then transferred to 100% ethyl acetate. Some of the specimens in 100% ethyl acetate were sonicated for 1 min in an ultrasonic cleaner to remove food material from the mouthparts; others were not sonicated so that the position of food on the mouthparts might be determined. The larvae were then either dissected or transferred whole to the SEM stubs after air-drying.

RESULTS

General Observations

Ephemerella needhami is a common stream-dwelling mayfly that occurs throughout eastern and central North America. It is generally found in association with filamentous algae. Our study population of larvae was always found in association with mats of *Cladophora* that developed in the Tippecanoe River each April and persisted through May. Densities of larvae on May 24, 1988, were 5.8 *Ephemerella needhami*/cm³ of *Cladophora* and 8.2 *Ephemerella needhami*/g (damp weight) of *Cladophora*. Emergence of adult *E. needhami* occurred in late May each year. Larvae in the field and laboratory consistently showed a strong preference to associate with the *Cladophora* filaments. In the field and in the laboratory, larvae were consistently positively rheotactic and preferred to climb on *Cladophora* filaments as opposed to other substrates such as rocks. In the laboratory, larvae were able to maintain their position among the filaments at current speeds comparable to those found in the field. Individuals in the artificial stream in the laboratory climbed and foraged among the *Cladophora* filaments during the daytime; no night observations were made.

Gut content analyses of larvae collected in the field and those observed in the laboratory revealed a diet consisting of detritus, *Cladophora* filaments, and epiphytic diatoms that occurred on the *Cladophora* filaments. Detritus was the most common component, and the larvae ingested relatively more detritus when detritus availability was high. Epiphytic diatoms were taken in similar proportions in all cases, but *Cladophora* intake declined when detritus intake increased. Details of proportionalities of diet and their significance are treated elsewhere.

Effects of Experimental Conditions on Feeding Behavior

Observations of feeding behavior of *E. needhami* larvae in the field and in the artificial stream were similar to those made under the more restricted conditions of the observation cells, with no observable difference in stereotypic feeding movements of the mouthparts. One aspect of the experimental conditions that did affect foraging behavior was the visibly larger load of detritus borne by *Cladophora* in the laboratory. Whereas *Cladophora* used in behavioral observations was freshly collected and thus bore a similar number of epiphytes compared to those in the field, once placed in the observation cells or artificial stream the *Cladophora* quickly picked up additional detritus.

Stereotypic Feeding Behavior

Resting Position

Larvae not actively feeding hold their mouthparts in a characteristic resting position (Figs. 1, 2, 3, and 4a) which is nearly hypognathous. The labial palps are normally somewhat extended and free of the other mouthparts. In a foraging larva they will constantly be moving, touching the *Cladophora* filament and associated material. The remainder of the labium is drawn anteriorly and dorsally to form the ventroposterior boundary of the preoral cavity. The glossae and paraglossae are in contact anteriorly with the posterior apices of the galealaciniae, which in turn are held with their anterior surfaces in contact with the superlinguae of the hypopharynx. The superlinguae contact the distal ends of the mandibles anteriorly; the lingua is held pressed against the mandibles at the molae. The mandibles are positioned with the distal apices separated by the width of the glossae. The labrum covers the mandibles anteriorly.

Feeding Cycles

Two distinct behavioral cycles were observed. One occurs when the larvae are removing detritus and other material from the *Cladophora* filaments and is

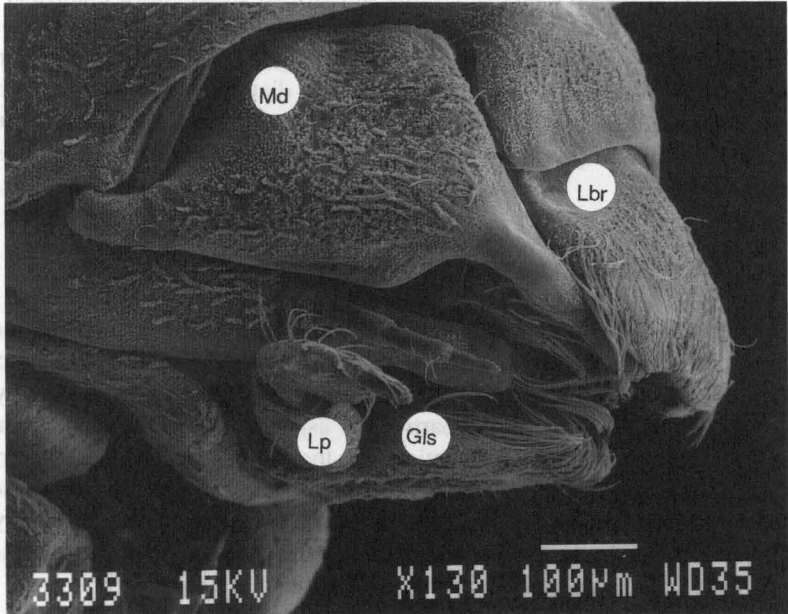


Fig. 1. SEM micrograph showing lateral view of mouthparts of *Ephemera needhami*. Scale bar = 100 μm . Gls, glossa; Lbr, labrum; Lp, labial palpus; Md, Mandible.

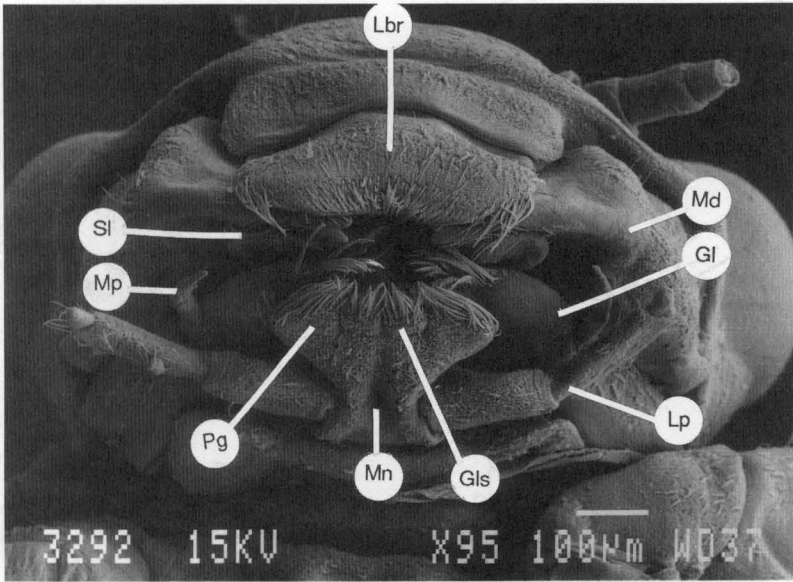


Fig. 2. Ventral view of *E. needhami* mouthparts. Scale bar = 100 μ m. Gl, galealacinia; Gls, glossa; Lbr, labrum; Lp, labial palpus; Md, mandible; Mn, mentum; Mp, maxillary palpus; Pg, paraglossa; Sl, superlingua.

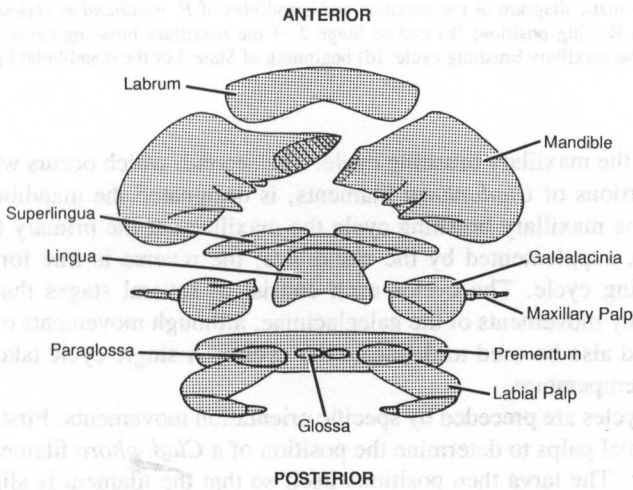


Fig. 3. Diagrammatic view of the relative positions of the mouthparts in *E. needhami*.

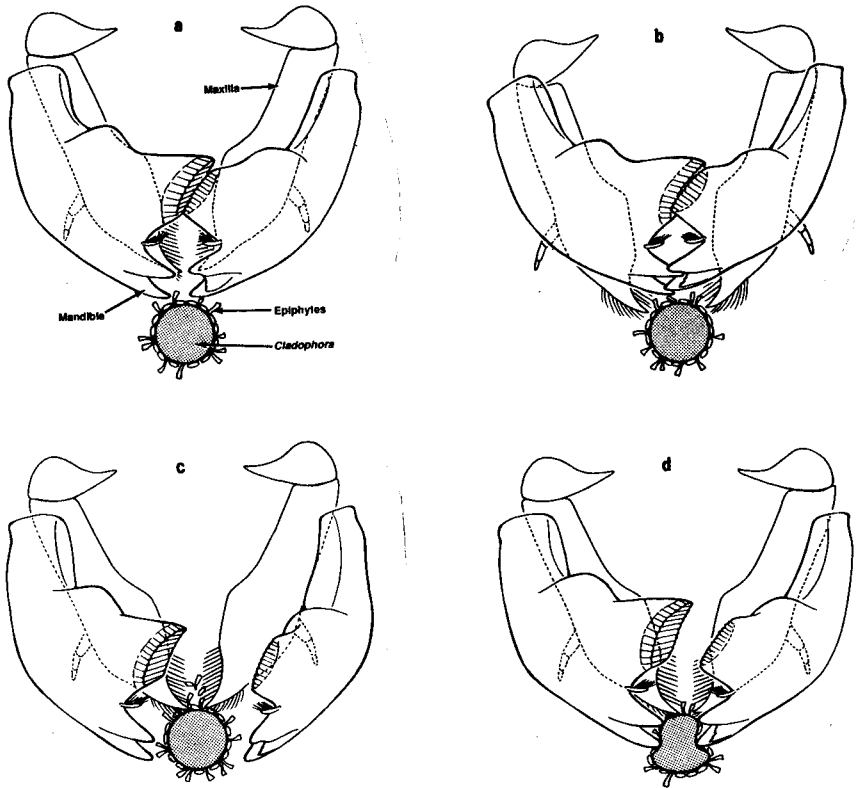


Fig. 4. Schematic diagram of the maxillae and mandibles of *E. needhami* at various stages of feeding. (a) Resting position; (b) end of Stage 2 of the maxillary brushing cycle; (c) end of Stage 3 of the maxillary brushing cycle; (d) beginning of State 3 of the mandibular biting cycle.

designated the maxillary brushing cycle. The second, which occurs when larvae bite off portions of *Cladophora* filaments, is designated the mandibular biting cycle. In the maxillary brushing cycle the maxillae are the primary food-gathering tools, supplemented by the mandibles; the reverse is true for the mandibular biting cycle. The cycles each consist of several stages that are here delineated by movements of the galealaciniae, although movements of the mandibles could also be used to delineate the cycles. A single cycle takes 0.3–0.5 s at room temperature.

Both cycles are preceded by specific orientation movements. First, the larva uses the labial palps to determine the position of a *Cladophora* filament relative to the body. The larva then positions itself so that the filament is aligned with its length parallel to the long axis of the body. Next the foreclaws are hooked

on either side of the filament aligned with the larva, or onto other nearby filaments, and are adducted, thus bringing the filament and the mouthparts together. The labial palps may assist in bringing the filament and mouthparts together. As the feeding cycles proper are about to commence, the larva is positioned with the algal filament traversing the preoral cavity, contacting the midline of the labrum anteriorly and the glossae posteriorly.

Maxillary Brushing Cycle

Stage 1. Initial Abduction of the Galealaciniae. As feeding commences, the galealaciniae move laterally outward while the mandibles move slightly inward toward the midline.

Stage 2. Final Orientation. The distal segments of the labial palps and/or the tibiae of the forelegs are adducted, bringing the head and filament into contact. This movement may be accompanied by a forward motion of the whole body induced by a rotation of the forelegs at the coxae. At this point the galealaciniae are fully open, and the mandibles fully closed (Fig. 4b).

Stage 3. Adduction of the Galealaciniae. The galealaciniae are adducted, moving medially with the terminal spines and setae (Fig. 5) being drawn over the filament surface. The spinous processes dislodge material from the filament; this material is filtered out by the lanceolate bipectinate setae on the crown of

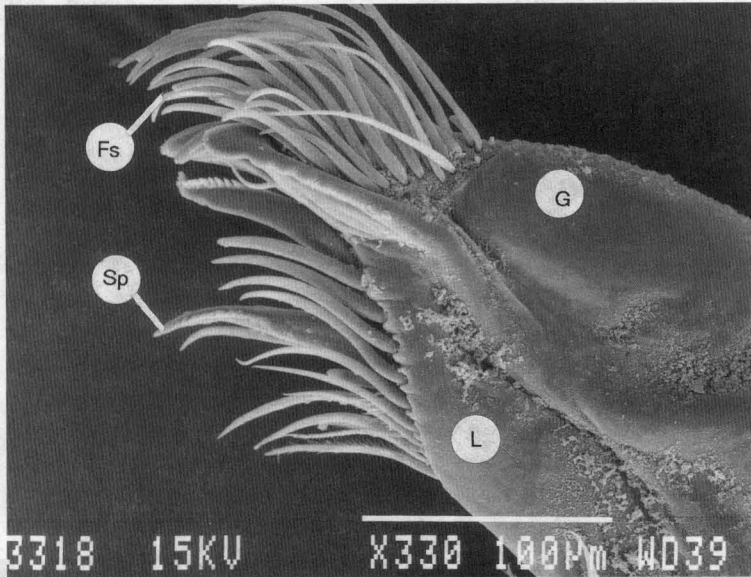


Fig. 5. Distal end of galealacinia of *E. needhami*, posterior view. Scale bar = 100 μ m. Fs, filtering setae; G, galea; L, lacinia; Sp, spinous process.

the galealaciniae (Fig. 6). The final position of the galealaciniae is with the distal ends meeting at the midline and inserted between the superlinguae and the lingua of the hypopharynx. While the galealaciniae are moving medially, the mandibles are being abducted laterally (Fig. 4c).

Stage 4. Food Deposition and Subsequent Abduction of the Galealaciniae. As the galealaciniae are abducted from the midline to begin a new cycle, food material is deposited on the superlinguae and lingua and, to a lesser degree, on the anterior surface of the paraglossae. The mandibles at this point are being adducted medially and may pick up detritus and other material from the *Cladophora* filament substrate. As the galealaciniae clear the hypopharynx, and the mandibles return to the midline, the mouthpart configuration is the same as it was in Stage 1. Feeding continues with a repetition of Stages 2, 3 and 4.

Mandibular Biting Cycle

The mandibular biting cycle is similar to the maxillary brushing cycle in many respects, with the main difference a replacement of the maxillae by the mandibles as the primary food-gathering tools. In our observations this cycle was performed only as a modification of an ongoing maxillary brushing cycle.

Stage 1. Adduction of the Galealaciniae. When feeding shifts from a max-

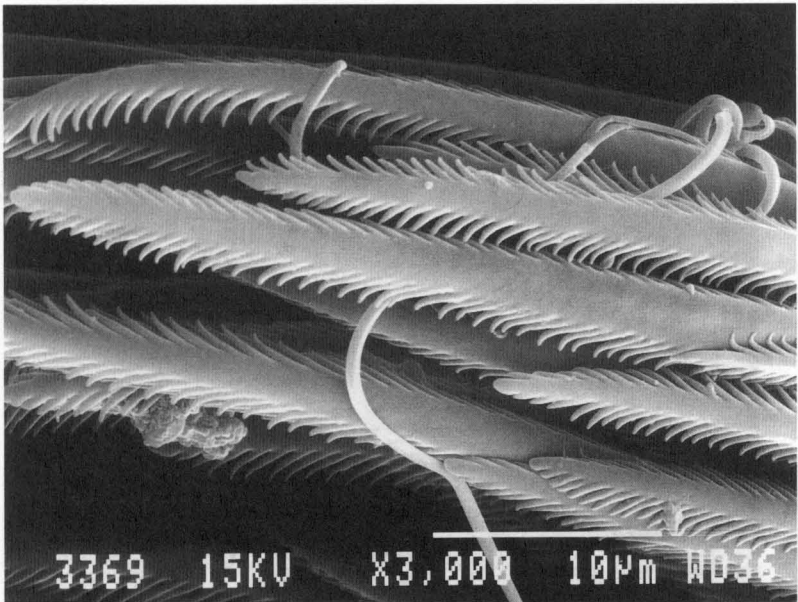


Fig. 6. Magnified view of bipectinate filtering setae on the galealacinia. Scale bar = 10 μm .

illary brushing cycle to a mandibular biting cycle, the Stage 3 adduction of the galealaciniae becomes the first stage of the mandibular biting cycle.

Stage 2. Final Orientation. Final orientation takes place with the galealaciniae closed and the mandibles fully open. The head and filament are brought into close contact in a fashion similar to that of the maxillary brushing cycle.

Stage 3. Abduction of the Galealaciniae and Biting. As the galealaciniae are abducted laterally, the mandibles are adducted medially and the distal ends of the mandibles bite into the filament (Fig. 4d). Often the pressure of the mandibles will cause the filament to bend abruptly, usually 90° in a direction ventral to the larva. When the filament has already bent, the closing of the mandibles acts to pull the filament slightly further into the preoral cavity.

Stage 4. Adduction of the Galealaciniae. As the mandibles reach the midline, the galealaciniae are adducted medially and may pass over the filament as they move inward. As they pass over the filament they gather available loose diatoms and detritus, in addition to material partially dislodged by the mandibles. The mandibles are abducted laterally as the galealaciniae reach the preoral cavity. The closing of the galealaciniae at this point serves to hold the filament in place while the mandibles are positioned for the next bite and may also force the filament further into the mouth. Feeding continues with a repetition of Stages 2, 3, and 4.

Predatory Feeding

One individual was observed to attack and ingest a midge (Chironomidae: Orthocladiinae: *Cricotopus*) that had been feeding on *Cladophora* and associated material. Because the mayfly was moving quickly, the initial stages of the attack and penetration of the midge cuticle were not observed. The mayfly fed using a maxillary brushing cycle, with both the maxillae and the mandibles packing midge tissue into the preoral cavity. The cuticle of the midge was not eaten. The mayfly consumed the posterior half of the midge over a period of 319 s, with individual cycles lasting about 0.3 s each.

The midge lived throughout the attack and even fed actively during its early stages; the midge was still alive when removed from the observation cell. 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.

Food Processing

Food brought to the preoral cavity by the maxillae in either cycle is deposited on the hypopharynx and paraglossae. Medially directed setae on the superlinguae and paraglossae strip food material from the apical setae of the galealaciniae during Stage 4 of the maxillary brushing cycle or Stage 3 of the

mandibular biting cycle and hold it in place. When the galealaciniae return in Stage 3 of the maxillary brushing cycle or Stage 4 of the mandibular biting cycle, they push the material stripped on the previous cycle farther medially toward the base of the hypopharynx. The hypopharynx in turn pushes the material at its base between the molae, which are moving apart. As the molae close (Stage 4 of the maxillary brushing cycle or Stage 3 of the mandibular biting cycle) they strain excess water from the material and force the material into the mouth.

Small pieces of food brought to the mouth by the mandibles may be retained by dorsomedially projecting setae on the inside of the labrum or by the medially projecting setae on the superlinguae. The material on the superlinguae is treated as already described; material on the labrum is forced dorsally by fresh material and is thus placed on the epipharynx to be pressed into the area between the molae. Filaments are directed into the oral cavity by the labial palps, galealaciniae, mandibles, and tip of the hypopharynx. Eventually the mandibles and/or the maxillae are able to cut the filament and it is swallowed. Filaments in the gut are reasonably intact.

DISCUSSION

Our studies of feeding behavior show that *E. needhami* is an opportunistic member of the *Cladophora* mat community that relies on two simple, closely related feeding cycles to obtain its food. The observations themselves, while requiring the organisms to be confined to several different artificial situations, were nonetheless consistent with each other. They also approximated feeding in the field as shown by gut content analyses, with larvae in laboratory and field conditions all feeding on the same food items. The stereotypic nature of feeding movements in larval mayflies, despite artificial conditions, has been well documented (Brown, 1961; Froehlich, 1964; McShaffrey and McCafferty, 1986, 1988).

The two feeding cycles complement each other in the type of food that is acquired. The maxillary brushing cycle allows loose material such as detritus that has been filtered out of the water column by *Cladophora* to be ingested; the mandibular biting cycle allows *Cladophora* filaments and more tightly bound material to be eaten. Together the two cycles account for all of the three main components of the diet—detritus, *Cladophora*, and diatoms. The direct intake of epiphytic diatoms was not observed; many of these diatoms are taken into the gut when the *Cladophora* filament to which they are attached is ingested. It is probable that some diatoms are removed from the algal filaments by the mandibles (Fig. 7) or the spinous processes on the ends of the galealaciniae (Fig. 5), particularly during the maxillary brushing cycle. In addition, measurements of the widths of *Cladophora* filaments found in the gut contents sug-

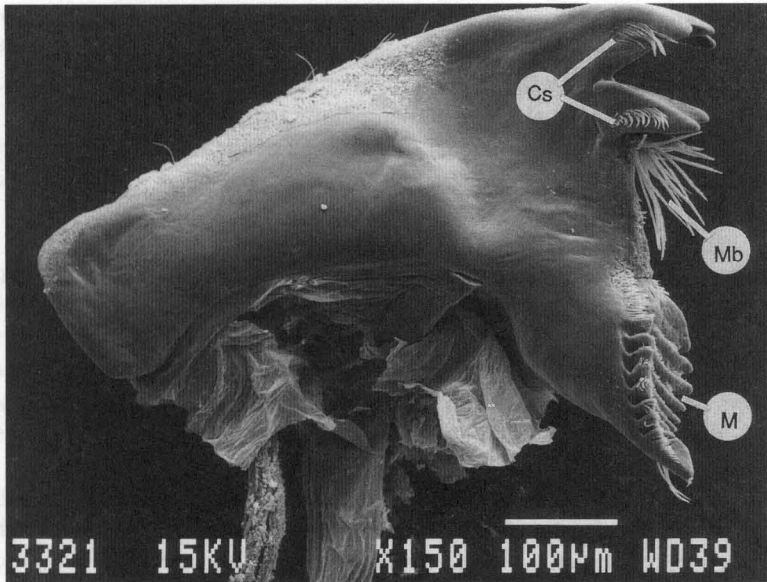


Fig. 7. Right mandible, posterior view. Scale bar = 100 μm . Cs, comb setae; M, mola; Mb, mandibular brush.

gest that a filament width of about 0.1 mm may be the upper size limit for ingestion by *E. needhami*. *Cladophora* in the field was measured at widths up to 0.15 mm; presumably the size limit is a function of some mechanical factor such as molar opening width or mandible strength.

The single predatory encounter most likely represents an isolated opportunistic attack. Although Hawkins (1985) found evidence that some western Ephemerellidae are predators, Sweeney and Vannote (1981) failed to find any animal parts in the guts of other *Ephemerella*. It should be noted, however, that the individual observed in this study consumed one-half of a midge larva and retained only a small, easily overlooked section of midge trachea in its gut. The level of predation by *E. needhami* in the field remains unknown.

Brown (1961) reported a feeding sequence for *Cloeon dipterum* that was essentially the same as the mandibular biting cycle described for *E. needhami*. The main difference was that *C. dipterum* used its labial palps to obtain food. Brown's (1961) account of *C. dipterum* feeding on filamentous algae was also similar to our observations of *E. needhami*. The tips of the mandibles were the primary food-gathering organs of *Baetis rhodani* (Brown, 1961), but otherwise it was also similar.

Although his descriptions did not give a precise accounting of sequential movements of the mouthparts, it is clear from Schonmann (1975, 1981) that the

overall feeding and food transport in *Siphonurus aestivalis* were similar to those in *E. needhami*, the main difference being the use of the labial and maxillary palps in *S. aestivalis* to acquire food. Schonmann (1975) was also able to document the use of the labial palps in manipulating algal filaments.

A comparison of the functional morphology of the mouthparts of *E. needhami* with *C. dipterum*, *B. rhodani*, *S. aestivalis*, and other mayflies is useful because it illustrates how behavioral and morphological differences reflect differing habitat and function. In our observations to date (McShaffrey and McCafferty, 1986, 1988, unpublished), we have observed a consistent pattern among mayflies in the primary food-gathering appendages used to obtain detritus or other fine particulate food. This pattern involved the presence of specialized filtering setae that are either pectinate or bipectinate, bearing one or two rows of setules perpendicular to the main setal shaft (Fig. 6). Such setae are also found on internal mouthparts, where it is important that food material be retained for further processing.

Ephemerella needhami has greatly reduced, possibly vestigial, maxillary palps, and the labial palps do not bear filtering setae (Fig. 1); neither of these mouthparts plays an active role in feeding on small particles. The labial palps of *C. dipterum* (Brown 1961) bear numerous setae, although the type was not specified, and the palps are active in feeding on fine particles of detritus. In contrast, the maxillary palps and labial palps of *B. rhodani* are bare and are not active in feeding on fine detritus (Brown, 1961). In *S. aestivalis*, both the labial and the maxillary palps are provided with apical brushes of setae and are active in acquiring small particles. Heptageniid mayflies also commonly have extensive fields of filtering setae on the labial and maxillary palps (Strenger, 1953; McShaffrey and McCafferty, 1986, 1988).

The differences in the distribution of these setae are probably related to habitat. The heptageniid mayflies and *S. aestivalis* feed on flat surfaces where detritus collects on surfaces that are wide relative to the width of the head capsule (Strenger, 1953; Schonmann, 1975; McShaffrey and McCafferty, 1986, 1988). On such surfaces it would be advantageous to cover a larger area with each sweep of the mouthparts and, thus, adaptive to use more of the mouthparts in food gathering. *Ephemerella needhami*, in contrast, feeds in an area where the surface on which the food lies is narrow, and extra coverage by additional mouthparts is not necessary. In any event, the labial palps of *E. needhami* are active in positioning the head in relation to the *Cladophora* filament and are thus not as available for a food-gathering role. *Cloeon dipterum* is somewhat intermediate, feeding both on filaments and on flat surfaces, and the labial palps can be used for food acquisition (Brown, 1961). *Baetis rhodani* faces a different problem; it must feed on particles that are firmly attached to the substrate and that are relatively large in comparison to the mouthparts (Brown, 1961). Filtering setae would presumably be of little use in such a situation.

Another pattern related to food gathering appendages is the modification of parts of the mandibles into combs used for removing particles from the maxillary palps. Among Heptageniidae, in which the distal ends of the mandibles do not reach the substrate, the comb structure of the mandibles is particularly noticeable (Strenger, 1953; McShaffrey and McCafferty, 1986); the trend itself is evident within the Heptageniidae, with well-developed maxillary palps correlated with highly comblike mandibles (McShaffrey and McCafferty, 1988). Comblike structures are not well developed in *E. needhami* and are represented only by a relatively few setae on the posterior surface of the mandible (Figs. 7 and 8), where they may act to strip food material from the galealaciniae. Comblike structures are present in *S. aestivalis* (Schonmann, 1981, Fig. 13d), which does utilize the maxillary palps to obtain food. *Cloeon dipterum* represents a condition similar to *E. needhami*, with only slight development of comblike structures on the mandibles (Brown, 1961, Figs. 3e-g). *Baetis rhodani*, with its mandibles used as the primary food-gathering organs (Brown, 1961), does not possess comblike structures on the mandibles (Brown, 1961, Fig. 5d).

In conclusion, it appears that strong similarities in feeding behavior and functional morphology exists in these mayflies (from several different families) that retain the generalized, primitive, hypognathous type of mouthparts. Vari-

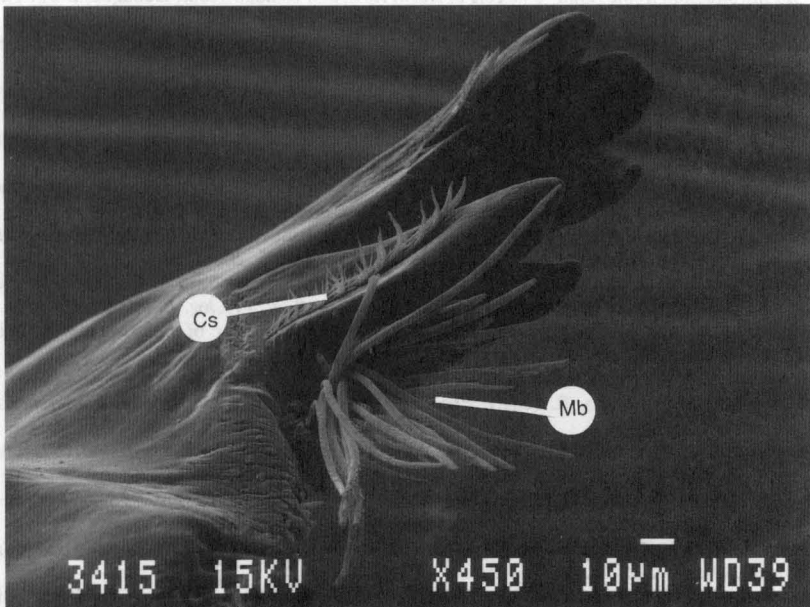


Fig. 8. Right mandible, distal end, dorsal view. Scale bar = 10 Cs, comb setae; M, mola; Mb, mandibular brush.

ations are related primarily to the development of setal fields and combs and the degree to which mouthparts, including palps, are involved in food gathering. These variations, in turn, appear to be generally related to the feeding microhabitat and substrate.

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