

Feeding behavior of *Stenacron interpunctatum* (Ephemeroptera:Heptageniidae)

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Abstract. Larvae of *Stenacron interpunctatum* (Ephemeroptera:Heptageniidae) were observed feeding under naturalistic conditions using macroscopic video techniques. The stereotypic feeding behavior is depicted as a cycle consisting of stages of coordinated movement of the entire suite of mandibulate mouthparts. Depending on experimental conditions this behavioral cycle was modified to enable individuals to brush loosely accreted material from the substratum, gather detritus from deposits, or passively filter detritus from the current. Larvae were most successful in feeding on loose particles of detritus. When presented with attached algae, larvae would attempt to brush the material from the substratum using the labial and maxillary palps with little success in removing tightly accreted material. Feeding observations combined with field and laboratory data on gut content and microhabitat distribution data suggest that *S. interpunctatum* larvae are opportunistic collectors (gatherers).

Key words: *Ephemeroptera*, *Heptageniidae*, *Stenacron interpunctatum*, feeding behavior, morphology, ecology.

An important aspect of any animal's ecology is its role as a consumer. In freshwater ecology, particularly in studies of running water, the consideration of feeding relationships of benthic macroinvertebrates has been crucial to conceptualizing community dynamics and predicting ecological relationships (Cummins 1973, 1974, Vannote et al. 1980). Despite the fundamental importance of such information, feeding habits are often inferred from reports of similar taxa because most species have not received critical autecological study. Conclusions about feeding have usually been based on gut content analyses and casual observations. Unfortunately, gut contents can be misleading because of seasonality and errors introduced in sampling, dissection, and identification of partially digested material (Shapas and Hilsenhoff 1976). It may not be clear which material in the gut is nutritionally important. Casual observations of behavior can seriously underestimate the complexity of an organism's feeding activities.

Perhaps the most difficult task in organizing feeding ecology data is the grouping of organisms into categories descriptive of similar feeding habits. Classifications based on food types are the oldest. Cummins (1973), however, has argued for the need of categories based on functional characteristics. As an example, larvae of the mayfly genus *Stenacron*, which is the

subject of the research reported here, have been placed in a "scraper" functional category by Cummins et al. (1984), defined as consisting of organisms feeding on "attached algae and associated material" (Cummins and Merritt 1984). "Gatherers", defined as organisms that collect detritus from sedimentary deposits, is another functional category in which *Stenacron* was placed (Cummins et al. 1984). Other authors have defined these groups differently; for example, Lamberti and Moore (1984) broaden the definition of scrapers to include organisms that collect material other than algae from crevices in the substratum.

We have studied the functional feeding role of *Stenacron interpunctatum* by analyzing functional morphology and feeding behavior. This approach allows us to define more accurately the feeding role of the animal, and also to make informed estimates about the functional roles of other organisms with similar morphology. Other studies of mayflies have combined observation and morphological analyses (Brown 1960, 1961, Froehlich 1964, Rawlinson 1939, Schönmann 1981, Strenger 1953, 1975). Our study, however, differs considerably by incorporating a recording device for detailed motion analyses, scanning electron microscopy (SEM) for analysis of fine structure and topology, and novel viewing angles. In addition, our primary observation system was designed to

duplicate natural stream conditions (i.e., flow, light levels, orientation) more closely than the studies cited above.

We have chosen *S. interpunctatum* as our prototypic subject because it is common in the eastern half of North America and easily cultured. Furthermore, mature larvae are large enough (head capsule width >2.5 mm) to observe with ease, and individuals continue to feed even under the high illumination often required for documentation. We view this study as ecologically important because *Stenacron* and its relatives in the family Heptageniidae are often important or even dominant in certain lotic habitats (Bednarik and McCafferty 1979). Our objectives in this study were to document the feeding behavior of *S. interpunctatum* and identify the structures used in feeding. Because this study is part of a larger, comparative investigation of the feeding behavior and associated morphology of larval mayflies, we have deferred critical study of the nutrition of this species, and we have not attempted to prepare a complete ethogram of its behavioral repertoire.

Methods

Organisms were collected from early spring to late fall from cobble substrate in the Tippecanoe River in north-central Indiana, and were maintained in the laboratory in large aquaria filled with substratum and water from the collection site. Circulation in the aquaria was provided by airstones placed on the bottom. Only large (head capsule width >2.5 mm) larvae were used for observation and videotaping.

Individuals were observed by the following techniques. Initially, to minimize possible distractions, individuals were observed in a large light-proof observational theater insulated to reduce sound vibrations. The observer was outside the theater, and by remote control operated the video camera (Panasonic WV-1850 with 1" Extended Red Newvicon S4119 pickup tube) mounted inside the theater for observation. The theater and monitoring system, which were designed for a study of burrowing behavior, were described in more detail by Keltner and McCafferty (1986). Light was provided either by an externally mounted fiber optic illuminator equipped with Kodak Wratten No. 87c filters or by infrared light-emitting diodes (LEDs). The

filters transmit less than 0.1% of the light below 780 nm, the LEDs transmit at 880 nm; thus the light used was essentially non-visible to humans. High reflectiveness by *Stenacron* eyes and the lack of observed responses to changes in infrared light intensity indicated that the infrared light sources were non-visible to the study organisms. Other observations were carried out under visible light which allowed smaller lens diaphragm openings to be used, thus increasing resolution and depth of field. A variety of lenses and lens extensions were employed to allow magnification up to 80 \times on a 9" (23 cm) high resolution black and white video monitor. A 1/2" (12.7 mm) VHS format Panasonic NV-8950 video recorder with freeze-frame, slow motion, and reverse option capabilities allowed images to be recorded and analyzed.

A larva was placed for observation in a cell built of 1/2" (12.7 mm) thick clear acrylic (Fig. 1), having a 1 \times 3-cm rectangular depression in the center. Several cells were constructed with depths ranging from 1 to 5 mm. At each end of the depression several small holes were drilled down into the material to join with larger holes leading out to the edge of the acrylic. Aquarium tubing was cemented into these larger holes. The depression was surrounded with self-adhesive automotive gasket material and covered with a 75 \times 25-mm glass microscope slide. The slide was held in place by a second piece of clear acrylic, 1/4" (6.35 mm) thick, that had its center removed to correspond with the depression; this hole was also surrounded by gasket material. The apparatus was held together by bolts inserted through holes in both pieces and secured with wing nuts. The observation cell was placed in the theater with the long axis in a vertical position and the glass slide facing the camera. The stage on which the cell was mounted was moved in three axes by electric motors.

Water at room temperature (20°C) was circulated through the cell by pumping or siphoning it into the cell through the lower tube and out the upper. The flow was controlled by a valve; however, current velocities around the larva (as measured by timing the movement of small particles) varied even within a given experiment. The larva could occupy a significant portion of the cross-sectional space within the shallowest observation cells; this had a dynam-

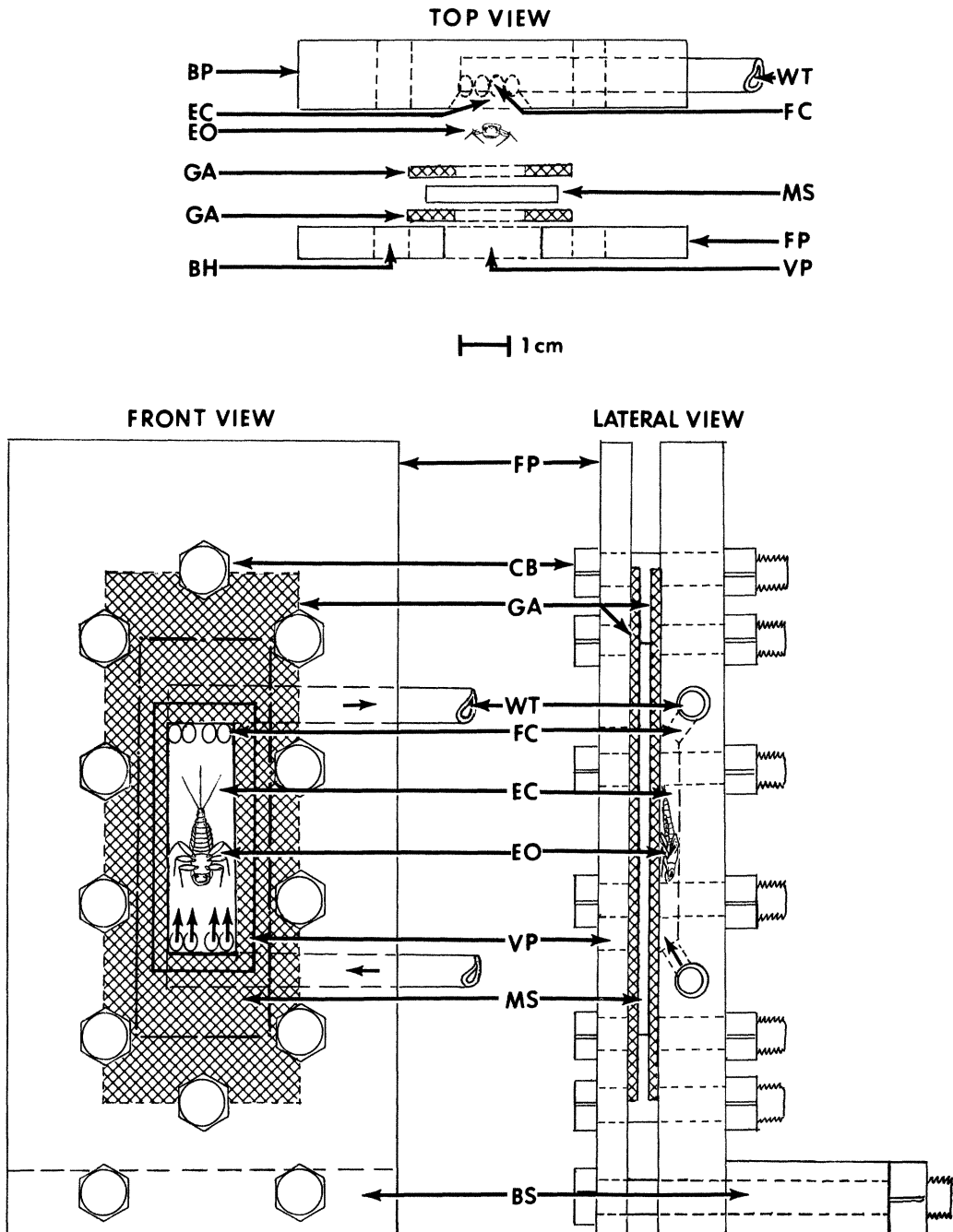


FIG. 1. Observation cell used for observations of feeding behavior in mayfly larvae, drawn to scale. Unlabelled arrows indicate direction of water flow. Abbreviations: BH = Bolt Hole, BP = Base Plate, BS = Base Support, CB = Clamp Bolt, EC = Excavated Chamber, EO = Experimental Organism, FC = Flow Collimator, FP = Face Plate, GA = Gasket, MS = Microscope Slide, VP = Viewing Port, WT = Water Tubing.

ic effect on local current velocities and produced a complicated pattern of streamlines of varying current velocities within the cell. For most experiments flow was adjusted until the larva began to orient. This adjustment was necessary because of the difficulty in measuring current velocity (or deciding which velocity was significant to the organism). Orientation usually occurred at "low" current velocities (0–5 cm/s).

Food was introduced into the observation cell by several means. Algae taken from the Tippecanoe River were cultured in the laboratory directly on the glass slide forming the viewing wall of the observation cell. The slides were covered primarily (95%) with *Cocconeis*; bacteria were common between these diatoms. The remaining 5% was covered by scattered fungal hyphae, *Oscillatoria*, *Cladophora*, *Melosira*, *Fragillaria*, *Chlorella*, rotifers, and protozoa. Slides were examined microscopically before and after the observation period. Feeding was considered effective if the slides contained patches where the algae had been removed, or if actual removal and ingestion were observed. Detritus taken from the holding tanks was placed in the cell and feeding was observed at low and high flow rates. Feeding on detritus was considered effective if ingestion was observed.

Motion analyses were carried out primarily by examination of the videotape recordings of the observation sessions of the organisms in the cells; however, this was supplemented by direct video observation. Over 20 individuals of *S. interpunctatum* were observed for a total period of over 50 hours in the course of this study. Ten of these individuals were videotaped in the observation cells; 236 feeding cycles from eight of these individuals (four larvae feeding on attached algae and four larvae feeding on detritus) were analyzed in detail using the single frame advance feature of the videotape recorder. This information was used to assemble a chronology of mouthpart movements which was checked against the remaining videotape. In all, several thousand feeding cycles were examined. Following the protocol of Keltner and McCafferty (1986), the observed feeding behavior was classified into stereotypic cycles describing different methods of obtaining and handling possible food material. Each cycle was divided into stages to describe the choreography of movement of the suite of

mouthparts. For our purposes the stages are delineated by changes in the movements of the labium and the labial palps.

Additional observations were made of organisms on more natural substratum in aquaria and in small artificial streams to assess the effect of the theater and observation cell on behavior, and to check the accuracy of the descriptions of the feeding cycles. These observations were made by eye, with and without a stereomicroscope, and with the video camera. These methods did not provide the detail and/or repeatability necessary for critical analysis of mouthpart movement; however, resolution is greater during the initial, direct observation than on videotape playback. We have found this also to be true for the species of mayflies and other aquatic invertebrates that have or are being studied using similar techniques.

Mouthpart structures were examined by light microscopy and SEM. This information was used to construct a moveable plastic model of the mouthparts to aid further understanding of their motion.

Gut contents of living larvae were placed on glass microscope slides and examined immediately with a compound microscope. Gut contents of individuals freshly collected in the field were compared to those held in the laboratory. Gut contents were classified as being mineral, organic detritus, diatoms, filamentous algae, unicellular algae, animal remains, or bacteria. No attempt was made to quantify proportions other than to note what type predominated.

Results

Field observations

The open canopy at the collection site permitted algal growth to cover the substratum. The aufwuchs community was more diverse than that cultured on slides in the laboratory. Additional taxa of diatoms such as *Gomphonema*, *Gyrosigma*, *Navicula*, and *Synedra* were also present. Certain taxa such as *Cladophora*, *Melosira*, and *Fragillaria* had seasonal blooms to a point where they visibly dominated the periphyton community. At times large areas of the substrate were covered by blackfly larvae and pupae, or by the silk retreats of *Petrophila* (Lepidoptera) or chironomid larvae.

The larvae collected in the field were, without exception, collected from the bottoms of

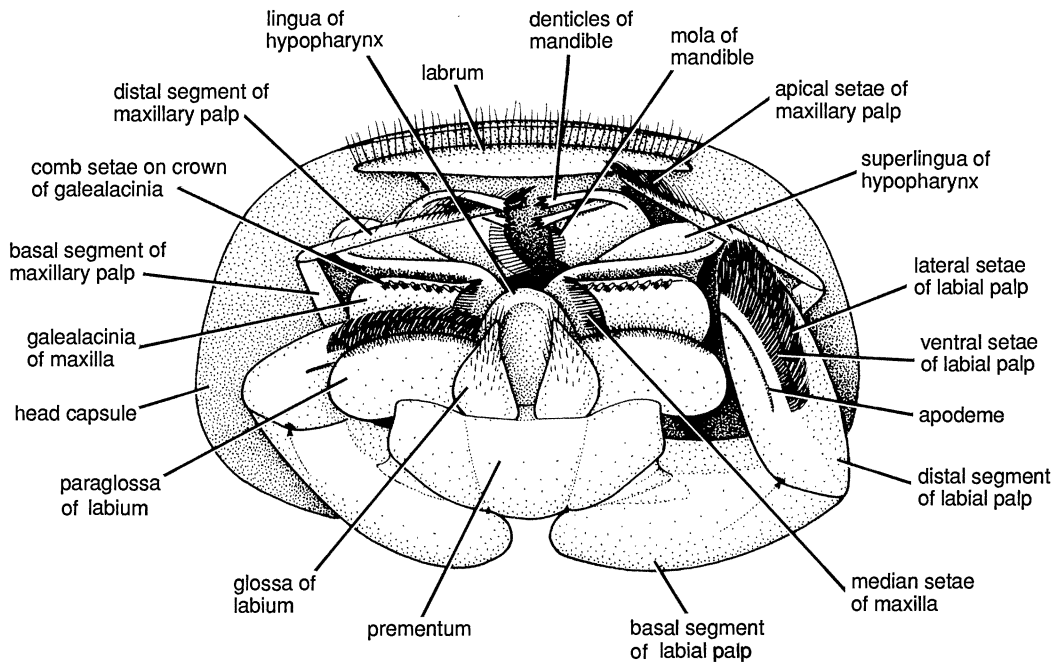


FIG. 2. Ventral view of the mouthparts of *Stenacron interpunctatum*. Mouthparts have been moved from the resting position to allow underlying structures to be seen.

stones. Although sampling was not quantitative, comparable numbers of *S. interpunctatum* larvae were found among the cobble substratum both in the open canopy areas and under an adjacent highway bridge where shading visibly reduced algal growth. Larvae were more commonly collected from areas of slower current.

Effects of experimental conditions on behavior

Mature larvae of *S. interpunctatum* were highly stereotypic in the movement of their mouthparts in all experimental enclosures (observation cells, artificial streams, holding aquaria with natural substratum). The few variations in feeding movements observed were apparently associated with food type and are described below. In every case, movements were independent of experimental enclosures.

External factors such as noise, vibration, changes in visible light intensity or water velocity did not affect the qualitative performance of feeding movements of *S. interpunctatum*. They did, however, affect the duration of movements and the release of stereotypic feeding movements. Feeding movements induced

by external stimuli ceased after 1–2 cycles of the mouthparts; those that appeared to be induced by the organism typically continued for at least 5 cycles. Feeding movements observed under visible light were identical to those viewed with infrared light. Specimens observed in the artificial streams and holding aquaria were negatively phototactic, positively thigmotactic and positively rheotactic.

Stereotypic feeding behavior

Resting position. When a larva is not feeding, its mouthparts (Figs. 2, 3, 4a–e) are held in a characteristic resting position (Fig. 5a). The distal segment of the labial palps are held folded inward so that they lie over the glossae and paraglossae. The labium as a whole is held adducted dorsally to close the preoral cavity ventrally. The galealacinae of the maxillae are positioned with their median setae touching the lingua of the hypopharynx; the galealacinae also are in contact ventrally with the labial palps and dorsally with the superlinguae of the hypopharynx. The distal segments of the maxillary palps are held folded over the anterior opening of the preoral cavity. The mandibles

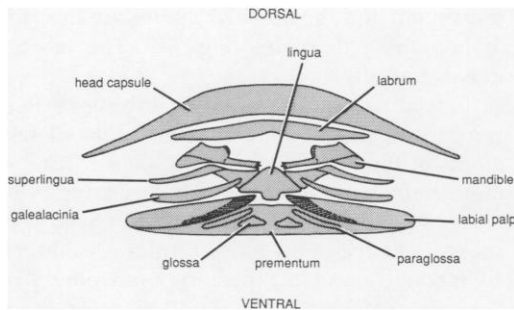


FIG. 3. Diagrammatic cross-section of the mouthparts of *S. interpunctatum*, showing relative vertical positions.

are held with the denticles separated, and the molae presumably closed. The labrum is held pressed against the head capsule dorsally and the mandibles ventrally.

Brushing cycle. A larva placed in the observation cell with algae grown on the glass slide performed a behavioral cycle we term brushing. A brushing cycle comprises several stages delineated by the movements of the labium. A single brushing cycle, as described below, takes approximately 1 second at 20°C. The mouthpart movements described below are often preceded by vigorous movement of the forelegs ahead (upstream) of the individual. The legs are repeatedly extended and then retracted, drawing the claws over the substratum; this movement ceases during the first cycle. We did not find any evidence that such movement of the forelegs displaces material adhering tightly to the substrate.

Stage 1.—Abduction of the basal segments of the labial palps: As feeding commences, the labium begins to swing ventrally towards the substrate. The basal segments of the labial palps swing posteriorly about 10° (Fig. 5b); this movement partially displaces the distal segments of the labial palps from contact with the glossae and paraglossae. At this point the basal segments of the maxillary palps swing posteriorly. The galealaciniae do not move in Stage 1 of the first brushing cycle, but in all subsequent brushing cycles they move medially at this point. The labrum begins to move down and backwards to shield the front of the other mouthparts.

Stage 2.—Abduction of the distal segments of the labial palps: Once the basal segments of the labial palps reach their posterior position, the

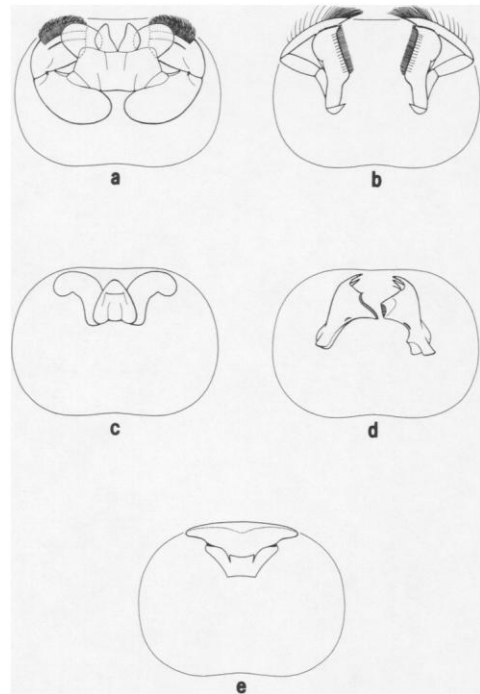


FIG. 4. Ventral view of mouthparts of *Stenacron interpunctatum*, ventral to dorsal sequence. a. Labium. b. Maxillae. c. Hypopharynx. d. Mandibles. e. Labrum.

distal segments of the labial palps are abducted, moving through a range of about 30°. As the apical tips of the labial palps clear the glossae and paraglossae, the labium completes its ventral swing coming to rest against the substratum with the labial palps fully extended, yet remaining under the contour of the head capsule (Fig. 5c). At this point the galealaciniae are abducted, moving laterally outward. The maxillary palps have been extended and reach beyond the lateral borders of the head capsule. The denticles of the mandibles begin to move laterally outward. The labrum completes its movement posteriorly and ventrally, effectively shielding the mouthparts under the head capsule from the current.

Stage 3.—Retraction of the labial palps: The labial palps are retracted from their extended position by a combination of an anterior swing of the basal segments of the palps and adduction of the distal segments of the palps. This movement is continuous and coordinated so that the palps always remain under the head

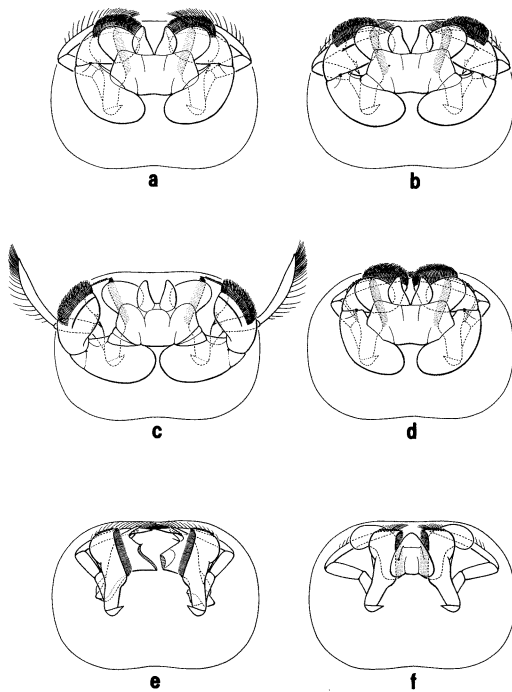


FIG. 5. Relative positions (all in ventral view) of the mouthparts of *Stenacron interpunctatum* during various stages of the brushing feeding cycle. a. Labium and maxillae, resting position. b. Labium and maxillae, Stage 1 of initial cycle. c. Labium and maxillae, Stage 2. d. Labium and maxillae, Stage 3. e. Maxillae, hypopharynx and mandibles, Stage 3. f. Maxillae and hypopharynx, Stage 1 of subsequent cycles.

capsule. As the distal segments of the labial palps move they brush (sweep) up material from the substratum with the profuse setae on the ventral and anterior surfaces. When the distal segments of the labial palps reach the paraglossae they are raised dorsally by a rotation of the basal segments of the palps so that they pass dorsal to the paraglossae and glossae. The distal segments of the palps reach a position that is more median than in the resting position (Fig. 5d). The entire labium is raised as soon as the distal segments of the labial palps are dorsal to the glossae and paraglossae. The galealaciniae follow the labial palps in moving medially; they also move somewhat ventrally. The maxillary palps sweep inward, brush over the substratum, and enter the preoral cavity dorsal to the superlinguae. The denticles of the mandibles complete their lateral outward

movement and the maxillary palps are inserted among these denticles (Fig. 5e). The labrum moves dorsally.

As feeding continues, this brushing cycle is repeated with the abduction of the basal segments of the labial palps as in Stage 1 (foreleg movement is not repeated). The brushing cycle is repeated unchanged except that in Stage 1 of subsequent cycles the galealaciniae are adducted medially, and the posterior movement of the basal segments of the maxillary palps draws the apical setae of the maxillary palps through the combs on the denticles of the mandibles.

Gathering cycle. When *S. interpunctatum* is presented with loose detritus, a gathering cycle is performed. The gathering cycle is similar to the brushing cycle except for the following. The mouthparts are not pressed tightly against the substratum in Stage 2, and the legs, particularly the forelegs, may bring detritus to the preoral cavity where it is swept up by the labial palps as they move inward in Stage 3. The lateral setae on the distal segments of the labial palps carry more material from the substratum than the ventral setae. In Stage 3 the apical setae of the maxillary palps bring a larger volume of detritus to the preoral cavity than in the brushing cycle; this material is combed out by the mandibular denticles when the maxillary palps are withdrawn in Stage 1.

When presented with filamentous algae such as *Cladophora* sp., the mouthparts are positioned in Stages 2 and 3 so that the labial palps brush over the filaments, removing epiphytes. The maxillary palps play a role in manipulating the filaments. It is possible for the organism to manipulate filaments into the preoral cavity; however, what could be interpreted as attempts to bite off and swallow pieces of such filaments were ineffective.

Filtering cycle. When a heavy load of detritus is moving in the current, *S. interpunctatum* alters its feeding behavior radically and becomes a passive filter feeder. The filtering cycle is less complex than the other cycles, and the labial palps are not used to gather food. The larva orients so that its head faces into the current and the longitudinal axis of the body is parallel to the flow. The mouthparts are held in the resting position except for the maxillary palps; these are extended until they are perpendicular to the flow. Particles of detritus adhere to the apical setae. Periodically the max-

illary palps are retracted into the preoral cavity as in Stage 3 of the brushing cycle. The detritus brought to the preoral cavity is combed out from the apical setae of the maxillary palps by the denticles of the mandibles as in Stage 1 of the brushing and gathering cycles; the detritus is then further processed in the manner described below, except that the labial palps do not gather additional food.

Food processing

Once food material has been acquired by the palps of either the labium or the maxillae in any of the cycles above, it must be positioned for ingestion. This process is carried on continuously during feeding and for several seconds after the last material is acquired from the substratum. The transfer is accomplished by successive fields of setae on the various mouthparts (Fig. 2) as described below.

After completion of at least one brushing or gathering cycle, and when the labial palps are extended again (Stage 1), the material on their setae is removed in two ways. The outward lateral movement (Stage 1) of the distal segments of the labial palps causes material to be combed from the ventral setae of the labial palps by the setae on the dorsal surfaces of the glossae and paraglossae. Material on the lateral setae of the distal segments of the labial palps is removed by the comb setae of the galealaciniae as they move medially in opposition to the outward movement of the labial palps (Stage 1). The material in the comb setae is brushed out as these setae are drawn base-first through the setae on the glossae and paraglossae by the ensuing outward lateral movement of the galealaciniae (Stage 2).

In all cycles, material on the maxillary palps is removed by the combs on the mandibular denticles as the palps are withdrawn (Stage 2). In the filtering cycle all material is brought to the mouth in this way.

Material left on the glossae and paraglossae is moved further through a number of processes. As the labial palps return to the preoral cavity (Stage 3), this material is displaced posteriorly, medially, and dorsally by the palps and the new load of material they bear. As the galealaciniae move medially (Stage 1), their median setae push the material between the superlinguae and the lingua (Fig. 5f). The lingua

bears rows of setae on its dorsum which guides the material to a point where it can be pressed against the mandibular molae for straining and ingestion. Presumably, material left on the denticles is brushed directly onto the dorsum of the hypopharynx by movements of the mandibles; we have not been able to observe this since this area is obscured by the other mouthparts.

The maxillary palps are used in all cycles to displace larger particles from the preoral cavity and to brush material from the comb setae on the galealaciniae. Once food acquisition ceases, the mouthparts (except for the labial palps) remain in motion as described above for several cycles, moving material into position to be ingested.

Gut content analysis

Organisms collected in the field had little variety in their gut contents. All guts contained mineral material and organic detritus. Diatoms were observed in the gut of only a few individuals collected early in November 1985, when a dense growth of diatoms, predominately species of *Melosira* and *Fragillaria*, covered the substratum in the Tippecanoe River. Whereas some of these diatoms were present in the gut, they were not predominant, and the diatom frustules were intact. None of the larvae collected in the field had filamentous algae, unicellular algae, or animal remains in their guts. Individuals held in the lab had gut contents similar to those newly collected in the field, although some of the individuals held in the laboratory did contain the diatom *Cocconeis* sp.

Discussion

In any behavioral study, it is important to assess the impact of experimental protocol on behavior. In our study the need to confine the organisms to a small area to allow for high magnification observation required an enclosure that did limit the overall behavior of the organism. Since our objective was only to document a small portion of the species' overall behavioral repertoire, this limitation was not a significant constraint because the portion of the behavior in which we were interested was not affected. The brushing cycle and the gathering cycle were performed in an identical fashion in the observation cell, in aquaria, and in the

artificial stream. Our observations of other Ephemeroptera, Trichoptera, Diptera, Odonata, Coleoptera, Amphipoda, Gastropoda, and other freshwater macroinvertebrates suggest that the cyclic movements of the mouthparts are stereotypic and vary little if any between individuals of the same age class of any one species. This conclusion is consistent with other insect feeding studies (Brown 1960, Chance 1970, Devitt and Smith 1985, Froehlich 1964, Pucat 1965).

This study shows that *S. interpunctatum* is an opportunistic feeder with a behavioral repertoire sufficient to allow it to feed in a number of different ways. The importance of detritus as a food source for this species has been documented by Lamp and Britt (1981); their quantitative gut content data agree with our qualitative observations. Our laboratory observations combined with ecological observations from the field suggest that this species is better classified as a collector-gatherer than as a scraper according to the categories of Cummins and Merritt (1984). In laboratory tests *S. interpunctatum* was not able to remove tightly adhering diatoms such as *Cocconeis* sp. from a glass slide; however, individuals on more natural substrata are apparently able to remove this diatom to some extent. The only alga that *S. interpunctatum* was observed to ingest was an extremely flocculent mass of diatoms with physical characteristics similar to loose detritus. Although the organisms are capable of manipulating filamentous algae and removing epiphytes from surfaces of these plants, they have difficulty biting off sections of the filaments. Filamentous algae, however, have been reported in the gut of *Stenonema modestum*, a closely related and morphologically similar species (Kondratieff and Voshell 1980).

Microhabitat data also suggest that this species is a collector-gatherer. We consistently found these larvae on the undersides of stones in crevices where detritus was deposited. Other studies (Wiley and Kohler 1980, Wodsedalek 1912) also stressed the occurrence of *S. interpunctatum* larvae on the undersides of stones.

Although direct observation and analysis of feeding behavior of earlier instars of *S. interpunctatum* were not conducted in this study, earlier instars of many species may be detritivores even if they later specialize on other food sources (Cummins 1973, Cummins and Merritt 1984). Since mature *S. interpunctatum* larvae pri-

marily ingest detritus (Lamp and Britt 1981), the importance of this food source in the diet of this species is significant.

The ability of *S. interpunctatum* to vary its feeding behavior to either filter or gather depending on the circumstances demonstrates its independence from a single resource such as periphyton. A more tenable classification of *S. interpunctatum* as primarily a collector has important consequences for ecological investigations incorporating or extrapolating from the river continuum concept.

On the basis of their mouthpart structure, heptageniids, in general, have sometimes been assumed to scrape their food. For example, Brown (1960) wrote that the crown setae of the maxillae are used to rake up diatoms; however, this statement actually was a misinterpretation of Strenger (1953) (in German) who described the function of these setae ("Kammborsten") as combs for the labial palps. We found that the orientation of these setae aligns them precisely with the labial palps, and that they cannot reach the substratum because of the position of the large labium between the maxillae and the substratum. The external chitinized "scraping bars" reported by Morgan (1911) on the distal segments of the labial palps in the heptageniid *Epeorus fragilis* are not present in *S. interpunctatum*. Examination of the distal segments of the labial palps of *S. interpunctatum* by light microscopy revealed structures which could be interpreted as scraping bars, but examination with SEM revealed that they were internal structures (probably apodemes). Further investigations will be needed to see if this is not the case for other heptageniids.

The only mouthparts of *S. interpunctatum* that reach the substratum are the labial palps and the tips of the maxillary palps. Both of these structures are heavily setose and not fit for scraping in the manner we have observed for radulae of gastropods and the mandibles of water penny beetle larvae (*Psephenus*). We have, however, seen the heptageniid *Heptagenia flavescens* scrape bacterial film from the substratum. The terminal ends of the maxillary palps of that species are reinforced and modified as a scraping tool, quite unlike the brush-like maxillary palps of *S. interpunctatum*. It is possible that the forelegs of *S. interpunctatum* may be capable of some scraping. They are active before the brushing cycle and are important in

bringing food to the mouth in the collecting cycle. The fact that we did not observe them to be effective in removing material from the substratum may be an experimental artifact.

From a functional-morphological standpoint, it is desirable to erect a new category of feeding—'brushing'—distinguished from scraping by the morphological structures used in acquiring material from the substratum. We propose that brushers include organisms that remove material from the substratum using setae, and that scrapers include organisms that use hardened structures such as mandibles or radulae to remove accreted material. Whereas such a distinction is valuable from a functional standpoint, its ecological significance may be less apparent and awaits data about what precise components of the aufwuchs can be removed by each of these functions and what components are nutritionally significant.

Analyses of the feeding behavior and functional morphology of a species are important tools in describing the ecological relationships of that species. Such studies are necessary before ecological assumptions based on morphology are made, and provide additional insight into the relevance of gut content data. As more of these studies are completed within taxonomic groupings and among taxa with similar morphology their usefulness will increase as an aid in understanding community dynamics and evolutionary trends.

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