Filter-feeding habits of the larvae of *Anthopotamus* (Ephemeroptera : Potamanthidae)

W.P. McCafferty[1]
Y.J. Bae[1]

Keywords : Ephemeroptera, Potamanthidae, *Anthopotamus,* filter feeding, behavior, morphology, detritus.

A field and laboratory investigation of the food and feeding behavior of larvae of the potamanthid mayfly *Anthopotamus verticis* (Say) was conducted from 1989 to 1991 on a population from the Tippecanoe River, Indiana (USA). Gut content analyses indicated that all size classes of larvae are detritivores, with over 95 % of food consisting of fine detrital particles. Videomacroscopy indicated that all size classes of larvae are filter feeders, able to utilize both active deposit filter feeding and passive seston filter feeding cycles in their interstitial microhabitat. Deposit filter feeding initially incorporates the removal of loosely deposited detritus with the forelegs. Seston filter feeding initially incorporates filtering by long setae on the forelegs and palps. Mandibular tusks are used to help remove detritus from the foreleg setae. A SEM examination of filtering setae indicated they are hairlike and bipectinate, being equipped with lateral rows of setules. The results show that previous assumptions that potamanthid larvae were collector/gatherers are erroneous. The results are applicable to congeners, and all potamanthids, including Palearctic and Oriental elements, are hypothesized to be filter feeders, differing only in some details of behavior.

Le régime trophique de type filtreur des larves d'*Anthopotamus* (Ephemeroptera : Potamanthidae)

Mots clés : Ephemeroptera, Potamanthidae, *Anthopotamus,* type trophique filtreur, comportement, morphologie, débris particulaires.

Une investigation sur le régime alimentaire et le comportement trophique des larves de l'Ephémère Potamanthidae *Anthopotamus verticis* (Say) a été menée à la fois sur le terrain et expérimentalement au laboratoire de 1989 à 1991, sur une population de la rivière Tippecanoe, Indiana (USA). L'analyse des contenus stomacaux a révélé que les larves de toutes les classes de taille sont détritivores et que 95 % de la nourriture ingérée est composée de fins débris particulaires. Une étude vidéo en macroscopie a montré qu'à toute classe de taille, les larves appartiennent au type trophique filtreur et qu'elles sont susceptibles de mettre en œuvre, dans leur microhabitat interstitiel, à la fois un mécanisme actif de filtration des dépôts et un cycle passif de filtration du seston (particules en suspension). La filtration trophique des dépôts débute par le balayage et le brassage des sédiments non compacts — ainsi remis en suspension — avec les pattes antérieures. La filtration du seston commence, elle, par la rétention des particules au niveau des longues soies des pattes antérieures et des palpes. Ensuite, le raclement de ces pattes sur la région antérieure très proéminente des mandibules contribue au retrait des particules filtrées par les soies. L'examen de ces soies filtrantes au microscope électronique à balayage montre qu'elles sont longues, fines et bipectinées (deux longues rangées de sétules latérales). Nos observations prouvent que l'hypothèse antérieure selon laquelle les larves de Potamanthidae seraient du type « collector/gatherer » est erronée. Ces résultats sont généralisables à toutes les espèces d'*Anthopotamus*. Toutes les espèces de Potamanthidae, y compris les représentants paléarctiques et orientaux, appartiennent même probablement au type trophique filtreur, avec tout au plus quelques différences de comportement.

1. Introduction

The mayfly genus *Anthopotamus* typifies the Potamanthidae, a Holarctic and Oriental family belonging to the superfamily Ephemeroidea, or

1. Department of Entomology, Purdue University, West Lafayette, IN 47907, U.S.A.

the burrowing mayflies. The interfamilial relationships of this family were recently treated by McCafferty (1991), who showed the family to represent a sister lineage to the larger and more widespread family Ephemeridae. Relationships within the Potamanthidae were treated extensively by Bae and McCafferty (1991), who showed the genus

Anthopotamus to represent a sister lineage to the Old World genus *Potamanthus*.

A moderately erosional/mixed substrate habitat in medium sized to large, shallow rivers applies to all potamanthid larvae (McCafferty 1975, Munn & King 1987, Watanabe 1988, Bae et al. 1990, Bae & McCafferty, unpublished, A.G.B. Thomas, personal communication). The microhabitat of *Anthopotamus*, the only North American genus of the Potamanthidae, was studied in detail by Bae and McCafferty (in manuscript). *Anthopotamus* larvae do not form walled, in-substrate burrows as larvae of most other Ephemeroidea (i.e., Ephemeridae and certain Polymitarcyidae) ; however, they do live interstitially amongst gravel and pebble-size substrate, or mixed substrates grading from sand to cobble. It is highly likely that the microhabitat of the other genera of Potamanthidae will prove to be similar to that of *Anthopotamus* (Bae & McCafferty 1991, in manuscript). Other aspects of the ecology of Potamanthidae are poorly known and based on rough field observations or more-or-less anecdotal information (Morgan 1913, Argo 1927, Berner 1959, McCafferty 1975, Bartholomae & Meier 1977, Cummins et al. 1984).

Potamanthid larvae have generally been considered to be detritivore collector/gatherers in terms of their functional feeding group or guild classification. Such a classification was given by Cummins et al. (1984) and Munn & King (1987), although Meier and Bartholomae (1980) suggested that they were periphyton grazers. Originally, Needham (1920) suggested the possibility that they were filter feeders because of the presence of rows of setae on the forelegs. Preliminary videomacroscopic observations of live larvae made by McCafferty (unpublished) in the mid 1980's did indeed suggest that the larvae were filter feeders. We therefore undertook a field and laboratory study to determine both the food resource being accessed by these mayflies as well as their mode of feeding behavior.

2. Methods

This study was, for the most part, fashioned after the recent studies on feeding behavior and functional morphology of aquatic macroinvertebrates by McShaffrey and McCafferty (1986, 1988, 1990).

Larvae of *Anthopotamus verticis* (Say) were recruited in June, 1989-1990, from the Tippecanoe River (White County, Indiana), a sixth order stream in the upper Wabash River drainage system. The river at our study site was approximately 50 m wide with water depth up to approximately 0.5 m. Diel maximum water temperature in June ranged from 22 to 28°. PH was 8.0-8.6. Substrate ranged from sand to large rocks, and current was 0.1-0.8 m/s.

Early, middle, and late instar larvae (ranging from 1.5-15.7 mm length, excluding caudal filaments) were sampled. Individuals were sorted to three size classes (< 5.1 mm, 5.2-10.0 mm, and > 10.0 mm) and held in aerated laboratory aquaria supplied with natural stream water at field temperature and with substrate taken from the field site (including associated microfauna and detritus).

We analyzed the gut contents of 10 freshly sampled individuals (as well as 10 individuals held in the laboratory for at least two weeks) from each size class during each summer. The procedures for these analyses were based on Cummins (1973).

Videomacroscopic analyses of feeding behavior were conducted by examining 10 individuals of each size class in 1989. General behavior and orientation was recorded in an artificial stream with a tripod-mounted, 8 mm color video camera. Detailed motion analysis of individual larvae placed in tank cells was performed using a low-light surveillance camera fitted with close-up lenses. The design and operation of the observation cell, particularly in terms of water flow and detrital movement and settling, was described in detail by McShaffrey and McCafferty (1988) in their report on *Rhithrogena*. Camera systems, including lighting conditions, were those described in detail by McShaffrey and McCafferty (1990, 1991) (see also McShaffrey and McCafferty (1986, 1988). The description and operation of the observational theater and VCR components used were described by Keltner and McCafferty (1986). The artificial stream was that used and described by McShaffrey and McCafferty (1990).

Scanning electron micrographs of mouthpart and leg ultrastructure associated with feeding were taken with a JEOL JSM-840 scanning microscope.

3. Results

The gut contents of all size classes of both freshly collected and laboratory-held *A. verticis* larvae

consisted almost entirely of fine detritus (> 95 % FPOM[1]). The remainder of the gut content consisted of diatoms, but never more than 5 % of the contents of any individual examined.

Observations of the habitat orientation of *A. verticis* larvae indicated that they preferred coarse-gravel and small-pebble substrates but often resided on the underside crevices of rocks imbedded in these mixed substrates. No favored directional orientation of the larvae was observed. Gill pulsation within interstices created an anterior to posterior microcurrent over the longitudinal plane of the bodies of the larvae.

Close-up videomacroscopy revealed that feeding usually was associated with the removal of fine detritus loosely deposited on substrate in the immediate anterior and anterolateral vicinity of the larvae. As the midlegs and hindlegs anchored the larvae, deposited detritus was removed by an arcing and sweeping motion of the forelegs. Essentially, the forelegs would straighten outward laterally and then the foretibiae and foretarsi were adducted together horizontally to in front of the head either anterior, dorsal, or ventral to the mandibular tusks. In this way the ventral setal field of the forelegs (Fig. 1 and 2) moved across substrate, displacing non accreted fine particulate matter. By sweeping in this fashion, the forelegs would stir up and suspend fine particles as well as actively filter suspended particles, including those being stirred up from deposits.

Also in this initial phase of feeding behavior, the head was lifted intermittently. In this fashion, the anteriorly projecting mandibular tusks (Fig. 1 and 2), and to some extent the dorsum of the head, excavated small substrate and further stirred up detritus. The mandibular tusks additionally functioned in the removal, or cleaning, of detritus from the setal field of the foretibiae and foretarsi. This was accomplished by alternately bringing the forefemora to an almost anteriorly directed position while the foretibiae and foretarsi were slightly bent inward. The foretibia and foretarsi were then bent to 90° or more to bring them to a position dorsal to the tusks, and the forefemora were then abducted so that the foretibiae and foretarsi were pulled across the tusks dorsally. This cleaning motion removed detritus that had been filtered and swept up by the forelegs. Such

detritus was then momentarily suspended in front and at the sides of the head within reach of the palps.

Frequency of the sweeping and cleaning movements of the forelegs was highly variable. As water lacking fine particulate matter was pumped through the observation cell, foreleg activity was more-or-less continuous.

One foreleg often repeated sweepings several times while the opposite leg gripped substrate. Sometimes right and left legs would alternately be used to sweep and clean, but with no consistent pattern. Forelegs would sweep on an average of three times per second when larvae were actively feeding. No consistent differences in any of this behavior was evident among the different size classes of larvae observed.

Besides this active, deposit filtering behavior, larvae of all size classes would commonly passively filter seston that had not been actively removed from the substrate. This was accomplished by the setal fields of both the forelegs (holding the forelegs somewhat outspread) and the palps (Fig. 2 and 3) passively catching seston in the current moving from anterior to posterior over the body. Foreleg movement across the tusks was also part of the passive, seston filtering behavior. Passive filtering was aided by the microcurrent generated by gill pulsation. Gills pulsated approximately nine times per second during ventilation. Ventilation was not always correlated with passive filter feeding, since it would also occur during non feeding periods or active filtering periods. Although both active and passive filtering were utilized by individuals, when fine detritus was continuously flushed through the observation cell, passive filtering was used exclusively.

Once detrital particles were suspended in the immediate vicinity of the head, either having been stirred up from deposits or being incumbent in the seston, the maxillary and labial palps synchronously and stereotypically filtered this material. This was accomplished by abduction and adduction of the terminal segments of the maxillary and labial palps, which would occur both alternatively and simultaneously. Fully abducted, the angle between the basal and terminal segments was 150° ; when adducted (the sweep motion), the angle was closed to approximately 50°. Approximately 4-12 palpal sweeps per second were performed, and this episode was usually followed by several seconds of rest. The relative activity of this palpal movement varied somewhat
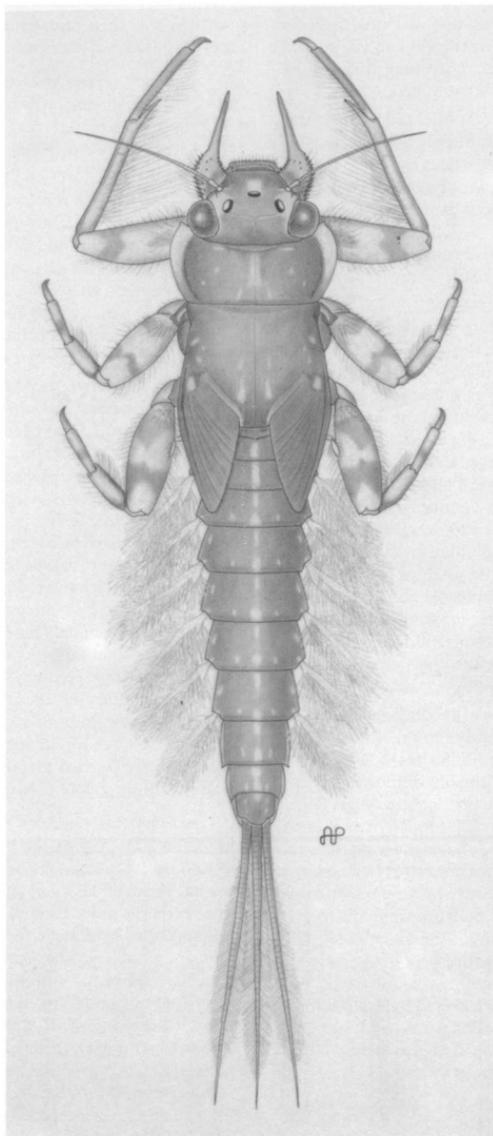
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1. Fine particulate organic matter.

Fig. 1. Dorsal view of *Anthopotamus verticis* larva (17 mm, including tails).
Fig. 1. Larve d'*Anthopotamus verticis* en vue dorsale (longueur : 17 mm, cerques compris).
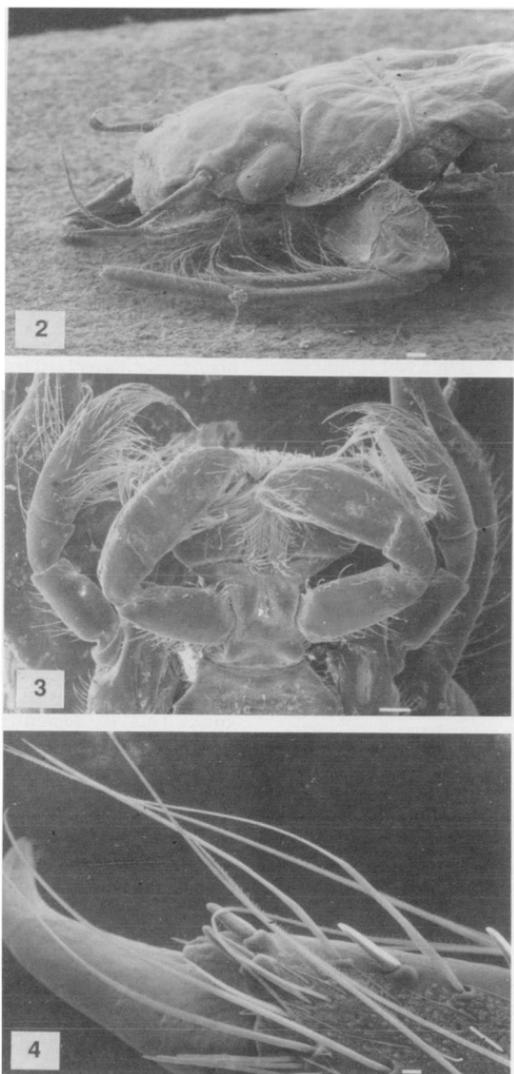
Fig. 2 to 4. Structures of *Anthopotamus verticis* larva. 2 : lateral view of head and thorax, bar = 100 μm. 3 : ventral view of mouth-parts, bar = 100 μm. 4 : claw and apical setae of foreleg, bar = 10 μm.

Fig. 2 à 4. Structures larvaires d'*Anthopotamus verticis*. 2 : tête et thorax en vue latérale, échelle : 100 μm. 3 : pièces buccales en vue ventrale, échelle : 100 μm. 4 : griffe et soies apicales d'une patte antérieure, échelle 10 μm.

depending on the detrital load in the water and the flow rate. With a large load of suspended detritus and flow, the palps were more passive in filtering.

The palpal sweep events described above were intermittently followed by the transfer of filtered particles to the pre-oral cavity. This was accomplished by detritus being combed out of the apical setae by pulling them through the denticles of the mandibles. This processing and eventual ingestion was similar to that described in detail for *Stenacron interpunctatum* by McShaffrey and McCafferty (1986). The movement of each labial palp during transfer was repeated seven to 10 times per second.

The filtering apparatus of the forelegs consists of three rows of well-developed hairlike setae, best developed on the foretibiae (Fig. 1 and 2) (also see Bae & McCafferty 1991, Fig. 71). These hairlike setae are bipectinate in that they each possess two rows of well-developed setules along the length of their shafts (Fig. 4). Filtering apparatus of palps consists of dense covering of hairlike setae on the terminal segments (Fig. 3) (see also Bae & McCafferty 1991, Fig. 45). These palpal setae also possess well-developed bipectinate setules on their shafts (see Bae & McCafferty 1991, Fig. 56).

4. Discussion

The results from our gut content analysis substantiate former reports that potamanthid mayflies are detritivores (Cummins et al. 1984, Munn & King 1987). The presence of a very small percentage of diatoms in the gut would appear to be incidental, and may be attributable to phytoplankton entering subterranean interstices. The interstitial microhabitat of potamanthid larvae (Bae and McCafferty, in manuscript) may be correlated with this detritivorous habit. Schwoerbel (1961) found a strong direct relationship between subterranean interstices, which tend to entrap particulate organic matter, and the presence of lotic detritivores.

Our feeding behavior data confirm Needham's (1920) assumption and the first author's preliminary observations that potamanthid mayflies are filter feeders (notwithstanding the fact that Needham had misidentified *A. verticis* as *Polymitarcys albus*). Our behavioral observations clearly show that *A. verticis* is a filter feeder [in part via deposit filtering sensu

McShaffrey & McCafferty (1988)] rather than a collector/gatherer as assumed by Cummins et al. (1984) and Munn & King (1987).

Anthopotamus larvae differ from strictly passive filter feeding mayflies such as larvae of *Isonychia* (Isonychiidae) (see Wallace & O'Hop 1979), which filter in the open stream current. *Anthopotamus* larvae, to a large degree, actively filter fine particulate organic matter (FPOM) that has been deposited amongst the substrate. They are, however, in part similar to certain passive filterers, such as larvae of *Pentagenia* (Ephemeridae) (Keltner & McCafferty 1986). The latter generate a microcurrent from which they are able to filter seston while burrowed in the substrate. Thus, *Anthopotamus* larvae are both *deposit filterers* and *seston filterers,* in the classification scheme of McShaffrey & McCafferty (1988).

Anthopotamus larvae clearly differ from macrobenthic scrapers, e.g., larvae of *Rhithrogena* (Heptageniidae) (see McShaffrey & McCafferty 1988) or collectors, e.g., larvae of *Stenacron* (Heptageniidae) (see McShaffrey & McCafferty 1986). *Anthopotamus* larvae lack specially armored maxillary and labial palps associated with scraping or collecting and do not demonstrate any concomitant scraping or collecting behavior. However, as pointed out by McShaffrey & McCafferty (1988), deposit filterers are often similar functionally, morphologically, and behaviorally to collectors of the brusher subcategory. This is demonstrated somewhat by *Anthopotamus*.

The morphology of *Anthopotamus* forelegs and mouthparts (Fig. 1-4), particularly the ultrastructure of the setation with regard to development of bipectinate hairlike setae (Fig. 4), is strongly associated with the filtering function (see also Bae & McCafferty 1991, Fig. 41-69). Such functional morphological correlations in aquatic arthropods have been variously discussed by Froehlich (1964), Farmer (1974), Soldán (1979), Strenger (1979), Wallace & Merritt (1980), Zimmerman & Wissing (1980), Braimah (1987 a and b), and McShaffrey & McCafferty (1988), among others. The results of this study and those of others detailing functional morphology suggest that certain behavior related to feeding can be predicted from the ultramorphology of feeding structures of benthic macroinvertebrates.

Our study also suggests, as have the studies of other mayflies by McShaffrey & McCafferty (1986, 1988, 1990) and C.G. Palmer (personal communication), that this type of investigation is prerequisite to fully documenting the feeding repertoire of benthic macroinvertebrates and hence a more comprehensive functional feeding group classification for use in freshwater ecology. Previously unknown plasticity as well as specificity of feeding habits are being discovered that are difficult to accommodate in the Cummins & Klug (1979) functional feeding group (FFG) system, which is so widely used by ecologists. Perhaps, some alternative classification system, as discussed by McShaffrey & McCafferty (1988) for microvores, will be necessary as analyses of aquatic community structure become more sophisticated.

Because *A. verticis* larvae are virtually identical morphologically with congeners, and because those congeners are known from similar habitats, our observations of filter-feeding behavior are likely applicable to all *Anthopotamus* species. Furthermore, we assume from examining the Old World genera *Potamanthus* and *Rhoenanthus,* which make up the remainder of the Potamanthidae, that they also are filter feeders. However, because the filtering setae on the forelegs and mouthparts of *Anthopotamus* are the most extensively developed among the genera (see Bae & McCafferty 1991), it is possible that subtle differences in feeding behavior or functional morphology exist in the family, and that *Anthopotamus* larvae are the most highly evolved in terms of filter feeding. In addition, since the mandibular tusks are not well developed anteriorly in the genus *Potamanthus,* they are not necessarily expected to play a functional part in helping to clean foreleg filtering hairs as is the case in *Anthopotamus* and probably *Rhoenanthus.* Behavioral studies of feeding in *Potamanthus* and *Rhoenanthus* will be necessary to determine any possible correlations between the differences in setal densities and distribution exhibited by these genera (see Bae and McCafferty 1991) and the mode and efficiency of filter feeding.

References

Argo V.N. 1927. — The North American species of the genus *Potamanthus,* with a description of a new species. *J. New York ent. Soc.* 35 : 319-330.

Bae Y.J. & McCafferty W.P. 1991. — Phylogenetic systematics of the Potamanthidae (Ephemeroptera). *Trans. Am. ent. Soc.* 117 (3-4) : 1-143.

Bae Y.J., McCafferty W.P. & Edmunds Jr. G.F. 1990. — *Stygifloris,* a new genus of mayflies (Ephemeroptera : Potamanthidae) from southeast Asia. *Ann. ent. Soc. Am.* 83 : 887-891.

Bartholomae P.G. & Meier P.G. 1977. — Notes on the life history of *Potamanthus myops* in southeastern Michigan (Ephemeroptera : Potamanthidae). *Gr. Lakes Ent.* 10 : 227-232.

Berner L. 1959. — A tabular summary of the biology of North American mayfly nymphs (Ephemeroptera). *Bull. Fla St. Mus.,* biol. Sci. 4 : 1-58.

Braimah S.A. 1987a. — Mechanisms of filter feeding in immature *Simulium bivittatum* Malloch (Diptera : Simuliidae) and *Isonychia campestris* McDunnough (Ephemeroptera : Oligoneuriidae). *Can. J. Zool.* 65 : 504-513.

Braimah S.A. 1987b. — Pattern of flow around filter-feeding structures of immature *Simulium bivittatum* Malloch (Diptera : Simuliidae) and *Isonychia campestris* McDunnough (Ephemeroptera : Oligoneuriidae). *Can. J. Zool.* 65 : 514-521.

Cummins K.W. 1973. — Trophic relations of aquatic insects. *Annu. Rev. Ent.* 18 : 183-206.

Cummins K.W., Edmunds Jr. G.F. & Merritt R.W. 1984. — Summary of ecological and distributional data for Ephemeroptera (mayflies), pp. 122-125 *in* Merritt R.W. & Cummins K.W. (eds.). An introduction to the aquatic insects of North America. Kendall/Hunt, Dubuque, Iowa.

Cummins K.W. & Klug M.J. 1979. — Feeding ecology of stream invertebrates. *Annu. Rev. Ecol. Syst.* 10 : 147-172.

Farmer A.S. 1974. — The functional morphology of the mouthparts and pereiopods of *Nephrops norvegicus* (L.) (Decapoda : Nephropidae). *J. nat. Hist.* 8 : 121-142.

Froehlich C.G. 1964. — The feeding apparatus of the nymph of *Arthroplea congener* Bengtsson (Ephemeroptera). *Opuscula ent.* 29 : 188-208.

Keltner J. & McCafferty W.P. 1986. — Functional morphology of burrowing in the mayflies *Hexagenia limbata* and *Pentagenia vittigera. Zool. J. Linn. Soc.* 87 : 139-162.

McCafferty W.P. 1975. — The burrowing mayflies (Ephemeroptera : Ephemeroidea) of the United States. *Trans. Am. ent. Soc.* 101 : 447-504.

McCafferty W.P. 1991. — Toward a phylogenetic classification of the Ephemeroptera : a commentary on systematics. *Ann. ent. Soc. Am.* 84 : 343-360.

McShaffrey D. & McCafferty W.P. 1986. — Feeding behavior of *Stenacron interpunctatum* (Ephemeroptera : Heptageniidae). *J.N. Am. benth. Soc.* 5 : 200-210.

McShaffrey D. & McCafferty W.P. 1988. — Feeding behavior of *Rhithrogena pellucida* (Ephemeroptera : Heptageniidae). *J.N. Am. benth. Soc.* 7 : 87-99.

McShaffrey D. & McCafferty W.P. 1990. — Feeding behavior and related functional morphology of the mayfly *Ephemerella needhami* (Ephemeroptera : Ephemerellidae). *J. Insect Behav.* 3 : 673-688.

McShaffrey D. & McCafferty W.P. 1991. — Videomacroscopy for the study of Ephemeroptera and other aquatic macroinvertebrates. pp. 15-24 *in* Alba-Tercedor J. & Sanchez-Ortega A. (eds.). *Overview and strategies of Ephemeroptera and Plecoptera.* Sandhill Crane Press, Gainesville, Florida.

Meier P.G. & Bartholomae P.G. 1980. — Diel periodicity in the feeding activity of *Potamanthus myops* (Ephemeroptera). *Arch. Hydrobiol.* 88 : 1-8.

Morgan A.H. 1913. — A contribution to the biology of mayflies. *Ann. ent. Soc. Am.* 6 : 371-426.

Munn M.D. & King R.H. 1987. — Ecology of *Potamanthus myops* (Walsh) (Ephemeroptera : Potamanthidae) in a Michigan stream (USA). *Hydrobiologia* 146 : 71-75.

Needham J.G. 1920. — Burrowing mayflies of our large lakes and streams. *Bull. Bur. Fish., Wash.* 36 : 266-304.

Schwoerbel J. 1961. — Über die Lebensbedingungen und die Besiedlung des hyporheischen Lebensraumes. *Arch. Hydrobiol.* 25 : 182-214.

Soldán T. 1979. — The structure and function of maxillary palps of *Arthroplea congener* (Ephemeroptera, Heptageniidae). *Acta ent. Bohemosl.* 66 : 300-307.

Strenger A. 1979. — Die Ernährung der Ephemeropterenlarven als funktionsmorphologisches Problem. pp. 299-306 *in* Pasternak (K.) & Sowa (R.) (eds.). Proceedings of the second international conference on Ephemeroptera. Panstowe Wydawnictwo Naukowe, Warsaw.

Wallace J.B. & Merritt R.W. 1980. — Filter-feeding ecology of aquatic insects. *Annu. Rev. Ent.* 25 : 103-132.

Wallace J.B. & O'Hop J. 1979. — Fine particle suspension feeding capabilities of *Isonychia* spp. (Ephemeroptera : Siphlonuridae). *Ann. ent. Soc. Am.* 72 : 353-357.

Watanabe N.C. 1988. — Life history of *Potamanthodes kamonis* in a stream of central Japan (Ephemeroptera : Potamanthidae). *Verh. Internat. Verein. Limnol.* 23 : 2118-2125.

Zimmerman M.C. & Wissing T.E. 1980. — The nutritional dynamics of the burrowing mayfly, *Hexagenia limbata*, pp. 231-257 *in* Flannagan (J.F.) & Marshall (K.E.) (eds.). *Advances in Ephemeroptera biology.* Plenum, New York.