

THE NUTRITIONAL DYNAMICS OF THE BURROWING MAYFLY, *HEXAGENIA*

LIMBATA *

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ABSTRACT

Aspects of the nutritional dynamics of the burrowing mayfly, *Hexagenia limbata*, were examined. Freshly deposited detritus and surface sediments were analyzed (organic, carbon, nitrogen, caloric contents) and compared with gut material from two size-classes of naiads (< 15 and \geq 15 mm). Both the chemical analysis and ATP-biomass carbon estimates suggest a higher nutritive potential for detritus. In both size-classes the ingested material consisted primarily of fine inorganic particles, and of the organic gut material, over 90% consisted of detrital aggregates. Analysis of the structure of the mouthparts and observations of feeding behavior were used to develop a description of the feeding process.

INTRODUCTION

To assess the importance of an organism in the utilization and cycling of nutrients, information is needed on its food habits and the quality and quantity of food ingested on a daily and seasonal basis. Although there are qualitative data available on the food materials ingested by *Hexagenia* (Neave 1932, Morgan and Grierson 1932, Hunt 1953, Fremling 1967, Walker 1970), there has been no real effort made to analyze feeding in relation to seasonal variation in the food materials available to the organism. Naiads of *Hexagenia*

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limbata can be classified as deposit feeders or gatherer-collectors, using the terminology of Cummins (1973). Collectors appear to utilize fine particulate organic matter (FPOM) that is primarily surface-colonized by bacteria (Anderson and Cummins 1979).

The material presented here is part of a larger study (Zimmerman 1977) of the life history and nutritional dynamics of *H. limbata*. Our approach to describing the nutritional dynamics of this species was to examine the quantity and quality of potential foods (i.e., surface sediments and freshly deposited detritus) available to naiads seasonally and to compare these characteristics to those of material actually ingested by nymphs and stored in the foregut. A description of the feeding apparatus and behavior is also given. The effects of temperature on the feeding intensity of *H. limbata* have been reported elsewhere (Zimmerman and Wissing 1978).

STUDY AREA

Brandenburg Pond is located in southwestern Ohio. It is roughly circular, with a diameter of 88 m, total surface area of 0.61 ha, and a maximum depth of 2.9 m. Rutter and Wissing (1975) and Zimmerman *et al.* (1975) have reported on the physical, chemical and biological characteristics of the pond. Sediment composition and distribution in the pond are shown in Figure 1 (Zimmerman *et al.* 1975). The mean particle-size diameter of zone 1 (2.8 ϕ ; medium sand) is larger than zone 4 (4.3 ϕ ; very fine sand). Zones 2 and 3 are intermediate in mean particle-size diameter (3.8 ϕ and 3.6 ϕ , respectively; fine sand). Mean separation with Duncan's New Multiple Range Test demonstrated that zones 1 and 4 are most dissimilar in all particle-size categories (Zimmerman 1977).

Hexagenia limbata naiads were abundant (often > 400 nymphs/m²) in zones 1 and 2 of the pond and sparse (often < 80 nymphs/m²) in zone 4 (Zimmerman *et al.* 1975). Late summer density estimates, taken from samples along two transects (Fig. 1), indicated that the mean population size remained relatively stable (approximately 351 nymphs/m²) during 1971-1976. Nymphs of various sizes can usually be collected from the pond as no short periods of synchronous emergence and mating exist. Instead, an emergence period extending from April through September was observed.

METHODS AND MATERIALS

Characteristics of Potential Food

To examine seasonal changes and to reduce variability due to sample site, surface sediments and detritus were collected monthly (November 1974 - November 1975) at two sites along the 1.2 and

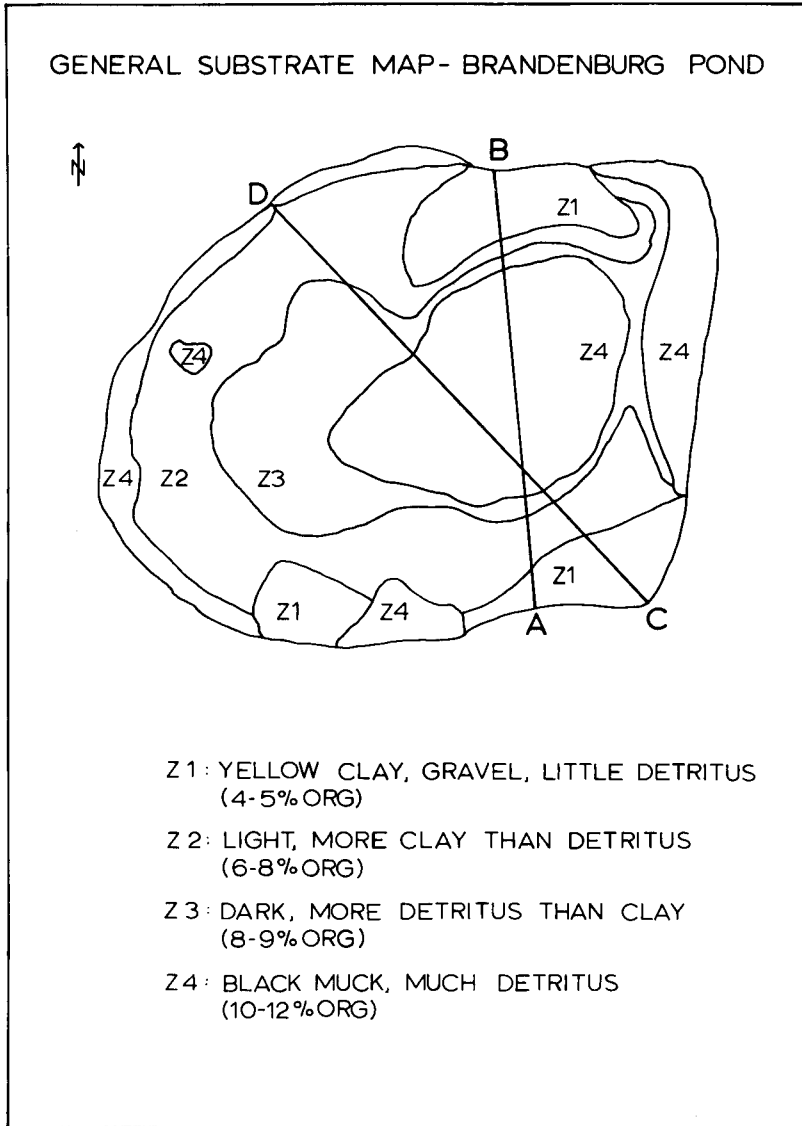


Figure 1. Types and distribution of sediments in Brandenburg Pond.

1.8 m contours in the southeast area of the pond (zones 1 and 2, respectively; see Fig. 1). Minimally disturbed surface sediments were collected with a K.B. gravity-type core sampler. Two replicate samples taken at each site were composed of the top 2 cm of sediment from four cores. All samples were transported to the laboratory on ice, oven-dried (60°C) to constant weight, and stored for later analysis. Suspended detritus, which settles to the bottom and hence becomes available as a potential food resource, was collected in paired acrylic plastic cylinders (9.5 cm d, 9 cm high) attached to bricks such that the effective collecting area (70.8 cm²) was approximately 20 cm above the bottom. The traps were suspended for three, 5-day periods monthly. At the end of each period the total contents of a trap were emptied into plastic containers, oven-dried (60°C) and weighed. The two sediment and detritus samples collected at each depth were analyzed separately for their caloric (cal/g ash-free dry weight), nitrogen (as % dry weight), organic (as % dry weight), and carbon (as % dry weight) contents. Caloric contents were determined with the modified iodate sulfuric acid-wet oxidation method of Karzinkin and Tarkovskaya (1964), as described in Hughes (1969). Total organic nitrogen was estimated from the micro-Kjeldahl method of the Association of Official Agricultural Chemists (A.O.A.C. 1970). Organic contents were determined from comparison of weighed samples before and after combustion in a muffle furnace (550°C for 3 h). Before the final weight was taken, the ashed material was wetted with double-distilled water to reintroduce the water of hydration of clay and other minerals (Weber 1973) and dried. Organic carbon contents of sediment and detritus samples were estimated by wet oxidation with chromic acid (Walkley and Black 1934), as described by Morgans (1956). During October, November and December of 1976, and April and May of 1977, total microbial ATP was acid-extracted (0.6 N H₂SO₄) from fresh and lyophilized sediments and from fresh detritus. The ATP extraction methods were modified (see Zimmerman 1977) from Lee *et al.* (1971a, b), Karl and LaRock (1975), and Perry (1974). An Aminco Chem Glow photometer (American Instrument Co.) coupled to a strip chart recorder was used to measure light intensity following the injection of 0.1 mL of a reconstituted lyophilized luciferan-luciferase firefly lantern extract (Sigma Chemical Co.) into 0.5 mL of an extracted ATP sample.

Ingested Foods

The gut contents of 25-80 naiads of two size-classes (< 15 (small) and ≥ 15 mm (large)) were removed monthly during November 1974 - October 1975 for determinations of their organic, nitrogen and caloric contents using the procedures outlined above. All nymphs were collected in areas corresponding to zones 1 and 2 of the pond (Fig. 1).

The biotic composition and range of detritus particle sizes in the gut contents of the two size-classes of naiads were determined monthly. Preliminary observations during November 1974 - April 1975 indicated that preserved (70% ETOH) gut contents from the entire digestive tracts did not lend themselves to detailed enumeration. Subsequently, the anterior one-third of the gut contents of five of the small and three of the large size-class of nymphs were dissected monthly from May 1975 - December 1975, placed in distilled water, and dispersed with forceps. The dispersed gut contents were washed onto a gridded Millipore filter (0.45 μm) (Cummins 1973). Two such filters were prepared for each size-class and examined microscopically at 100, 200 and 450X. Determinations of biotic composition were made on the basis of 20 randomly chosen ocular grid squares (each square = 0.12 mm^2 at 200X). Particles were enumerated as a percentage of total present and were placed in the categories of organic detritus, diatoms, filamentous algae, and animal fragments. In addition, estimates of the areas (maximum length x maximum width; at 100X) of 40 detrital particles were made from each filter.

From September 1976 - March 1977, anterior gut contents of nymphs were observed periodically with a scanning electron microscope (SEM) (Coates and Welter 1966). The contents were prepared for observation with the technique of Paerl and Shimp (1973). Gut contents were filtered on Nucleopore filters (0.4 μm), fixed (20% v/v glutaraldehyde solution buffered in 0.1 M sodium cacodylate), dehydrated in a graded ETOH series, transferred to 100% methanol, critical-point-dried (liquid CO_2 as transition fluid), mounted on aluminum stubs, sputter-coated with palladium-gold (40:60), and examined at 15 kV accelerating voltage.

Feeding Apparatus and Behavior

Naiad feeding behavior was observed in the field (from observations near shore) and laboratory. In the laboratory, nymphs were placed in 3 cm-wide aquaria filled with sediment and pond water. In addition, movements of mouthparts of nymphs placed with their ventral sides up in hanging drop slides (1.75 mm deep) were observed with a binocular microscope.

Mouthparts of naiads of various sizes (range = 10-25 mm) were observed with the SEM at an accelerating voltage of 1 kV. Whole nymphal heads or heads plus forelegs were separated from the thorax, preserved in 70% ETOH, and prepared for viewing as described above.

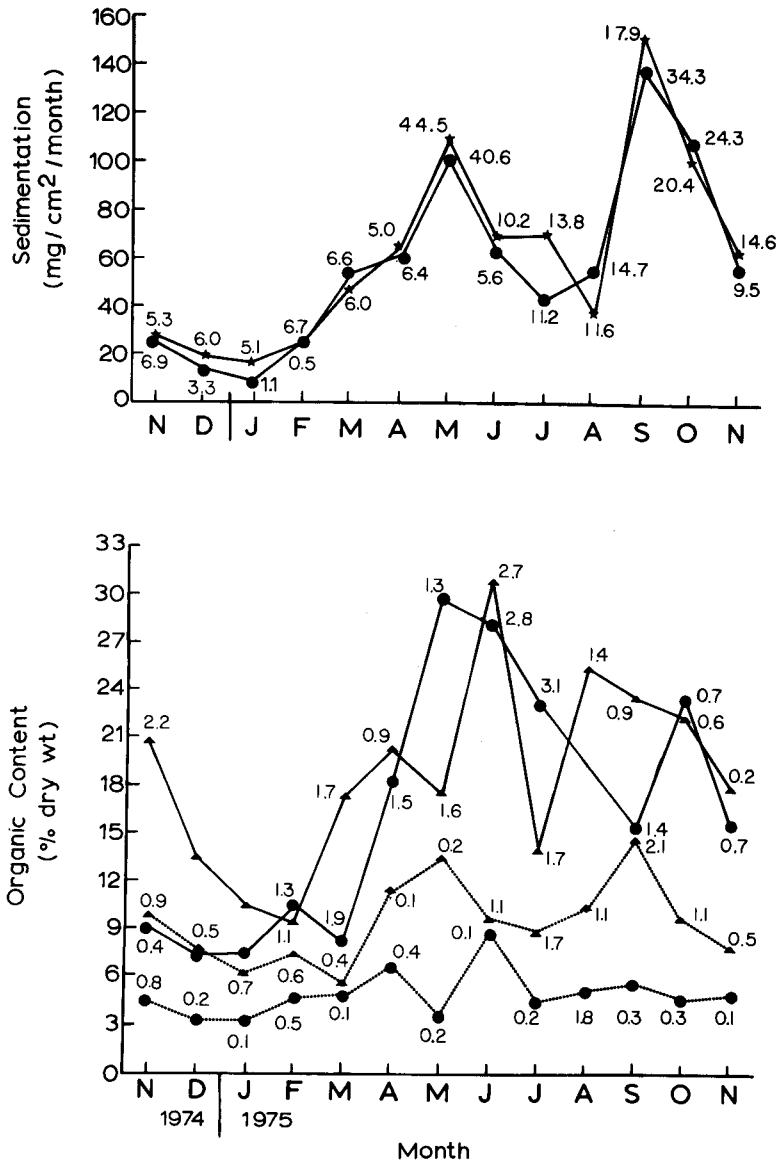


Figure 2. Sedimentation rates (mg-dry wt/cm²/month) and organic contents (% dry wt) of detritus and surface sediments from Brandenburg Pond. Numbers represent the standard errors of the means. Sedimentation: * 1.2 m; • 1.8 m. Organic content, detritus: ●---● 1.2 m; ▲---▲ 1.8 m; surface sediments: ●---● 1.2 m, ▲---▲ 1.8 m.

RESULTS AND DISCUSSION

Potential Food Materials

Mean monthly sedimentation rates (mg-dry wt/cm²/month) and organic contents (% dry weight) of detritus and surface sediments are shown in Figure 2. The rates of sedimentation revealed a distinct seasonal pattern of low sedimentation during winter and high sedimentation during spring, summer and autumn. The monthly median rates of sedimentation at the two sites were similar. The highest rates of sedimentation were recorded in May and September, during and following a period of mixing, respectively. Distinct seasonal trends in the organic contents of detritus and sediments were not observed. However, during all but two months (November and December, 1974) the organic contents of detritus were always higher than those of surface sediments. The relationship between resuspended bottom sediments and water turbulence has been discussed by a number of investigators (Davis 1968, Steele and Baird 1972, Pennington 1974, Gasith 1975, and Jones 1976). The low organic content of the detritus indicates that during all months a large fraction of the material collected in the traps is resuspended sediment. As algal blooms develop very infrequently in this system (the pond may be considered oligotrophic), tripton of high organic content is never present in high concentrations.

Mean monthly nitrogen, carbon, and caloric contents of sedimentary detritus and surface sediments are shown in Figures 3 and 4. No distinct trends between sites or among seasons were observed for detritus nitrogen and carbon contents (Fig. 3). The caloric contents of detritus, at both depths, were higher in the May-September period (i.e., the range at 1.8 m = 4374-3366 cal/g ash-free dry wt) than in the November-March period (range = 3598-2919 cal/g ash-free dry wt). There appeared to be two peaks (April and August) in monthly nitrogen, carbon and caloric contents of the sediments (Fig. 4). During the winter the sediment nitrogen content was low or not detectable. Most studies of sedimentation have shown that material settling on the bottom has higher carbon, nitrogen and caloric contents than that of sediments in the same area. This has been attributed to the degree of oxidation of materials in the sediments (Pamatmat and Bhagwat 1973).

Annual grand mean values for the organic, caloric, carbon and nitrogen contents (Table 1) of detritus were always higher than those for sediments at each depth. Thus, it appeared that freshly deposited detritus has more nutritive potential for the naiads of *H. limbata*. However, Mann (1972) has noted that many animals that feed on sedimentary deposits are more nutritionally dependent on the microbiota than on the nonliving organic debris. Newell (1965) suggested that bacterial carbon and nitrogen are present in quantities sufficient to account for a large proportion of sediment carbon and

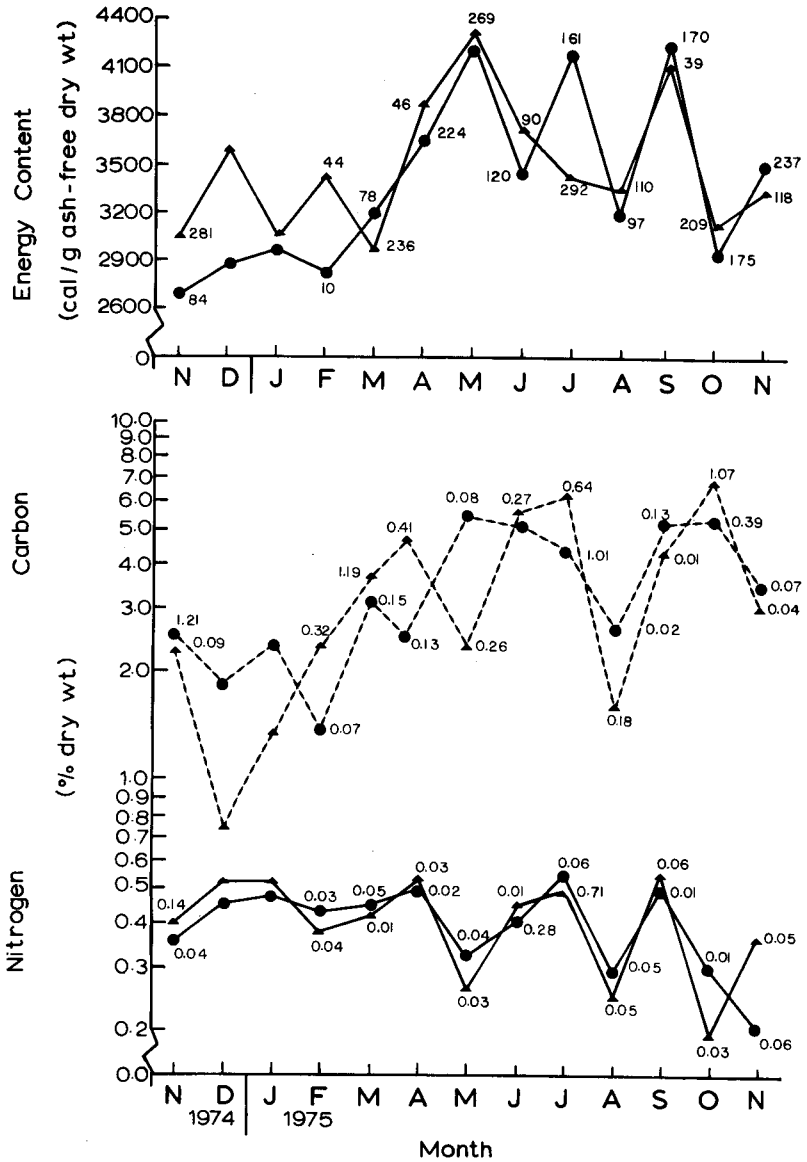


Figure 3. Percentage nitrogen and carbon (dry wt) and caloric contents (cal/g ash-free dry wt) of sedimentary detritus in Brandenburg Pond. Numbers represent the standard errors of the means. ● 1.2 m; ▲ 1.8 m.

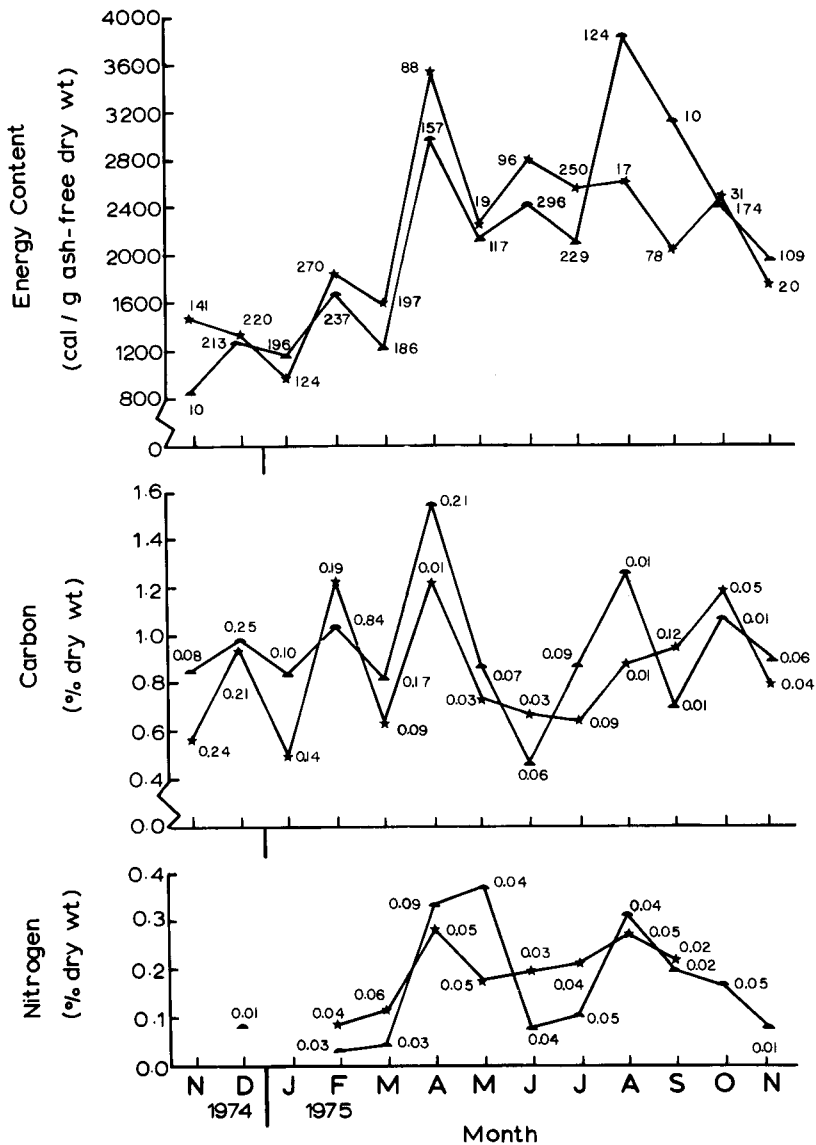


Figure 4. Percentage nitrogen and carbon (dry wt) and caloric contents (cal/g ash-free dry wt) of surface sediments from Brandenburg Pond. Numbers represent the standard errors of the means. * 1.2 m; ● 1.8 m.

Table 1. Annual grand mean values for organic, carbon (C), nitrogen (N), (as percentage dry weights), caloric contents (cal/g ash-free dry wt) and C:N ratios of detritus and surface sediments from Brandenburg Pond. Numbers in parentheses represent standard errors of the means.

Characteristic						
	Depth (m)	Organic (% dry wt)	Caloric (cal/g ash-free wt)	Carbon (% dry wt)	Nitrogen (% dry wt)	C:N
Detritus	1.2	16.5 (2.2)	3390 (154)	3.61 (0.42)	0.40 (0.03)	9.1:1
	1.8	18.7 (1.7)	3505 (125)	3.50 (0.53)	0.41 (0.03)	8.5:1
Sediments	1.2	5.0 (0.4)	2092 (195)	0.86 (0.07)	0.12 (0.03)	7.2:1
	1.8	9.3 (0.7)	2079 (239)	0.95 (0.07)	0.13 (0.04)	7.3:1

nitrogen, and Dale (1974) observed high correlations between carbon and nitrogen concentrations and bacterial numbers in sediments. He noted further that bacteria alone do not probably account for the total carbon and nitrogen in sediments. It seems reasonable that the primary source of carbon and nitrogen in sediments would include the total microbial community, consisting of bacteria, protozoans, fungi and epipelagic algae. The potential nutritive contribution by the microbial community in sediments and detritus from Brandenburg Pond is shown by their low C:N ratios (see Table 1) and by preliminary values for ATP-biomass carbon (Table 2). Lee *et al.* (1971a) and Perry (1974) have reported values of sediment ATP ranging from 0.34-9.4 $\mu\text{g ATP/g dry wt}$ and 11.24-50.5 $\mu\text{g ATP/g dry wt}$ for nine Wisconsin lakes and Marion Lake, respectively. In this study, the highest values for fresh surface sediment were observed in April and May (range = 9.9-14.7 $\mu\text{g ATP/g dry wt}$).

The organic carbon estimates (as % dry wt) reflected the organic carbon present in living and dead material (Fig. 3 and 4). The biomass carbon values were based only on living material (Table 2). Comparison of the two sets of values provide information on what fraction of the sediment or detritus was tied up in live microbes. If it is assumed that the 1974-1975 carbon values (Figs. 3 and 4) were representative of any year, then most of the organic carbon present at any time is in microbial biomass. For example, the December and April organic carbon estimates for detritus and sediments at 1.2 m were 1.7 and 0.93%, and 2.5 and 1.2%, respectively. The corresponding ATP-biomass carbon estimates (converted to % dry wt) for these months were 0.9 and 2.5%.

Analysis of Ingested Foods

Changes in the organic, nitrogen and caloric contents of gut material from two size-classes of naiads are shown in Figure 5. Values of the gut material for both size-classes were similar during each interval. In general, the highest values for each group were observed during March-September. This trend was especially evident in data on the caloric content of gut material (e.g., for large nymphs, March-September range was 5588 cal/g ash-free dry wt, while the November-February range was 4329-4286 cal/g ash-free dry wt). The organic and caloric contents of gut material were always higher than values for sedimentary detritus and surface sediments (Fig. 3 and 4). However, the nitrogen contents of gut material, though higher than values for surface sediments, were similar to values for sedimentary detritus. For example, for large nymphs the July nitrogen content of ingested material was 0.63% of dry weight, while the sediment and detritus nitrogen values at 1.2 m were 0.21 and 0.54% of dry weight, respectively. These results suggest that *H. limbata* naiads utilize the freshly-deposited detritus as food. However, the contributions of gut secretions and the effects of

Table 2. Surface sediment and detritus ATP-biomass carbon values for Brandenburg Pond, 1976-1977. Biomass carbon calculated by multiplying the ATP measurements by 250 (Holm-Hansen, 1973).

Year	Depth (m)	No. of Samples	Biomass ATP ($\bar{x} \pm SE$ $\mu\text{g/g}$ dry wt)	Biomass Carbon ($\bar{x} \pm SE$ $\mu\text{g/g}$ dry wt)
1976				
Lyophilized sediments				
October	1.2	3	3.5±0.2	875±38
November	1.2	3	4.2±0.1	1042±22
December	1.2	3	3.9±0.1	967±36
1977				
Fresh sediments				
April	1.2	3	9.9±0.1	2487±13
	1.8	3	12.6±0.1	3147±29
May	1.2	3	16.6±0.4	4141±92
	1.8	3	14.7±0.3	3645±73
Detritus				
May	1.8	2	15.8±0.3	3945±70

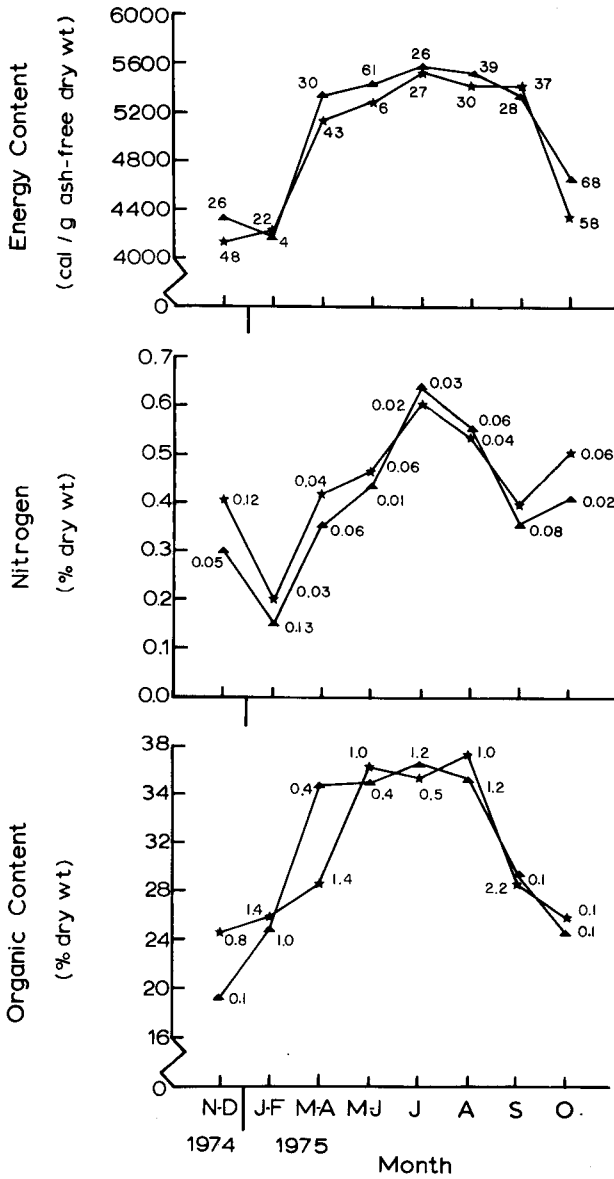


Figure 5. Percentage organic and nitrogen (dry wt) and caloric contents (cal/g ash-free dry wt) of gut contents from two size groups (< 15 and ≥ 15 mm) of *H. limbata* naiads. Numbers represent the standard errors of the means.
 * < 15 mm naiads; ▲ ≥ 15 mm naiads.

digestive processes on the organic, nitrogen and caloric values of gut materials are not known.

Results of the visual analysis of the gut contents of the two size-classes of nymphs are shown in Table 3. In both groups, detrital aggregates accounted for over 90% of the organic fraction of the gut material on a monthly basis. Diatoms were present (< 5% of total gut contents) in the foreguts of nymphs in all months except July. Filamentous algae and plant remains were of minor importance in the diet, and no animal fragments were encountered. Shapas and Hilsenhoff (1976) obtained similar results (92% detritus and 8% diatoms) for ten *H. limbata* nymphs collected in early spring. Though his data were only qualitative, Hunt (1953) reported that no significant differences were discernible in the amounts or composition of material ingested by *H. limbata* of different sizes or during different seasons. Although no animal fragments were observed in the gut contents, Rutter (1972) noted the presence of an oligochaete (*Sparganophilus* sp.) protruding from the mouthparts of a late instar naiad taken from Brandenburg Pond. Cummins (1973) has noted that the food items digested more rapidly, and hence seldom observed in gut contents, may actually have the highest nutritive value. In aquatic insects, these would probably include soft-bodied Diptera and Oligochaeta. Recently, Moore (1977) has concluded that the importance of algae in the diet of aquatic insects is highly variable and dependent on the species, age and habitat. Brown (1960) observed that many of the algae removed from the hindguts of the detritivore *Chloeon dipterum* were viable. However, Cummins (1973) has emphasized that organic compounds secreted or leaked by the algae also may be of nutritional importance to the consumer organism. Furthermore, Monk (1976) has observed weak cellulase activity in a number of aquatic insects, including ephemeropterans.

Mean size (μm^2) and range of detrital aggregates in the foreguts of the two size groups of naiads are also shown in Table 3. The mean sizes ($19,375 \mu\text{m}^2$) of detrital particles in the guts of small nymphs were significantly different ($p \leq 0.05$; Student's *t*-test) from those ($38,239 \mu\text{m}^2$) in large nymphs. These clumps of particles can be seen in the contents from freshly-dissected guts and are not artifacts of filtration. It is possible that naiads mechanically compact these particles while straining debris through the molar surfaces and that the size differences are due to the variability in the size of the molar ridges between the large and small size-classes (see description of molar surfaces below). Treatment of the particles with acetone, which causes a white precipitate on contact with mucopolysaccharides (= mucus), revealed that these aggregates may also be held together by this material. Bacteria are known to secrete sticky acidic polysaccharides (Corpe 1970, Floodgate 1972) and have been linked to formation of detrital aggregates in freshwater systems (Paerl 1973, 1974, 1975; Rodina 1963). Recently, Canfield and Backman (1978) reported high

Table 3. Summary of the food habits of two size-classes (<15 and \leq 15 mm) of *H. limbata* naiads. Analyses are based on food material removed from the anterior one-third of the digestive tract.

	Month							
	M	J	J	A	S	O	N	D
Naiads \geq 15 mm:¹								
Detritus remains								
% of total ²	95.8	97.7	96.9	96.5	98.2	97.2	96.8	95.6
mean size (μm^2) ³	36,750	47,050	39,070	38,800	40,250	36,405	45,285	37,052
size range of particles (μm^2)	3,000 to 159,600	3,000 to 161,000	2,800 to 144,000	1,200 to 160,000	2,000 to 156,000	600 to 159,600	650 to 165,000	575 to 158,000
Diatoms								
% of total	3.1	1.3	0	3.2	1.2	2.5	3.2	4.4
Filamentous algae								
% of total	1.1	1.0	3.1	0	0.6	0	0	0
Plant remains								
% of total	0	0	0	0.3	0	0.3	0	0
Animal remains								
% of total	0	0	0	0	0	0	0	0
Naiads < 15 mm:								
Detritus remains								
% of total	97.3	96.0	97.0	99.4	97.3	95.9	97.2	97.2
mean size (μm^2)	18,670	17,200	18,588	19,875	18,990	18,622	20,847	18,932
size range of particles (μm^2)	800 to 72,000	600 to 87,800	700 to 73,800	1,200 to 86,800	400 to 120,900	1,300 to 60,000	600 to 85,100	950 to 68,130
Diatoms								
% of total	2.4	1.0	0	0.6	2.5	3.8	2.5	2.5
Filamentous algae								
% of total	0.3	3.0	3.0	0	0.2	0.3	0.3	0
Plant remains								
% of total	0	0	0	0	0	0	0	0
Animals remains								
% of total	0	0	0	0	0	0	0	0

¹ Size range of nymphs \geq 15 mm was 15-25 mm; size range of nymphs < 15 mm was 8-14 mm.

² Percent detritus, diatoms, filamentous algae, animal, and plant remains based on total particles present and not size or weight. Estimates for detritus do not include inorganic particles.

³ Size based on maximum length x maximum width of organic detritus and does not include inorganic particles.:

concentrations (range = 4-274 million/L) of detrital aggregates (size range = 4-200 μm dia.) in the seston of nine Iowa lakes and reservoirs.

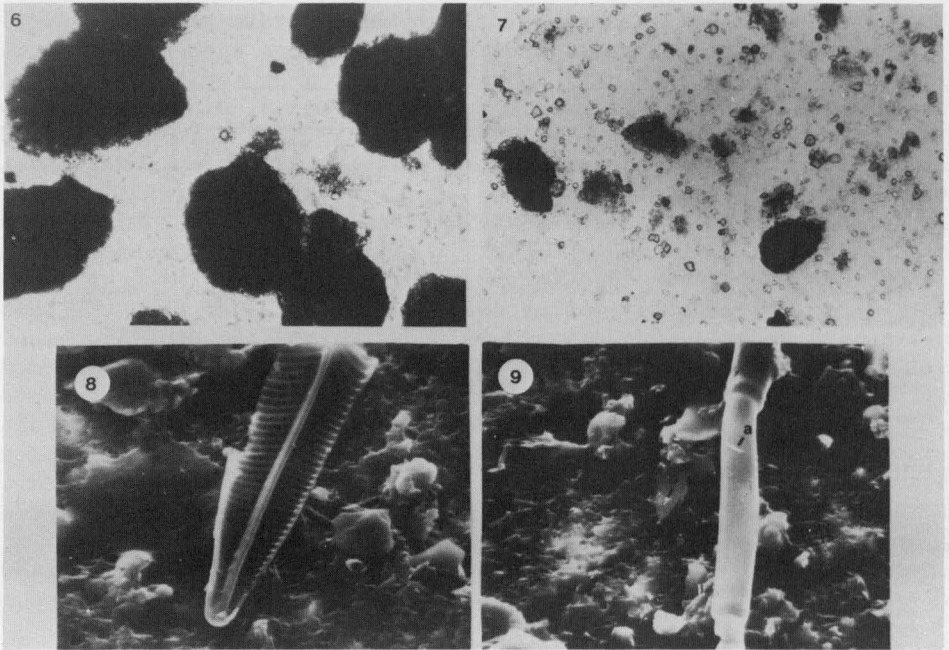


Plate 1. Figs. 6 and 7. Light micrographs of Millipore-filtered gut contents of *H. limbata* naiads. 13, large detrital aggregates at 100X; 14, a region of the filter showing smaller detrital aggregates and particles at 100X.

Figs. 8 and 9. Scanning electron photomicrographs of Nucleopore-filtered gut contents of *H. limbata* naiads. 8, fractured diatom frustule at 2700X; 9, filamentous algae at 2500X (a = colony of (?) bacteria attached to filamentous algae; b = (?) bacterium attached to inorganic particle). Accelerating voltage at 16 kV.

(Figs. 6 - 9 reduced 50% for reproduction).

Light and SEM micrographs of gut contents of *H. limbata* are shown in Plate 1. The light micrographs (at 100X) depict the size range of detrital particles (Figs. 6 and 7). The number and size range of inorganic particles (especially sand and clay) observed were large. Walker (1970) enumerated the inorganic and organic particles of *H. munda* naiads and found that 90% of the gut material was composed of sand and clay particles. Examination of the gut contents with the SEM supported the observation that the most abundant component of the gut contents is fine inorganic particulate material (many particles $<1 \mu\text{m}$; Figs. 8 and 9). Diatoms, pollen grains, filamentous algae, fungal hyphae, and bacteria were observed with the SEM. Many of these were associated with the detrital aggregates. Over 90% of the diatom frustules in the gut contents of naiads were fragmented (Fig. 8). While some appeared to be colonized by microbes, and ingested in that state, others seemed to have been fragmented by the animal during feeding. The grinding action of the molar surface of naiad mandibles, in combination with inorganic particles, may fragment the silicate frustules. Richardson and Gaufin (1971) concluded that sand particles in the foregut of the stonefly nymph, *Pteronarcys californica*, are used for grinding food and are regurgitated after this process. Regurgitation of sand particles does not seem to occur in deposit feeders. In fact, Cummins (1973) has suggested that these materials have nutritional value, owing to adsorbed organic material and associated bacteria.

Feeding Behaviour and Apparatus

It was difficult to observe the mechanism by which fine detritus is swept into the preoral cavity, processed by the molars, and swallowed. The following account of the feeding process is derived from microscopic analysis of the structure (Figs. 10-25) and movements of the mouthparts, laboratory and field observations of feeding behaviour, and from scattered reports in the literature (Morgan 1913), Needham 1920, Needham *et al.* 1935, Spieth 1941, and most recently McCafferty 1971). Most of the literature descriptions involve *Hexagenia recurvata*, now described as *Litobranchea recurvata* (McCafferty 1971, Edmunds *et al.* 1976). The most detailed description of the morphology, function and articulations of the mouthparts of mayflies was reported by Brown (1965) who studied two baetid forms (*Chloeon dipterum* and *Baetis rhodani*).

Food material is brought to the mouthparts of *H. limbata* in two ways. Nymphs occasionally approach the mouth of their burrows and dislodge surrounding material with their forelegs. Food material is also brought into contact with the mouthparts as the gills beat, thereby forcing water and debris into the burrow. On numerous occasions, I observed "puffs" of debris entering and leaving the burrows. The fine detritus debris is presumably collected by the labial palps, galea-laciniae, and canines, and swept into the preoral cavity, while

the hypopharynx is retracted, by the movements of the galea-laciniae. The food is retained in the ventral part of the preoral cavity by setae and spines situated on the labrum (inner surface and outer edge, Fig. 11) and tips of the hypopharyngeal lobes (Fig. 25). Debris is forced towards the mouth by the mandibles, as they close, and by the pressure exerted through the protraction of the hypopharynx. A relatively dry bolus of food is prepared for swallowing by the straining and crushing action of the molar surfaces. Support for these observations can be derived from a detailed examination of the structure of the mouthparts.

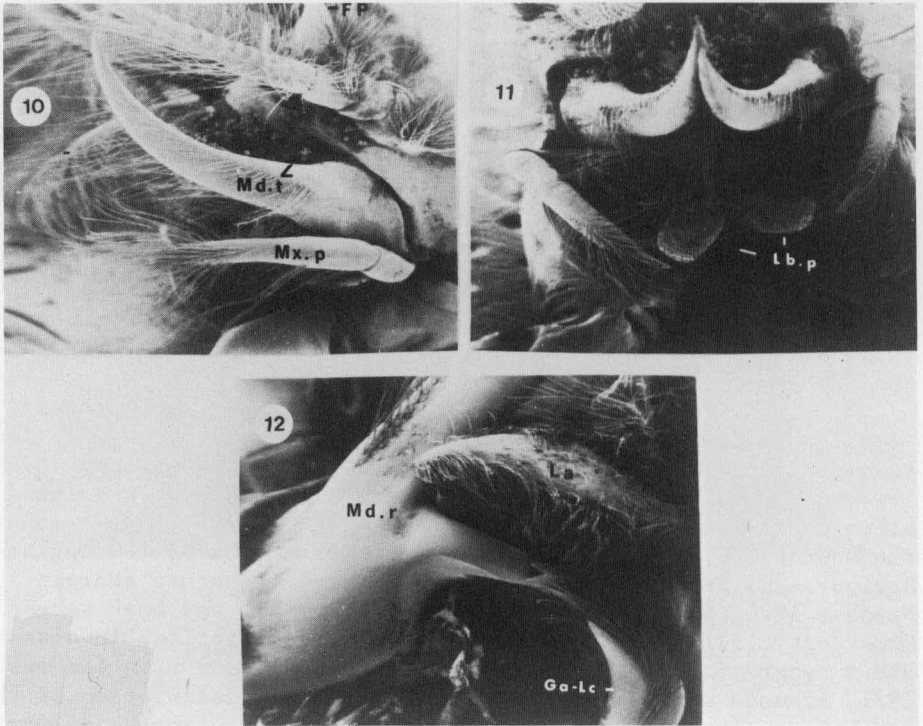


Plate 2. Figs. 10-12. Scanning electron photomicrographs of feeding appendages of *H. limbata* naiads. 10, side view of head at 68.2X; oblique view of head at 53.2X; 12, ventral view of head with labium and right maxilla removed exposing right mandible at 61.0X. Abbreviations: FP = frontal process; Ga-Lc = galea-lacinia of maxilla; La = labrum; Md. t = mandibular tusk; Md. r = right mandible; and Mx. p = maxillary palp. (Figs. 10-12 reduced 50% for reproduction).

The most noticeable diagnostic features of the head of *H. limbata*, as well as other *Hexagenia* species, are the long, curved tusks (mandibular tusks) extending beyond the head, and the dome-shaped prominence (frontal process) on the front of the head (Fig. 10) The maxillary and labial palps also extend beyond the head. All

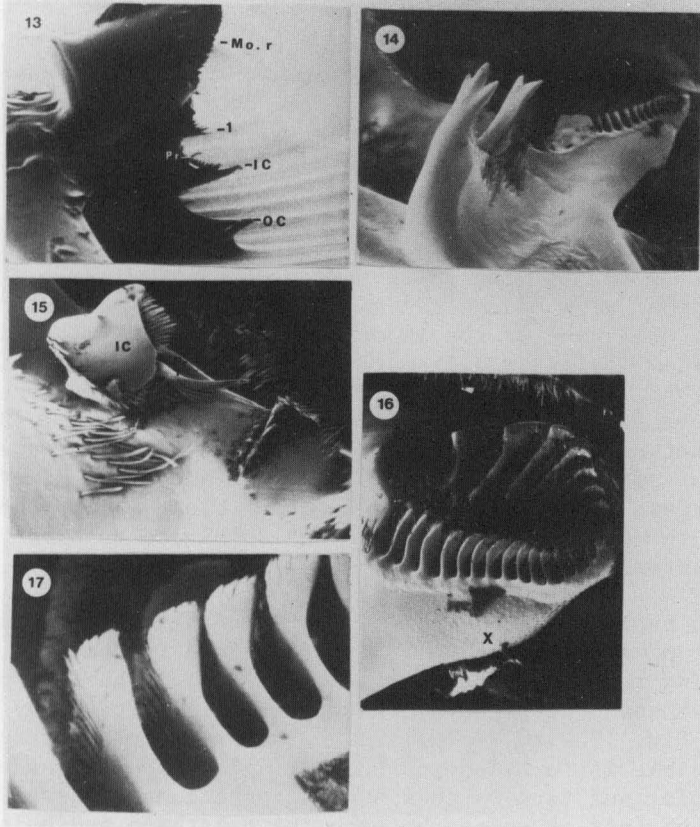


Plate 3. Figs. 13-17. Scanning electron photomicrographs of various aspects of the right mandible of *H. limbata* naiads. 13, profile of dissected right mandible at 87.7X; 14, ventral view of dissected mandible exposing canines and molar surfaces at 123.4X (note inner canine has two teeth); 15, median view of inner canine showing position of prostheca at 418.7X; 16, right molar surface at 286.1X (note, X = anterior surface); 17, close-up of anterior ridges of molar surface at 1100X. Abbreviations: IC = inner canine; Mo. r = right molar; OC = outer canine; and Pr = prostheca. Note, no 1 in Figures 13 and 15 are spines which lie between inner canine and molar surface. (Figs. 13-14 reduced 50% for reproduction).

mouthparts have an assortment of setae, spines and bristles which are directed toward the oral opening and apparently aid in food handling (Figs. 10 and 11). The proximal portions of the mandibles, maxillae, and labium are enclosed anteriorly by the clypeo-labral lobe, and the posterior surface of the lobe forms the anterior wall of the preoral cavity. In addition to the mandibular tusks, each mandible is composed of two canines (composed of two or three teeth), a prostheca, a number of spines and a molar surface (Figs. 13-21). The canines are on the median side of the tusk near the base, and, when the mandibles are in normal position (Fig. 12), they extend downward and probably function in grasping food. The food is passed from the canines to the grinding surface of the molars. Asymmetry in the structure of the right (Figs. 13-17) and left (Figs. 18-21) mandibles is produced by the arrangement and structure of the canines, prostheca and molar surfaces. The apex of the outer canine of the right mandible contains three teeth, while the inner canine contains two teeth (Fig. 14). The dorsal surface of each canine is cup-shaped and numerous spines line the outer edge. This is more easily seen in the dorsal view of the canines from the left mandible (Fig. 18). At the lateral base of the inner canine lies the bristled prostheca (also called lacinia mobilis or mandibular palp), which is freely movable, but lacking muscles (Fig. 15). Its significance in feeding has not been determined (Needham *et al.* 1935, Berner 1950, Brown 1965). Between the prostheca and the right molar surface is a thick cluster of spines (Figs. 13 and 15). The anterior end of the right molar surface bears 14 ridges, which are blunt and toothed. These traverse the entire molar surface and terminate as blunt projections on the posterior side (Figs. 16 and 17).

Both canines of the left mandible contain three teeth, and the perimeter of their cup-shaped dorsal surface is composed of two alternating rows of toothed spines (Fig. 18). The left prostheca is stouter than the right and bears several short, horny spines (compare Fig. 19 with Fig. 15). The anterior molar surface of the left mandible is formed by 12 blunt ridges which traverse the body of the molar and terminate as sharp projections (Figs. 20 and 21). There is no tuft of spines between the prostheca and molar surface of the left mandible.

When the mandibles are closed, the canines of the left mandible lie anterior to (overlap) those of the right, and the ridges of the molar surfaces overlap (Fig. 12). Brown (1965) noted that the spines and teeth are sharpest and most numerous on the mandibles of larvae that have recently undergone ecdysis. These structures become worn with use. A worn molar surface from a right mandible is shown in Figure 22. The wear exerted by the sediments on the molar surfaces during feeding may account in part for the large number of instars (approximately 40) that may occur in this species (N.W. Britt, personal communication).

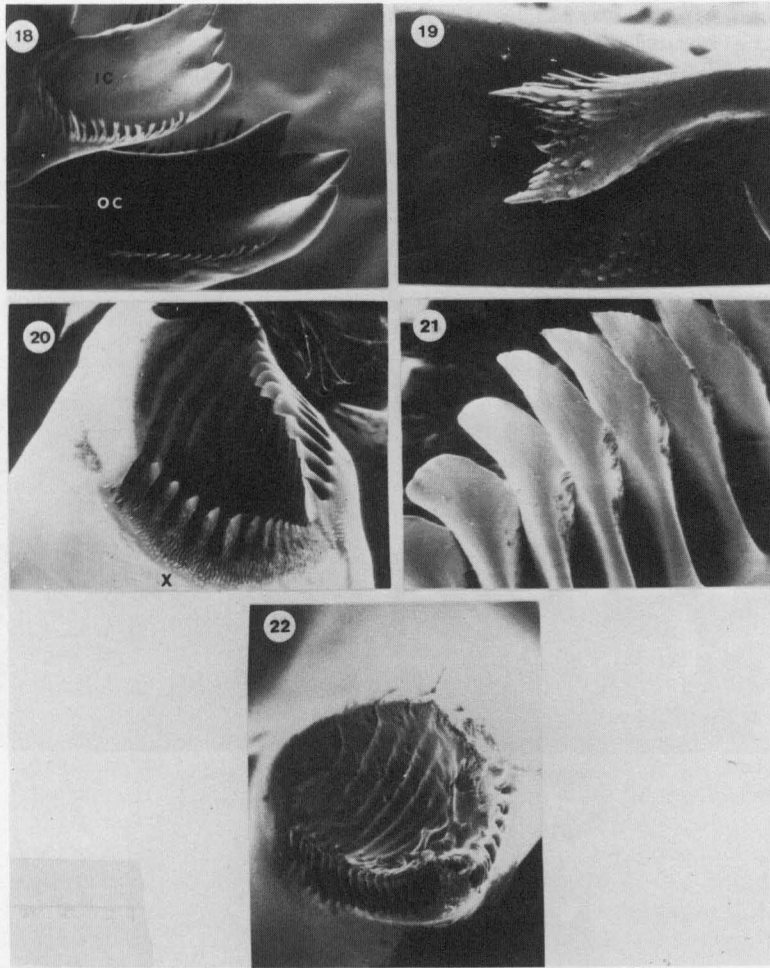


Plate 4. Figs. 18-22. Scanning electron photomicrographs of various aspects of the left mandible of *H. limbata* naiads. 18, lateral view of canines at 370.9X (note, inner canine has three teeth); 19, prosthema of left mandible at 840.1X; 20, left molar surface at 269.1X (note, X = anterior surface); 21, close-up of ridges on posterior molar surface at 827.6X; worn molar surface from the right mandible at 256.8X. Abbreviations: IC = inner canine; and OC = outer canine. (Figs. 18-22 reduced 50% for reproduction).

The positions of the maxillary and labial palps of *H. limbata* are shown in Figure 23. The palpi of the maxillae consist of three segments and terminate in a blunt, apical spine. The galea-laciniae of the maxillae are acute apically, with one large bidenticulate apical spine and two small subapical spines (not easily seen in Fig. 23). Though not distinct in Figure 25, the hypopharynx is composed of two superlinguae and a median sublingua.

The labium is formed by two palpi, each consisting of two segments and two inner paraglossae (Fig. 23). The dorsal surface of the terminal segment of a palp bears numerous spines (Fig. 24). The only differences in the morphology of the feeding appendages of large (none > 25 mm observed) and small (none < 10 mm observed)

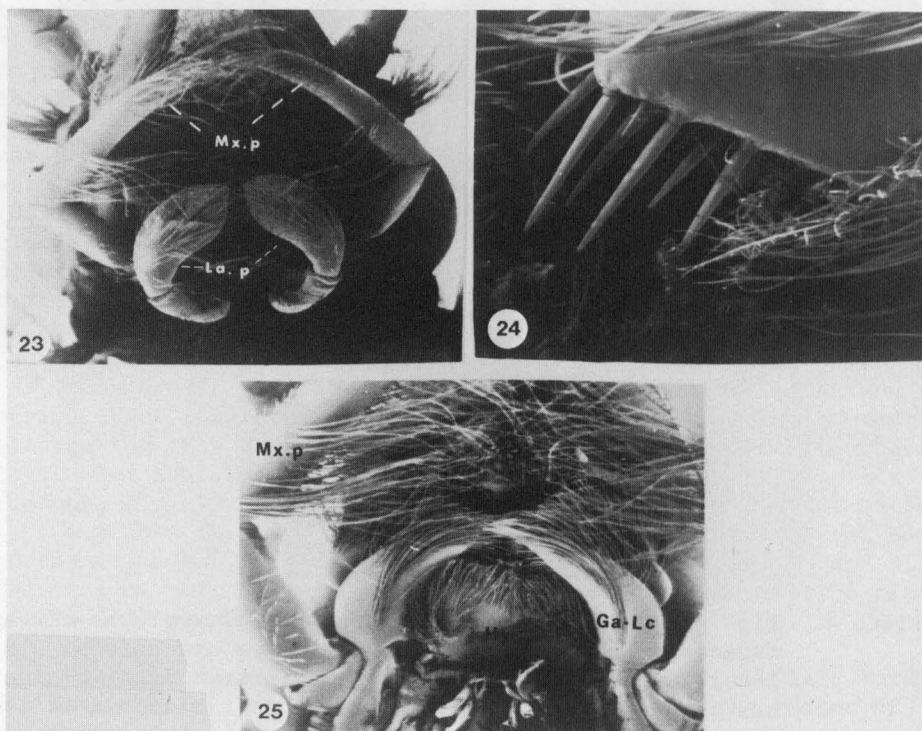


Plate 5. Figs. 23-25. Scanning electron photomicrographs of various aspects of ventral view of naid head. 23, ventral view at 45.5X; 24, apical view of terminal segment of labial palp at 436.0X; 25, ventral view of head with labium removed exposing maxillae and hypopharynx at 61.9X. Abbreviations: Ga-Lc = galea-lacinia; Hy = hypopharynx; La. p. = labial palp; Mx. p. = maxillary palp. (Figs. 23-25 reduced 50% for reproduction).

naiads were in the sizes of structures, which in turn are dependent on length (or age) of the organism.

In summary, it appears that all size-classes of *H. limbata* feed in a similar manner and ingest material of high caloric, organic, nitrogen and carbon contents (i.e., the most freshly-deposited detritus). This material also appears to have a high microbial content. Other data indicate that naiads feed continuously, and at most temperatures (range = 10-25°C) ingest over 100% of their dry body weight per day (Zimmerman and Wissing 1978). An estimate of how much sediment is processed by the *H. limbata* population in the pond may be made by multiplying the densities of nymphs by their ingestion rates calculated from equations given in Zimmerman and Wissing (1978). When this is done for nymphs with mean lengths of 8, 12, 18 and 22 mm (for zone 1 of pond, using densities reported in Zimmerman *et al.* 1975; assume temp. = 20°C), the estimates of the quantities of sediment ingested are 1116, 1416, 1893 and 587 mg/m²/day, respectively. For all size-classes combined, this value would be 5.01 g/m²/day. Such information indicates that a deposit feeder such as *H. limbata* can contribute significantly to detritus-processing in small aquatic ecosystems.

RESUME

On a examiné les aspects des dynamiques nutritives de l'éphémère fouisseuse, *Hexagenia limbata*. On a analysé le détritius nouvellement déposé et les sédiments superficiels (les volumes organiques, du carbone, de l'azote, et calorique) et comparés avec la matière dans l'intestin antérieur des larves de deux classes de taille (< 15 et ≥ 15 mm). Et l'analyse chimique et les devis du ATP-biomasse carbone suggèrent un potentiel nutritif plus haut du détritius. Dans les deux classes de taille, la matière ingerée se compose surtout de fines particules inorganiques, et plus de 90% de la matière organique dans l'intestin antérieur se compose de agrégats de détritius. On a utilisé l'analyse de la structure des pièces buccales et les observations du comportement alimentaire pour développer une description du procès alimentaire.

ZUSAMMENFASSUNG

Diese Arbeit behandelt Aspekte der Ernährungsdynamik der sich eingrabenden Eintagsfliege, *Hexagenia limbata*. Frisch abgeschiedener Detritus und Oberflächensedimente wurden analysiert (organischer Gehalt, Wärmegehalt, Kohlestoff - und Stickstoffgehalt) und verglichen mit Darmmaterial von Najaden zweier Größenklassen. (< 15 und ≥ 15 mm). Beides, die chemische Analyse und ATP-Biomasse-Kohlenstoff Schätzungen lassen vermuten, daß Detritus ein höheres Ernährungspotential besitzt. Bei beiden Größenklassen enthielt das verschlungene

Material hauptsächlich feine, anorganische Partikel. Des organische Darmmaterial bestand zu mehr als 90% aus Detritalaggregaten. Eine Analyse der Struktur der Mundteile und Beobachtungen bezüglich des Ernährungsverhaltens wurden verwendet, um daraus eine Beschreibung des Nahrungsaufnahme Prozesses zu entwickeln.

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