

Bioenergetics of the burrowing mayfly, *Hexagenia limbata*, in a pond ecosystem

MELVIN C. ZIMMERMAN, THOMAS E. WISSING and ROBERT P. RUTTER

With 3 figures and 6 tables in the text

Introduction

Mayflies of the genus *Hexagenia* (Ephemeroptera: Ephemeridae) are often abundant in the benthos of lakes and streams throughout North America, where they constitute an important food resource for some secondary consumers. General ecological relationships of *Hexagenia* spp. have been studied by a number of investigators (HUNT 1953; BRITT 1955 a, b; DORRIS & COPELAND 1962; SWANSON 1967; CARLANDER et al. 1967; CRAVEN & BROWN 1969; HUDSON & SWANSON 1972); however, little information is available on the contributions of these organisms to energy flow in freshwater communities.

WELCH (1968) and MANN (1969) have reviewed the calculated energy budgets for a number of aquatic invertebrates. More recently, STOCKNER (1971), KIMERLE & ANDERSON (1971), and LAWTON (1971) have reported on the ecological energetics of *Hedriodiscus truquii*, *Glyptotendipes barbipes*, and *Pyrrhosoma nymphula*, respectively. Similar studies of *Hexagenia* have not been carried out.

The energy budget equation for an aquatic insect can be expressed as:

$$C = F + U + Ev + R + P,$$

where C is the energy consumed, F is the energy lost as faeces, U is the excretory energy loss, Ev is the energy loss through moulting (exuviae), R is the respiratory energy loss, and P is the energy accumulated as growth (LAWTON 1971). The present study was designed to obtain energy budgets for nymphs of the major size-classes of *Hexagenia limbata* in a pond ecosystem. The energy relationships which were investigated were the caloric equivalents of ingestion, egestion, respiration, and growth.

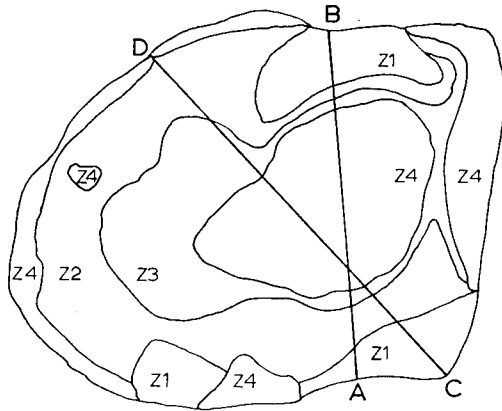
Study area

Brandenburg Pond is located approximately 3 km southeast of Oxford, Ohio. The pond is roughly circular with a diameter of about 88 m, total surface area of 6,133 m², and a maximum depth of 2.9 m. Substrate composition and distribution, as determined by RUTTER & WISSING (1975), are shown in Fig. 1.

Methods

A sampling program was designed to monitor changes in the numbers and biomass of nymphs in each of four zones in the pond (see Fig. 1). However, only the data on numbers will be presented in this paper.

Two transects (A—B, C—D), containing 13 and 15 permanent sampling stations, respectively, were sampled with a 15-cm EKMAN grab on alternate weeks from 15 May to 12 September, 1972. The number of nymphs per m² in each of four size-classes (5—9, 10—14, 15—19, 20—24 mm) was recorded for the different substrate types. Dissolved



- Z1: YELLOW CLAY, GRAVEL, LITTLE DETRITUS
(4-5% ORG)
- Z2: LIGHT, MORE CLAY THAN DETRITUS
(6-8% ORG)
- Z3: DARK, MORE DETRITUS THAN CLAY
(8-9% ORG)
- Z4: BLACK MUCK, MUCH DETRITUS
(10-12% ORG)

Fig. 1. Substrate types and distribution in Brandenburg Pond. Sampling stations were located along two transects (A—B, C—D).

oxygen (ppm) and water temperature ($^{\circ}\text{C}$) were determined at each station with an oxygen meter and thermistor.

Estimates of ingestion and food-turnover times were made in the laboratory. Nymphs were allowed to feed in two series of small plastic containers containing filtered pond water and the yellow-clay (Series I) and black-mucky (Series II) substrates characteristic of certain areas of the pond. Nymphs with empty digestive tracts were placed in Series-I containers and observed against a bright background at 2-hour intervals to determine the time required to fill the digestive tract. Nymphs with guts filled completely with yellow-clay substrate were then transferred to Series-II containers. Food-turnover time was determined by recording the movement of the interface between the yellow and black substrates, after nymphs were serially sacrificed and their digestive tracts were opened to expose the interface. Sixty-four and 44 nymphs were followed through Series I and II, respectively.

Daily food intake of three size-classes (10—14, 15—19, 20—24 mm) of nymphs was estimated by multiplying the mean dry weight (105 $^{\circ}\text{C}$ for 24 hours) of gut contents by the number of times the contents were turned over in a 24-hour period. Dry weight of gut contents of the smallest nymphs (5—9 mm) was determined from a graphical relationship between gut content weights and lengths of nymphs of all size-classes. During March, 1972, gut contents were removed from nymphs (10—14, 15—19, 20—24 mm) collected in Zones 1 and 3. This material was then oven-dried and combusted in a PHILLIPSON microbomb calorimeter (PHILLIPSON 1964).

Faeces of nymphs ($n = 708$) in the larger size classes (15—19, 20—24 mm) were collected during the summer. Nymphs were periodically introduced into an inverted plastic container (3.76 l) filled with filtered pond water. Faecal material produced over the 24-hour period after introduction was collected in a vial attached to the

container and refrigerated. Approximately 30 g of surface sediment were also collected monthly (March—August, 1972) with a 20-cc syringe from EKMAN grab samples (KAJAK 1971) taken in each of the four zones. During October to November, 1972, suspended detritus, which settles on the bottom and hence becomes available as a potential food resource, was collected in an acrylic plastic cylinder lowered to the bottom of the pond (depth = 1.7 m). The caloric contents of dried (105 °C for 24 hours) samples of faeces, sediments, and detritus were determined with the modified iodatesulfuric acid wet oxidation method of KARZINKIN & TARKOVSKAYA (1964), as described in HUGHES (1969).

Respiratory metabolism was measured in 300-ml BOD bottles, containing pond water, which were lowered to the bottom at a depth of 1.6 m. Three to five nymphs of a particular size-class were exposed for 14-hour diurnal and 10-hour nocturnal time periods. Dissolved oxygen was determined with the sodium-azide modification of the WINKLER method (TARAS et al. 1971). Oxygen consumption was expressed as mg oxygen per nymph per day.

Daily energy budgets (in cal/nymph/day) were constructed for the four size-classes of nymphs in Zones 1 and 3. Ingestion (I) was calculated by multiplying the daily food intake of a particular size-class by the cal/g value of the gut contents. The caloric content of gut material of the smallest size-class (5—9 mm) was not determined experimentally; instead the average caloric value of gut contents from the three larger size-classes was used. Calculations of daily egestion were based on 1) the assumption that all inorganic material ingested by the organism is egested, and 2) the observation that roughly one-half of the organic fraction of the ingested material appeared in the faeces. The caloric equivalent of egestion (E) was obtained by multiplying the dry weight of material egested over a 24-hour period by the caloric content (670 cal/g) of the faeces. Daily energy of respiration (R) was determined with an oxycaloric coefficient of 3.38 cal per mg oxygen consumed (KIMERLE & ANDERSON 1971). A component designated as larval growth (G) was calculated by difference and was assumed to reflect energy apportioned to moulting (Ev) and to the formation of new body tissue (P). The caloric equivalent of excretion (U) was not determined experimentally, but was estimated from data reported for the neuropteran, *Sialis lutaria* (STADDON 1955). Excretory energy losses for the small size-classes (5—9, 10—14, 15—19 mm) were estimated, on a proportional mean weight basis, from the calculated energy loss of the 20—24 mm size-class (0.39 cal/day).

The estimates of daily energy flow, along with the data on number of nymphs per m², were used to calculate energy budgets for four time intervals of 30 days during late spring and summer. Energy budgets constructed for Zones 1 and 3 were used to calculate budgets for nymphs in Zones 2 and 4, respectively, since the organic content and physical characteristics of substrates in these zones were similar (see Fig. 1).

Results and discussion

Water temperature during the study period averaged 23.5 °C (range = 19.5—26.5 °C). The oxygen profiles show that low oxygen levels (< 1.0 ppm) occurred at depths greater than 2.0 m (Fig. 2); however, during a period of high wind (14 Aug.), mixing did occur.

Results of the feeding experiments indicate that nymphs turn over the contents of the digestive tract as often as five times per day. Ingestion of food material by Series-I nymphs less than 20 mm was more rapid than that recorded for individuals greater than 20 mm (4.4 and 5.1 hours, respectively). The respective food-turnover times for the same nymphs in the Series-II containers were 4.4 and 5.5 hours. The dry weight of gut contents of the smallest size-class (5—9 mm) was determined as 1.35 mg from a semi-log plot of the rela-

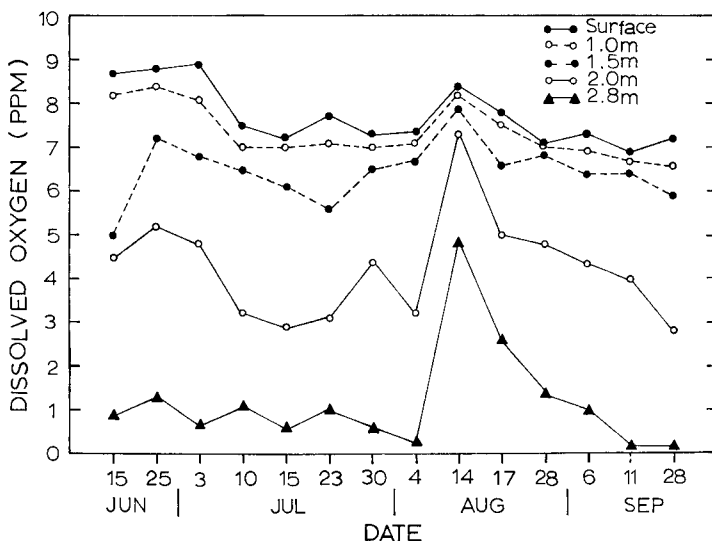


Fig. 2. Dissolved oxygen profiles for Brandenburg Pond during June–September, 1972.

relationship between gut content weights and lengths of the larger size-classes. The corresponding daily food intake was calculated as 7.4 mg. It was assumed in calculating daily food intake that nymphs feed continually during a 24-hour period. The original experiments on food-turnover times were carried out under conditions of constant light. When these were repeated in the dark, the organisms continued to ingest and to process food material. Rapid food-turnover rates have been reported for a number of benthic invertebrates (GORDON 1966; HARGRAVE 1971). Furthermore, frequent feeding is generally common among immature insects (WALDBAUR 1968).

The caloric and organic contents of potential food materials varied greatly. The grand mean energy values for the monthly samples of surface sediments increased from Zones 1 through 4 ($1,016 \pm 15$, $1,225 \pm 12$, $1,725 \pm 6$, and $2,254 \pm 11$ cal/g ash-free weight, respectively), as did the organic content (5.4 ± 0.2 , 6.8 ± 0.3 , 7.3 ± 0.1 , and $8.9 \pm 0.2\%$). Variability in the monthly values for surface sediments was noted in each zone. This could reflect differences among the various sampling sites or seasonal variation in the composition and degree of oxidation of the organic fraction in the sediments. The mean energy content of detrital material was 724 ± 36 cal/g dry weight or 3,719 cal/g ash-free weight (\bar{x} organic content = 25.0%). Caloric values for gut contents are given in Tab. 1. Interestingly, the caloric and organic contents of gut material were much higher than those of surface sediments in the four zones.

The observed differences in the energy and organic contents of surface sediments, detrital material, and gut contents suggest that nymphs selectively ingest organic matter of high caloric content. The exact composition of this material is unknown at this time, though its high energy content would indicate that benthic algae, protozoans, bacteria, and small amounts of organic detritus are

Tab. 1. Caloric and percentage organic contents of gut material from four size-classes of *H. limbata*. Mean values are given for two determinations on pooled samples. SE = standard error of mean.

Zone	Size-class (mm)	Caloric content (cal/g dry weight)	± SE	Caloric content (cal/g ash-free dry weight)	± SE	Organic content (%)	± SE
1	5—9	1,826 ^a					
	10—14	2,008	57	5,646	164	35.6	0.8
	15—19	1,560	2	5,125	5	30.4	0.1
	20—24	1,911	62	5,249	172	36.4	0.6
3	5—9	1,798 ^a					
	10—14	1,723	9	4,786	26	36.0	0.2
	15—19	1,714	50	4,566	132	37.5	0.7
	20—24	1,957	21	5,189	58	37.7	0.6

^a Caloric value (in cal/g dry wt.) of gut material from nymphs in 5—9 mm size-class determined by averaging values from other size-classes. Values for organic and caloric content (in cal/g ash-free wt.) were not determined.

probably consumed, along with large amounts of indigestible inorganic matter. Some evidence as to the mode of feeding in *Hexagenia* is derived from the observation that nymphs will seldom leave their burrows, but will occasionally approach the mouth of the tube and dislodge surrounding material (HUNT 1953).

The mean energy content of replicate samples of faeces was 670 ± 50 cal/g dry weight or 3,766 cal/g ash-free weight (\bar{x} organic content = 17.8%). Both the caloric and organic contents of the faeces were higher than the values for surface sediments but lower than those for gut material (see Tab. 1). HUGHES (1970) reported that the energy value for faeces from the marine bivalve, *Scrobicularia plana*, was roughly 1.8 times higher than that for sediments.

The respiration experiments exposed nymphs to natural changes in photo-period and ambient water temperature. Small nymphs (5—9 mm) exhibited a higher metabolic rate than large individuals (20—24 mm). For example, the 14-hour diurnal value for the 5—9 mm size-class was 0.72 mg O₂ consumed/g wet weight/hr, and the 10-hour nocturnal value was 0.76 mg O₂/g wet weight/hr. Corresponding values for 20—24 mm individuals were 0.41 and 0.48 mg O₂/g wet weight/hr. On the average, nymphs in the larger size-classes (15—19, 20—24 mm) consumed 0.82 and 1.07 mg O₂/individual, respectively, during a 24-hour period, whereas the respective values for individuals in the smaller size-classes (5—9, 10—14 mm) were 0.17 and 0.48 mg O₂/individual.

Daily energy budgets (in cal/nymph/day) were constructed for the four size-classes in Zones 1 and 3 (Tab. 2). Ingestion in each size-class was calculated by using the mean cal/g value for the gut contents, which appears to more closely approximate the true energy content of ingested material than the caloric values for surface sediments and detrital material. The assimilated fraction of ingested energy averaged 68% in both zones.

Energy budgets for the four zones over four 30-day periods are given in Tabs. 3 through 6. Nymphal densities and energy flow were greatest during

Tab. 2. Daily energy budgets (in cal/nymph/day) for four size-classes of *H. limbata*. I = Ingestion, E = Egestion, U = Excretion, R = Respiration, and G = Growth.

Zone	Size-class (mm)	I = E + U ^a + R + G ^b	Assimilation efficiency $\frac{I - (E + U)}{I} \times 100$
1	5—9	13.51 = 4.09 + 0.13 + 0.59 + 8.70	69
	10—14	26.10 = 7.17 + 0.22 + 1.63 + 17.08	72
	15—19	36.50 = 13.74 + 0.30 + 2.77 + 19.69	62
	20—24	61.92 = 17.94 + 0.39 + 3.62 + 39.97	70
3	5—9	13.31 = 4.06 + 0.13 + 0.59 + 8.53	69
	10—14	22.40 = 7.12 + 0.22 + 1.63 + 13.43	67
	15—19	40.12 = 12.59 + 0.30 + 2.77 + 24.46	68
	20—24	64.38 = 17.65 + 0.39 + 3.62 + 42.72	72

^a Calculated from data reported in STADDON (1955).

^b By difference.

the first interval (15 May—13 June; Tab. 3). During this period, 5—9 mm nymphs dominated the population, with a density of 911/m² in Zone 1. The densities of the four size-classes steadily declined during the remaining intervals (Tabs. 4—6). The relatively low density of nymphs in Zone 4 at all times was probably related to low levels of dissolved oxygen in this area during the summer (see Fig. 2).

Periodic changes in size-class distribution were also observed (Fig. 3). This was especially noticeable in Zone 4, where nymphs in the larger size-classes (15—19, 20—24 mm) were generally dominant, though in varying percentages relative to the other size-classes present. The temporal changes in size-class composition of the zones could reflect the influence of factors such as predation, emergence, and movement. Reports of changes in the distribution of larval stages of *H. limbata* through migration are scattered in the literature. HUNT (1953) and SWANSON (1967) observed movements of young nymphs from densely populated shore areas to deeper water. HUDSON & SWANSON (1972) suggested that migration is most intense when the population density exceeds 100 individuals/m². Migratory movements might also occur during periods of low water, when substrate along the shoreline is exposed, or during times of low oxygen levels in deep waters. Whatever the cause, it is clear that changes in the density and composition of the nymphal population in a particular zone can influence energy flow in that area of the pond (see Tabs. 3—6).

The net growth efficiency (growth/assimilation or K_2 ; IVLEV 1945) of *H. limbata* averaged about 88% for the four size-classes. A high growth efficiency in this species may not be unusual, since larvae appear to remain in their burrows for long periods of time and, hence, expend little energy in movement. MCNEILL & LAWTON (1970) have suggested that poikilotherms with short generation times (< 2 years) tend to lose less of their assimilated energy through respiration than do animals with long life cycles. Thus, organisms with short life cycles can potentially maintain high rates of production throughout their lives. *H. limbata* seems to conform to this hypothesis, since nymphs in Branden-

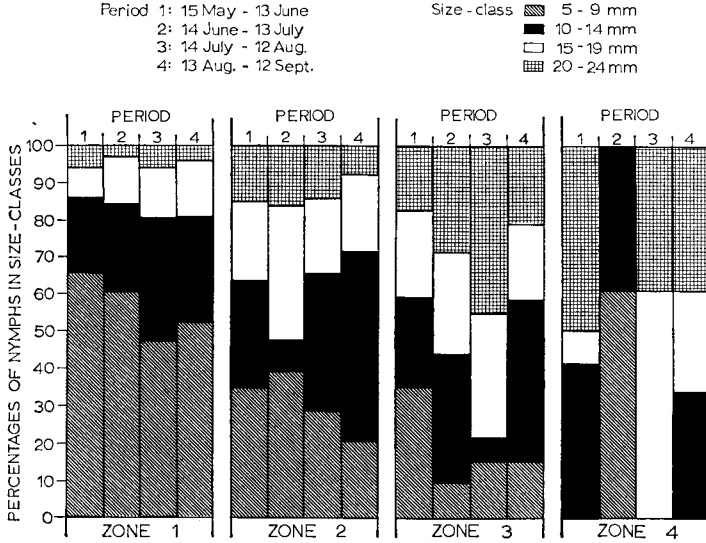


Fig. 3. Changes in the percentages of four size-classes of *H. limbata* nymphs in Zones 1—4 of Brandenburg Pond. Values are given for four 30-day periods in 1972.

Tab. 3. Densities and energy budgets (in Kcal/m²) of major size-classes of *H. limbata* during the period 15 May — 13 June, 1972. SE = Standard error of mean. I = Ingestion, E = Egestion, U = Excretion, R = Respiration, G = Growth.

Zone	Size-class (mm)	Mean no. of larvae/m ² (±SE)	I = E + U ^a + R + G ^b
1	5—9	911.0 (±105)	369.3 = 111.8 + 3.6 + 16.1 + 237.8
	10—14	281.5 (±98)	220.4 = 60.5 + 1.9 + 13.8 + 144.2
	15—19	116.0 (±22)	127.1 = 47.8 + 1.0 + 9.6 + 68.7
	20—24	69.1 (±6)	128.4 = 37.2 + 0.8 + 7.5 + 82.9
2	5—9	174.6 (±30)	70.8 = 21.4 + 0.7 + 3.1 + 45.6
	10—14	152.4 (±43)	119.4 = 32.8 + 1.0 + 7.5 + 78.1
	15—19	101.6 (±25)	111.2 = 41.9 + 0.9 + 8.4 + 60.0
	20—24	73.0 (±8)	135.6 = 39.3 + 0.9 + 8.0 + 87.4
3	5—9	26.7 (±10)	10.6 = 3.2 + 0.1 + 0.5 + 6.8
	10—14	17.8 (±6)	11.9 = 3.8 + 0.1 + 0.9 + 7.1
	15—19	17.8 (±4)	21.4 = 6.7 + 0.2 + 1.5 + 13.0
	20—24	13.3 (±3)	25.7 = 7.1 + 0.2 + 1.4 + 17.0
4	5—9	0.0 (±0)	0.0 = 0.0 + 0.0 + 0.0 + 0.0
	10—14	15.9 (±2)	10.7 = 3.4 + 0.1 + 0.8 + 6.4
	15—19	3.3 (±0)	3.8 = 1.2 + 0.1 + 0.3 + 2.2
	20—24	12.7 (±0)	24.5 = 6.7 + 0.1 + 1.4 + 16.3

^a Calculated from data reported in STADDON (1955).

^b By difference.

Tab. 4. Densities and energy budgets (in Kcal/m²) of major size-classes of *H. limbata* during the period 14 June—13 July, 1972. Details as in Tab. 3.

Zone	Size-class (mm)	Mean no. of larvae/m ² (\pm SE)	I = E + U ^a + R + G ^b
1	5—9	595.1 (\pm 95)	241.5 = 73.0 + 2.4 + 10.5 + 155.3
	10—14	224.7 (\pm 63)	175.9 = 48.3 + 1.5 + 11.0 + 115.1
	15—19	128.4 (\pm 20)	140.6 = 52.9 + 1.2 + 10.7 + 75.8
	20—24	29.6 (\pm 3)	55.0 = 16.0 + 0.4 + 3.2 + 35.4
2	5—9	115.5 (\pm 24)	46.8 = 14.1 + 0.5 + 2.0 + 30.2
	10—14	22.5 (\pm 5)	17.6 = 4.9 + 0.1 + 1.1 + 11.5
	15—19	104.8 (\pm 17)	114.7 = 43.2 + 0.9 + 8.7 + 61.9
	20—24	50.8 (\pm 0)	94.2 = 27.3 + 0.6 + 5.5 + 60.8
3	5—9	8.9 (\pm 0)	3.5 = 1.1 + 0.0 + 0.2 + 2.2
	10—14	31.1 (\pm 5)	20.8 = 6.6 + 0.2 + 1.5 + 12.5
	15—19	26.7 (\pm 6)	32.1 = 10.1 + 0.2 + 2.2 + 19.6
	20—24	26.7 (\pm 6)	51.5 = 14.1 + 0.3 + 2.9 + 34.2
4	5—9	9.5 (\pm 0)	3.8 = 1.2 + 0.0 + 0.2 + 2.4
	10—14	6.4 (\pm 0)	4.3 = 1.4 + 0.0 + 0.3 + 2.6
	15—19	0.0 (\pm 0)	0.0 = 0.0 + 0.0 + 0.0 + 0.0
	20—24	0.0 (\pm 0)	0.0 = 0.0 + 0.0 + 0.0 + 0.0

^a Calculated from data reported in STADDON (1955).

^b By difference.

Tab. 5. Densities and energy budgets (in Kcal/m²) of major size-classes of *H. limbata* during the period 14 July—12 August, 1972. Details as in Tab. 3.

Zone	Size-class (mm)	Mean no. of larvae/m ² (\pm SE)	I = E + U ^a + R + G ^b
1	5—9	338.2 (\pm 27)	137.1 = 41.5 + 1.3 + 6.0 + 88.3
	10—14	251.8 (\pm 31)	197.2 = 54.2 + 1.7 + 12.3 + 129.0
	15—19	88.9 (\pm 3)	97.3 = 36.6 + 0.8 + 7.4 + 52.5
	20—24	46.9 (\pm 2)	87.0 = 25.2 + 0.5 + 5.1 + 56.2
2	5—9	101.6 (\pm 15)	41.2 = 12.5 + 0.4 + 1.8 + 26.5
	10—14	139.7 (\pm 17)	109.3 = 30.0 + 0.9 + 6.8 + 71.6
	15—19	73.0 (\pm 3)	79.9 = 30.1 + 0.7 + 6.1 + 43.0
	20—24	50.8 (\pm 7)	94.3 = 27.3 + 0.6 + 5.5 + 60.9
3	5—9	8.9 (\pm 0)	3.5 = 1.1 + 0.0 + 0.2 + 2.2
	10—14	4.4 (\pm 0)	3.0 = 0.9 + 0.0 + 0.2 + 1.9
	15—19	22.2 (\pm 5)	26.7 = 8.4 + 0.2 + 1.8 + 16.3
	20—24	26.7 (\pm 4)	51.5 = 14.1 + 0.3 + 2.9 + 34.2
4	5—9	0.0 (\pm 0)	0.0 = 0.0 + 0.0 + 0.0 + 0.0
	10—14	0.0 (\pm 0)	0.0 = 0.0 + 0.0 + 0.0 + 0.0
	15—19	9.5 (\pm 0)	11.5 = 3.6 + 0.1 + 0.8 + 7.0
	20—24	6.4 (\pm 0)	12.3 = 3.4 + 0.1 + 0.7 + 8.1

^a Calculated from data reported in STADDON (1955).

^b By difference.

Tab. 6. Densities and energy budgets (in Kcal/m²) of major size-classes of *H. limbata* during the period 13 August—12 September, 1972. Details as in Tab. 3.

Zone	Size-class (mm)	Mean no. of larvae/m ² (± SE)	I = E + U ^a + R + G ^b
1	5—9	273.0 (±11)	110.6 = 33.5 + 1.1 + 4.8 + 71.2
	10—14	149.2 (±15)	116.8 = 32.1 + 1.0 + 7.3 + 76.4
	15—19	73.0 (±12)	79.9 = 30.1 + 0.7 + 6.1 + 43.0
	20—24	22.2 (±5)	41.3 = 12.0 + 0.3 + 2.4 + 26.6
2	5—9	80.0 (±7)	32.4 = 9.8 + 0.3 + 1.4 + 20.9
	10—14	195.6 (±6)	153.1 = 42.1 + 1.3 + 9.6 + 100.1
	15—19	80.0 (±7)	87.6 = 33.0 + 0.7 + 6.6 + 47.3
	20—24	26.7 (±2)	49.5 = 14.3 + 0.3 + 2.9 + 32.0
3	5—9	12.7 (±0)	5.0 = 1.6 + 0.0 + 0.2 + 3.2
	10—14	38.1 (±2)	25.6 = 8.1 + 0.3 + 1.9 + 15.3
	15—19	19.1 (±0)	22.9 = 7.2 + 0.2 + 1.6 + 13.9
	20—24	19.1 (±0)	36.8 = 10.1 + 0.2 + 2.1 + 24.4
4	5—9	0.0 (±0)	0.0 = 0.0 + 0.0 + 0.0 + 0.0
	10—14	4.4 (±0)	3.0 = 0.9 + 0.0 + 0.2 + 1.9
	15—19	4.4 (±0)	5.3 = 1.7 + 0.0 + 0.4 + 3.2
	20—24	4.4 (±0)	8.8 = 2.5 + 0.1 + 0.5 + 5.7

^a Calculated from data reported in STADDON (1955).

^b By difference.

burg Pond appear to have a life cycle of 1 to 2 years (RUTTER & WISSING 1975). High assimilation efficiencies (> 60 %) are generally characteristic of herbivores and carnivores (WELCH 1968; LAWTON 1970), though *H. limbata* is probably more omnivorous in its food habits. The values of assimilation efficiency obtained in this study ($\bar{x} = 68\%$) indicate that food material ingested by the nymphs is relatively high in digestibility and hence may be assimilated more efficiently than that consumed by strict detritivores.

The results of our study illustrate in part the functional importance of this species in the pond community. They also point out the critical need for methods of better characterizing the food habits of aquatic insects. Recently, CUMMINS (1973) has outlined techniques for the preparation and enumeration of the gut contents of aquatic insects. This kind of information, coupled with an analysis of the food resources available to the organism, would provide a more realistic basis for assessing the composition and nutritive value of ingested food material and hence lead to a more meaningful description of energy flow in this and other species of aquatic insects.

References

- BRITT, N. W., 1955 a: Stratification in western Lake Erie in summer of 1953: effects on the *Hexagenia* (Ephemeroptera) population. — *Ecology* 36, 239—244.
- 1955 b: *Hexagenia* (Ephemeroptera) population recovery in western Lake Erie following the 1953 catastrophe. — *Ecology* 36, 520—522.
- CARLANDER, K. D., CARLSON, C. A., GOOCH, V. & WENKE, T., 1967: Population of *Hexagenia* mayfly naiads in Pool 19, Mississippi River, 1959—1963. — *Ecology* 48, 873—878.

- CRAVEN, R. E. & BROWN, B. E., 1969: Ecology of *Hexagenia* naiads (Insecta — Ephemeroidea) in an Oklahoma reservoir. — *Amer. Midl. Nat.* **82**, 346—358.
- CUMMINS, K. W., 1973: Trophic relations of aquatic insects. — *Ann. Rev. Entomol.* **18**, 183—206.
- DORRIS, T. C. & COPELAND, B. J., 1962: Limnology of the middle Mississippi River. III. Mayfly populations in relation to navigation water-level control. — *Limnol. Oceanogr.* **7**, 240—247.
- GORDON, D. C., 1966: The effect of the deposit feeding polychaete *Pectinaria gouldii* on the intertidal sediments of Barnstable Harbor. — *Limnol. Oceanogr.* **11**, 327—332.
- HARGRAVE, B. T., 1971: An energy budget for a deposit-feeding amphipod. — *Limnol. Oceanogr.* **16**, 99—103.
- HUDSON, P. L. & SWANSON, G. A., 1972: Production and standing crop of *Hexagenia* (Ephemeroptera) in a large reservoir. — *Studies in Natural Sciences* **1**, 42 p. Eastern New Mexico Univ.
- HUGHES, R. N., 1969: Appraisal of the iodate-sulphuric acid wet-oxidation procedure for caloric content of marine sediments. — *J. Fish. Res. Bd. Canada.* **26**, 1959—1964.
- 1970: An energy budget for a tidal flat population of the bivalve *Scrobicularia plana* (DA COSTA). — *J. Anim. Ecol.* **39**, 357—381.
- HUNT, B. P., 1953: The life history and economic importance of a burrowing mayfly, *Hexagenia limbata*, in southern Michigan lakes. — *Bull. Inst. Fish. Res., Mich. Dept. Conserv.* **4**, 151 p.
- IVLEV, V. S., 1945: The biological productivity of waters. — *Usp. Sovrem. Biol.* **19**, 98—120 (transl. by W. E. RICKER, 1966, *J. Fish. Res. Bd. Canada* **23**, 1727—1759).
- KAJAK, Z., 1971: Benthos of standing water. — In: W. T. EDMONDSON & G. C. WINBERG (ed.), *A manual on methods for the assessment of secondary productivity in fresh waters. IBP Handbook* **17**, 25—65. Blackwell Scientific Publications, Oxford. 358 p.
- KARZINKIN, G. S. & TARKOVSKAYA, O. I., 1964: Determination of caloric value of small samples. — In: E. N. PAVLOVSKII (ed.), *Techniques for the investigation of fish physiology*, 122—124. Israel Program Sci. Transl. Oldbourne Press, London.
- KIMERLE, R. N. & ANDERSON, N. H., 1971: Production and bioenergetic role of the midge *Glyptotendipes barbipes* (STAEGER) in a waste stabilization lagoon. — *Limnol. Oceanogr.* **16**, 646—659.
- LAWTON, J. H., 1970: Feeding and food energy assimilation in larvae of the damselfly, *Pyrrosoma nymphula* (SULZ) (Odonata: Zygoptera). — *J. Anim. Ecol.* **39**, 669—689.
- 1971: Ecological energetics studies on larvae of the damselfly *Pyrrosoma nymphula* (SULZ) (Odonata: Zygoptera). — *J. Anim. Ecol.* **40**, 385—423.
- MANN, K. H., 1969: The dynamics of aquatic ecosystems. — *Advances Ecol. Res.* **6**, 1—81.
- MCNEILL, S. & LAWTON, J. H., 1970: Annual production and respiration in animal populations. — *Nature* **225**, 472—474.
- PHILLIPSON, J., 1964: A miniature bomb calorimeter for small biological samples. — *Oikos* **15**, 130—139.
- RUTTER, R. P. & WISSING, T. E., 1975: Distribution, abundance, and age structure of a population of the burrowing mayfly, *Hexagenia limbata*, in an Ohio pond. — *Ohio J. Sci.* **75**, 7—13.
- STADDON, B. W., 1955: The excretion and storage of ammonia by the aquatic larva *Sialis lutaria* (Neuroptera). — *J. Exp. Biol.* **32**, 84—94.
- STOCKNER, J. G., 1971: Ecological energetics and natural history of *Hedriodiscus truquii* (Diptera) in two thermal spring communities. — *J. Fish. Res. Bd. Canada.* **28**, 73—94.
- SWANSON, G. A., 1967: Factors influencing the distribution and abundance of *Hexagenia* nymphs (Ephemeroptera) in a Missouri River reservoirs. — *Ecology* **48**, 216—225.

- TARAS, M. J., GREENBERG, A. E., HOAK, R. D. & RAND, M. C. (eds.), 1971: *Standard methods for the examination of water and wastewater*. — Amer. Public Health Assoc., Amer. Water Works Assoc., and Water Pollution Control Federation, Washington, D. C. 874 p.
- WALDBAUR, G. P., 1968: The consumption and utilization of food by insects. — *Advances Insect Physiol.* **5**, 229—282.
- WELCH, H. E., 1968: Relationships between assimilation efficiencies and growth efficiencies for aquatic consumers. — *Ecology* **49**, 755—759.

Discussion

MARCHANT: What was the percentage decrease in O₂ concentrations in your bottles over the period of your respiration determinations?

ZIMMERMAN: We have not computed a % decrease but from initial concentrations of 7—7.5 ppm the average decrease was 1—2 ppm during the time intervals.

ERIKSEN: Did you merely place the nymphs in a glass bottle or did you provide some kind of artificial substrata? Burrowing mayflies try to burrow and oxygen consumption from that activity can magnify respiration 5 or 6 times in *H. limbata*. Therefore respiration in your tables may be too high.

ZIMMERMAN: We did not provide any artificial substrate. The respiration experiments were run in the field under conditions of ambient temperature and light in an attempt to minimize hyperactivity.