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Production ecology of burrowing mayflies in a Kansas reservoir

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With 5 figures and 3 tables in the text

Introduction

This study estimates the production of the burrowing mayfly *Hexagenia limbata* in a large Kansas reservoir. The objectives include estimating annual production and comparison of production between years. These estimates are comparable with estimates of other components of the reservoir ecosystem and with other *Hexagenia* populations.

One of the few comparable estimates of *Hexagenia* sp. production in reservoirs was made at Lewis and Clarke Reservoir (HUDSON & SWANSON 1971). Estimates of stream mayfly production have been made by WATERS (1962) and WATERS & CRAWFORD (1973). Production of the whole stream invertebrate community has been estimated by HYNES & COLEMAN (1968) and modified by HAMILTON (1969).

Methods and materials

1) Sampling methods

The *Hexagenia limbata* population was surveyed in Tuttle Creek Reservoir, Manhattan, Kansas, during 1972 and 1973. An intensive sampling program was conducted in McIntire Cove with other surveys in the main reservoir, Carnahan, Mill and Tuttle Coves (Fig. 1).

The McIntire Cove survey design consisted of a major transect running the length of the cove and two minor transects running perpendicular to the first across the cove (Fig. 2). Seven stations were located on the major transect with two on one perpendicular transect and five on the other. All stations were sampled in duplicate. In March 1973 the design was changed to three length and three width sections with triplicate sampling at each of the nine locations (Fig. 2). Stations were sampled monthly from October to May and at two week intervals from June to September.

The main reservoir was surveyed by sampling five strata at two stations per stratum. These two stations were located on opposite sides of the reservoir and each station was sampled in triplicate (Fig. 1). Carnahan, Mill and Tuttle coves were surveyed by triplicate samples collected at a randomly chosen station in each cove.

Standing crop estimates of mayfly nymphs were made for all areas of the reservoir for January to September 1973. McIntire Cove was surveyed from July 1972 to September 1973. Samples of nymphs were collected with an EKMAN dredge, washed through a number thirty (0.60 mm) sieve and hand sorted in white enamel pans. The length weight relationship was determined by weighing no less than ten nymphs in each length class (Fig. 3). This relationship was assumed to be constant during the study.

Egg densities in McIntire Cove were estimated from gravity core samples collected from July to September 1973. The top few centimeters of sediment and water above it were removed and placed in a saturated sucrose solution at the lab (ANDERSON 1959). Eggs were decanted off the mixture when sediments had settled out.

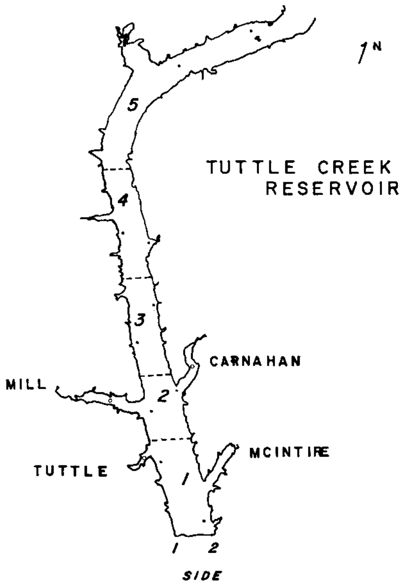

Fig. 1. Map of Tuttle Creek Reservoir, Manhattan, Kansas, indicating the areas sampled during 1972 and 1973. These areas include five strata in the main reservoir, Carnahan, Mill and Tuttle Coves. A map of McIntire Cove is presented in Fig. 2.

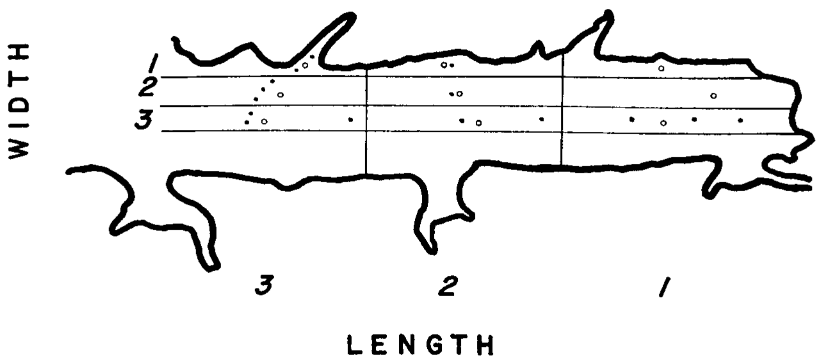

Fig. 2. Map of McIntire Cove sampling design used in 1972 and 1973. The stations along the transect design are indicated by solid circles, while those sampled after March 1973 are represented by open circles.

Emerging sub-adult *Hexagenia* density was surveyed by one meter square emergence traps placed on the reservoir surface. Insect sticky traps, constructed from twelve ounce soft drink cans coated with Stickem Special (Mapco Products), sampled sub-adult activity. Activity and emergent density had a significant positive relationship which allowed calculation of emergent density on days when only activity data was collected.

Mean annual standing crop for nymphs was calculated by a regression of density against time and then calculating mean annual standing crop at the mid-point of the year. A parabolic adjustment was chosen to fit the relationship between density of nymphs and time. This analysis was performed with a one way analysis of covariance where the four years were the main effect. A separate regression was made for each size class due to the different relationship between density and time for the various size classes of nymphs.

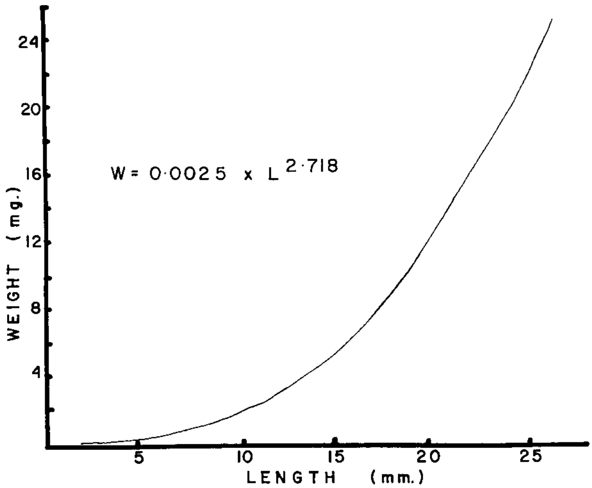

Fig. 3. The length (L) weight (W) relationship for *Hexagenia* nymphs from Tuttle Creek Reservoir derived from a least squares regression which had a R^2 of 0.94.

Standing crop data provided a basis for construction of a life table. All standing crop estimates are expressed in numbers per m^2. Egg development time was assumed to be 22 days from data of HUNT (1953) at comparable lake temperatures. Sub-adult development takes only one day since emergence occurs late in the evening and the molt to adult usually occurs late the following afternoon.

The development time of nymphs was calculated for two millimeter length increments beginning at six millimeters. Growth rate of nymphs was estimated from March to July when no eggs were hatching which would bias the calculation. The resulting growth rate was assumed to be representative of all nymphs. The growth pattern of nymphs appears to be continuous and not really separable into stages. Equally spaced length increments such as in this study are chosen to allow calculation of production estimates but do not represent biological units such as instars.

2) Production models

Production for this study is the amount of tissue per unit area per unit time either added to or lost from the population (CLARKE 1946). This is comparable to net production in plants since respiratory loss is not considered.

$$P = B_{t+1} - B_t \qquad (1)$$

where P is production in mg/m²/time, B_{t+1} is the biomass of the population at time t + 1 and B_t is the biomass of the population at time t.

HYNES & COLEMAN (1968) introduced a general model for secondary production which was corrected and modified by HAMILTON (1969). Assumptions of the model and probable consequences of violation for each assumption are presented by HAMILTON (1969). The model is:

$$p = c \sum_{j=1}^{c} (\bar{n}_{j+1} - \bar{n}_j) \times \frac{(\bar{B}_j + \bar{B}_{j+1})}{2} \qquad (2)$$

where: P is the annual production in mg/m²/year
$\bar{n}_j$ is the mean annual density of nymphs of size j
$\bar{B}_j$ is the mean biomass of nymphs of size j
c is the number of size or life stages in the life cycle.

This model assumes that the organism takes the same time to pass through each size class. If large deviations from this assumption exist, a correction of standing crop must be made. One method is presented by HAMILTON (1969):

$$\bar{n}_j^* = \bar{n}_j \, (P_e/P_a) \tag{3}$$

where $\bar{n}_j^*$ is the adjusted standing crop, P_e is the estimated proportion of the life cycle spent in a stage ($P_e = 1/c$), P_a is the actual proportion of the life cycle spent in a stage, and c is the number of life stages the organism passes through.

Calculation of annual production for McIntire Cove was made using the modified HYNES & COLEMAN (1968) model (2) and the adjustment (3) for standing crop. Production for the entire reservoir was estimated by weighting the McIntire estimate for each segment of the reservoir by the ratio of standing crop in McIntire to the standing crop in that segment. Surface area for each section was then used to obtain a weighted average annual production per square meter for the reservoir.

Comparison of annual production over several years was made from nymphal mean annual standing crop estimates in McIntire Cove. Data was obtained from KLAASSEN & MARZOLF (1971) and MARZOLF (1973) for the years 1969 to 1971. Annual production was then calculated by the modified HYNES & COLEMAN (1968) model for the nymphal portion of the population.

Results

One life cycle or one *Hexagenia* year was defined from the time eggs were laid in July to the time sub-adults emerged the following emergence season.

Mean annual standing crop for *Hexagenia* nymphs in McIntire Cove was 172.05, 126.93, 110.32, and 216.63 mg/m² for the years 1969—70, 1970—71, 1971—72, and 1972—73, respectively (Tabs. 1 and 2). Standing crop for eggs from July to September 1973 averaged 2117.76 per m² which gives an annual mean of 557.22 eggs per m² (Tab. 1). The average density of emerging sub-adults during the 1973 emergence season was 0.78 per m² which averaged over the whole year gives a density of 0.13 per m² (Tab. 1).

The relationship between standing crop expressed both as mg/m² and numbers per m² and time is presented in Fig. 4. During fall months both biomass and the numbers of nymphs increased due to hatching of eggs and individual growth. In the period from January to emergence in July numbers decreased but biomass increased. This period was used to calculate individual nymphal growth rate by regressing mean individual weight against time measured in days.

A *Hexagenia* life table for the year 1972—73 was constructed from standing crop estimates (Tab. 1). Standing crop was adjusted for development time at each life stage and production was then calculated by the modified HYNES & COLEMAN model. Annual production for McIntire Cove was estimated as 1118.34 mg/m² and mean annual standing crop was 216.63 mg/m². Annual turnover ratio or annual production divided by mean annual standing crop was 5.38.

Extrapolation from McIntire Cove production estimates to a production estimate for the entire reservoir is presented in Tab. 3. In this calculation the proportion of the total 64.03 km² of reservoir surface and ratio of nymphal density to that of McIntire Cove are used for each section and the sections then added. During the year 1972—73 a total of 28,647 kg was produced by

Tab. 1. Production for McIntire Cove 1972—73 using the modified Hynes-Coleman model for calculating annual production from standing crop estimates.

Life stage	Annual mean standing crop (n) no/m²	Cohort time/stage days	Proportion of time in each stage (P_a)	Adjustment factor (P_e/P_a)	Adjusted standing crop (*) no/m²	Number lost at stage no/m²	Average weight at loss mg	Cohort production mg/m²	Annual production mg/m²
Egg	557.22	22	0.0601	2.0799	1,158.95				
Nymph						1,037.37	0.0017	1.76	14.11
<6	124.89	47	0.1284	0.9735	121.58				
						78.75	0.3268	25.74	205.88
7—9	58.05	62	0.1694	0.7379	42.83				
						25.18	0.7592	19.12	152.93
10—12	22.76	59	0.1612	0.7754	17.65				
						10.46	1.7639	18.45	147.60
13—15	8.65	55	0.1503	0.8317	7.19				
						3.35	4.0980	13.73	109.83
16—18	5.20	62	0.1694	0.7379	3.84				
						1.36	9.5211	12.95	103.59
>18	3.14	58	0.1585	0.7886	2.48				
						0.41	15.7889	6.47	51.79
Sub-adult	0.13	1	0.0027	15.6250	2.07				
						2.07	22.9000	47.40	379.22
Total	782.04				1,356.59				1,164.96

Annual production adjusted for 4% of nymphs with a two year life cycle 1,118.34 mg/m².
Annual turnover ratio 5.38, mean annual standing crop 216.63 mg/m².
Annual nymphal production 719.84 mg/m², standing crop 167.26 mg/m².

Tab. 2. Calculation of annual nymphal production in McIntire Cove for the years 1969 to 1972.

Nymph size (mm)	Annual mean standing crop (no/m²)	Adjusted standing crop (no/m²)	Adjusted standing crop (mg/m²)	Number lost at stage (no)	Cohort production (mg/m²)	Annual production (mg/m²)
Year 1969—1970						
6	113.40	110.39	23.41			
				51.40	16.80	134.38
7—9	79.94	58.99	31.97			
				34.46	26.16	209.30
10—12	31.64	24.53	30.88			
				14.05	24.78	198.26
13—15	12.61	10.48	30.65			
				6.74	27.62	220.96
16—18	5.06	3.74	25.42			
				2.15	20.47	163.76
18	2.01	1.59	29.71			
			172.05			926.67
Year 1970—1971						
6	73.25	71.31	16.63			
				38.39	12.55	100.37
7—9	44.61	32.92	17.84			
				18.98	14.41	115.28
10—12	17.98	13.94	17.55			
				7.40	13.05	104.42
13—15	7.86	6.54	19.13			
				4.30	17.62	140.97
16—18	3.03	2.24	15.22			
				0.07	0.67	5.33
18	2.75	2.17	40.55			
			126.93			466.37
Year 1971—1972						
6	30.52	29.71	6.93			
				10.09	3.30	26.40
7—9	26.59	19.62	10.63			
				8.31	6.31	50.47
10—12	14.58	11.31	14.24			
				2.95	5.20	41.63
13—15	10.06	8.36	24.45			
				5.39	22.09	176.71
16—18	4.03	2.97	20.18			
				1.16	11.04	88.36
18	2.30	1.81	33.89			
			110.32			383.54

the mayfly population, or 447.40 mg/m². Mean annual standing crop over the whole reservoir was 47.39 nymphs per m², or about 3×10^9 nymphs in the reservoir.

Comparing the density of nymphs in McIntire Cove from 1969 to 1973 reveals a decreasing standing crop and production from 1969 to 1972 followed

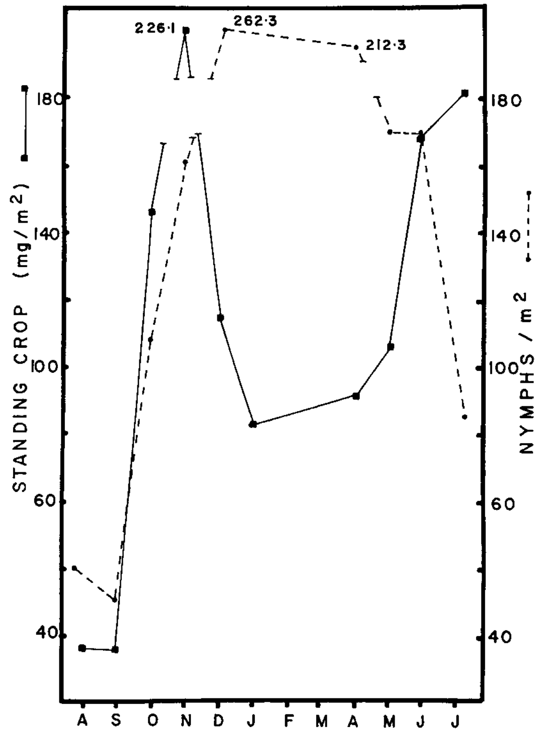

Fig. 4. Standing crop of *Hexagenia* nymphs from McIntire Cove expressed in numbers and milligrams per square meter.

Tab. 3. Calculation of annual production for Tuttle Creek Reservoir using McIntire Cove production data and standing crop of each section.

Section of lake	% of Total area	Area (km²)	Standing crop of nymphs (no/m²)	Ratio of standing crop to McIntire	Annual prod. per unit area (mg/m²)	Total production (kg)
McIntire	1.842	1.180	118.52	1.000	1,118.36	1,319.66
Carnahan	1.601	1.026	118.51	1.000	1,118.36	1,147.44
Mill	0.747	0.479	51.85	0.437	488.72	234.10
Tuttle	2.950	1.890	14.81	0.125	139.79	264.21
Stratum						
I	25.213	16.152	16.67	0.141	157.69	2,546.98
II	9.738	6.239	74.07	0.625	698,97	4,360.90
III	12.176	7.800	68.44	0.577	645.29	5,033.28
IV	17.229	11.038	116.67	0.984	1,100.46	12,146.92
V	28.512	18.266	9.24	0.078	87.23	1,593.38
Total	100.000	64.030				28,646.87

Mean annual production 447.40 mg/m².

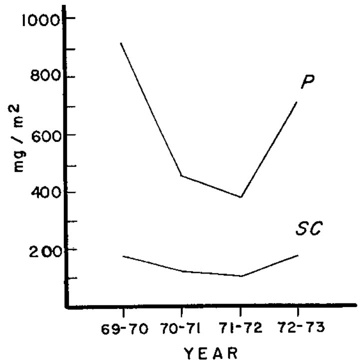

Fig. 5. Annual *Hexagenia* nymph production (P) and mean annual nymphal standing crop (SC) for the years 1969 to 1973 from data collected in McIntire Cove.

by an increase in both in 1972—73 (Fig. 5). Production was more varied than standing crop reaching a maximum of 926.67 and a minimum of 384.54 mg/m², while standing crop only varied from 172.05 to 110.32 mg/m². Annual nymphal turnover ratios were 5.38 and 4.30 in 1969—70 and 1972—73; but turnover ratios were 3.67 and 3.48 in 1970—71 and 1971—72 (Tab. 2). A comparison of *Hexagenia* production between years should include all life stages or make assumptions about the densities of the unsampled stages. This study assumes that relative nymphal production and standing crop are indicative of production and standing crop of the entire population.

Discussion

Annual production (1972—73) of *Hexagenia* has been estimated as 447.40 mg/m² for the whole reservoir. Hudson & Swanson (1972) estimated *Hexagenia* production in Lewis and Clarke Reservoir between 1,498 and 2,407 mg/m². These higher production values result from a higher standing crop in Lewis and Clarke Reservoir.

It is difficult to determine why Lewis and Clarke populations are more dense than those of Tuttle Creek Reservoir unless it reflects the length of time populations have been established. Data from Lewis and Clarke 1962 to 1969 suggests the population was established in 1962 at a density of 14 nymphs per m² (Hudson & Swanson 1972). The *Hexagenia* population in Tuttle Creek Reservoir has been more recently established. Thomas (1970) surveyed Tuttle Creek Reservoir from 1965 to 1968 and found no *Hexagenia* nymphs while Schwartz (1970) found 7.7 nymphs per m² comprising 32 per cent of the benthos in a 1968 survey.

The population in Lewis and Clarke Reservoir has an annual turnover ratio of 2.7 compared to 5.38 for Tuttle Creek Reservoir. This is reflective of high percentages of the Lewis and Clarke population with a two year life cycle. In Tuttle Creek Reservoir less than 4 per cent of the population required two years to develop in the year 1972—73. Annual turnover ratios in Tuttle Creek Reservoir are comparable with those determined for the stream mayfly *Ephemerella subvaria* which also takes one year to complete its life cycle (Waters & Crawford 1973).

Mayfly production as indexed by nymphal production in McIntire Cove declined from 1969 to 1972 and then increased in 1972—73. The years of low production also had low turnover ratios. Low turnover ratios indicate a large percentage of the population is completing the life cycle in two years, while high turnover ratios indicate a large percentage of the population is completing the life cycle in one year. In 1972—73 when the turnover ratio for the nymphal portion of the population was 4.30 only 4 per cent of the nymphs were overwintering for the second year.

Hudson & Swanson (1972) calculated a turnover ratio of 2.7 for *Hexagenia* nymphs with a high percentage completing the life cycle in two years. Waters &

Crawford (1973) calculated a turnover ratio of 5.8 to 6.3 for the stream mayfly *Ephemerella subvaria* which has an annual life cycle. The *Hexagenia* population in Tuttle Creek Reservoir appears to have a life cycle that is longer than one year, but shorter than two years. This results in a variation in the annual turnover ratio from year to year because the insects can only emerge during the summer. They must individually have either a one or two year life cycle, while the population has an average life cycle between one and two years.

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Discussion

Williams: Is it possible that your low standing crop estimates are due to the sampler (Ekman dredge) not collecting all of the fauna — due to their deep burrowing behaviour?

Horst: No. The sediments over much of the reservoir are thin, i.e. they've only been deposited over one decade and can often be sampled in their entirety with an Ekman dredge. Such samples include the total benthic fauna since the underlying substrate is undisturbed and not likely penetrable.

Macan: To what size of error are such calculations subject? How do numbers caught range from sample to sample?

Horst: The variance around sample means is quite small. Tuttle Creek Reservoir is an inundated flood plain with an extraordinarily flat basin. The deposition of lacustrine sediments has resulted in an homogeneous benthic environment. This may help to account for the low variance.

HUDSON: Did you not add egg production into your estimate twice (adult females and deposited eggs)? One of these estimates belongs to another generation.

HORST: The method we used could be corrected for egg production by adjustment of the adult life stage. The magnitude of this bias is probably minor when viewed in relationship to the precision of the estimate.

RESH: Have you tried following cohorts and using either ALLEN's or instantaneous growth techniques?

HORST: The characteristics of *Hexagenia* make the identification of cohorts difficult if not impossible. The variance in production estimates using the HYNES-COLEMAN and ALLEN curves is probably largely a function of the ability to define cohorts. It is therefore not appropriate to use the ALLEN method for this *Hexagenia* population.