POPULATION DYNAMICS OF THE BURROWING MAYFLY *HEXAGENIA LIMBATA*[1]

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Abstract. Population regulation of burrowing mayflies was investigated by modeling the population dynamics of *Hexagenia limbata* at Tuttle Creek Reservoir, Kansas, USA. Census data were obtained for the egg, nymph, and adult life stages to construct the basic statistics for life tables.

Estimates were derived for survivorship of nymphs during 4 yr and for egg and adult survivorship in four areas in 1 yr. Fecundity was estimated from a random sample of adult ♀♀. Density dependence between segments of the life history was tested by key factor analysis and also by discrete time simulation.

Population growth rate, calculated using the exponential model, had a negative linear relationship with population density, suggesting regulation at some life stage within the cycle. Population growth rates calculated for Leslie matrices with different nymphal survivorships but constant egg and adult survivorship also had a negative linear relationship with population density. Therefore, it is concluded that the population is regulated in the aquatic environment in the nymphal portion of the life cycle.

Key words: Ephemoptera; Hexagenia limbata; *Kansas*; *mayflies*; *modeling*; *population dynamics*; *population regulation*; *reservoirs.*

Introduction

The life history of the burrowing mayfly *Hexagenia limbata* was described by Hunt (1953) and Fremling (1960). Several more quantitative studies estimated population density of nymphs (Swanson 1967, Cowell and Hudson 1968, Klaassen and Marzolf 1971). Life tables were constructed by Hudson and Swanson (1972) for calculating secondary production of mayflies.

Little effort, however, has been made to utilize models for population growth and regulation to study *Hexagenia* populations. The life table approach presented by Birch (1948) and the matrix approach described by Leslie (1945) are based on the theory of exponential growth. Until recently the life table method has been more popular with ecologists, perhaps due to lack of familiarity with matrix algebra (Emlen 1973).

The objectives of this paper are to present models which describe the life history of *Hexagenia limbata* at Tuttle Creek Reservoir, Kansas, and to use the models to analyze the dynamics and regulation of the population.

Population Dynamics Models

Fretwell (1972) developed a model which utilizes stages in the life cycle to partition the population density through time. The objective of the model is to observe equilibrium population densities in terms of numbers of individuals.

It is assumed that each of n life stages in the life cycle follows from the previous one in a density dependent manner

$$N_i = N_{i-1}[f_{i-1}(N_{i-1})] \tag{1}$$

where N_i is the density of the ith life stage in numbers of individuals and f_i is a monotonic function in N; and assume that if $i = 1$, $i - 1 = n$. Thus, if $N_i/N_{i-1} > 1$, the transition is reproduction; otherwise, the transition is stable or a decline in density.

When the population is in equilibrium the finite growth rate (R) is equal to 1 and the density of stage i in the next generation (N'_i) will equal the density of stage i in the present generation (N_i)

$$N'_i = R N_i \tag{2}$$

then,

$$N'_1 = N_n f_n(N_n) = N_{n-1} f_{n-1}(N_{n-1}) f_n(N_n) \ldots$$
$$= N_1 \prod_{i=1}^{n} f_i(N_i). \tag{3}$$

Several values of N_i will satisfy the equilibrium situation, some of which will be unstable, in the sense that slightly higher or lower values of N_i will grow away from the equilibrium. Fretwell (1972) argues that an organism with density dependence in several life stages can have more than one stable equilibrium population density. This model can only be used after estimates or assumptions about all the $f_i(N_i)$, which are related to the survivorship and fecundity, have been made.

The life table and the matrix approach both utilize
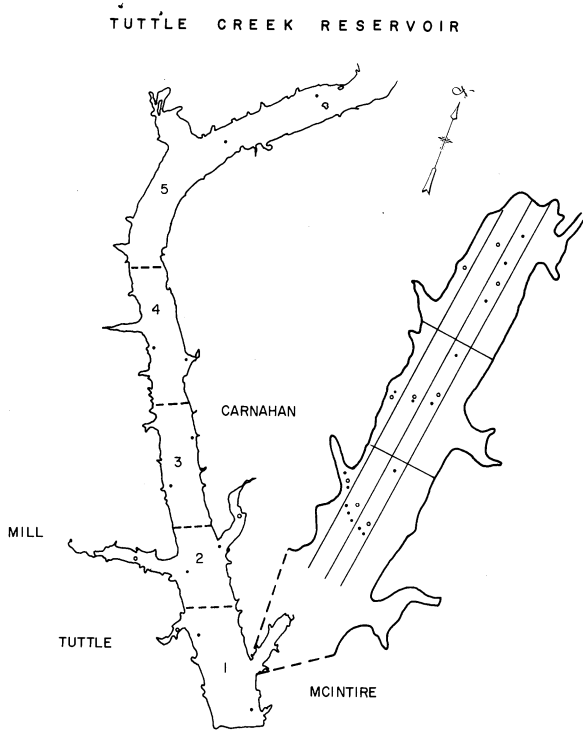
TUTTLE   CREEK   RESERVOIR

FIG. 1. Map of Tuttle Creek Reservoir, Kans. depicting sampling locations in Carnahan, Tuttle, and Mill coves, including an enlargement of the more intensely sampled McIntire Cove. The McIntire Cove stations sampled before March 1973 are represented by closed circles; those sampled after March 1973 by open circles.

the same survivorship and fecundity parameters. These models further assume these parameters are constant over the projected time. The matrix model is

$$N_{t+1} = A N_t \qquad (4)$$

$$
\begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ \cdot \\ \cdot \\ N_n \end{bmatrix}_{t+1}
=
\begin{bmatrix}
M_1 & M_2 & \ldots & M_{n-1} & M_n \\
S_1 & 0 & \ldots & 0 & 0 \\
0 & S_2 & \ldots & 0 & 0 \\
\cdot & \cdot & \ldots & \cdot & \cdot \\
\cdot & \cdot & \ldots & \cdot & \cdot \\
0 & 0 & \ldots & S_{n-1} & 0
\end{bmatrix}
\begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ \cdot \\ \cdot \\ N_n \end{bmatrix}_{t}
\qquad (5)
$$

where S_i is the probability of survivorship of an individual from the $i-1$ stage to the ith stage and M_i is the fecundity of females at stage i. This is an expansion of Eq. (2) and the value of R can be obtained from Eq. (5) as the maximum characteristic root of the A matrix (Leslie 1945). The instantaneous population growth rate (r) is the natural logarithm of the finite population growth rate (Emlen 1973).

METHODS AND MATERIALS

The *H. limbata* population was surveyed in Tuttle Creek Reservoir, Kansas in 1972 and 1973. A may-

fly year was defined from egg laying in mid-July to emergence in August of the following year. An intensive sampling was made of the McIntire Cove population at 2-wk intervals from May to October and once per month for the rest of the year. Carnahan, Mill, and Tuttle coves were sampled once per month during the summer of 1973 (Fig. 1). Adults were sampled nightly at all locations using both emergence and sticky traps during the emergence season. Nymphal densities for McIntire Cove from 1969 to 1972 were obtained from data of Klaassen and Marzolf (1971) and G. R. Marzolf (*personal communication*).

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. The 16 stations in this design were sampled in duplicate. In March 1973 the design was changed to three length and three width sections with triplicate sampling in each of the nine locations. Carnahan, Mill, and Tuttle coves were surveyed by triplicate samples collected at a randomly chosen fixed station in each cove (Fig. 1).

Eggs were collected using a gravity corer. The top few centimeters of sediment and water above it were mixed in a saturated sucrose solution and the eggs were decanted after the sediment had settled.

Nymphs were collected from Ekman dredge samples which were washed through a no. 30 sieve. The samples were then hand sorted in white enamel pans. Nymphs were grouped by size since individual instars could not be determined.

Emerging subimago density was surveyed by 1-m² emergence traps placed on the surface of the reservoir. Adult activity was surveyed by sticky traps (containers of $\approx$ ⅓ liter capacity coated with adhesive) placed in trees at the edge of the reservoir. Six sticky traps were placed around McIntire Cove and one was placed in each of the other coves. A linear relationship existed between adult activity and emerging density which was used to determine emerging density when emergence trap data were missing.

Mean annual standing crop of nymphs was determined for 1969–1973 by regressing nymphal density against the time of sampling in a one-way analysis of covariance in which the 4 yr were the main effect. A separate analysis was performed for each size-class of nymph since the density peak passed consecutively from smaller to larger nymphs. All regressions were parabolic; since the density of each size nymph generally increased for a time after the eggs were laid, reached a maximum, and then declined to a minimum.

Egg and adult mean standing crops for the year

TABLE 1. *Hexagenia* life tables for 1969–1974. Parameters are annual mean number $(\overline{N})/m^2$, SE, adjusted mean number $(\overline{N}^*)/m^2$, survivorship (S), fecundity (F), and development time (DT) in days

| Year | Parameter | Egg | Nymph (mm) | | | | | | Adult |
			<6	7–9	10–12	13–15	16–18	>18	
	DT	22	47	62	59	55	62	58	1
1969	$\overline{N}$		113.40	79.94	31.64	12.61	5.06	2.01	
	SE		30.04	15.31	6.83	2.90	2.17	2.05	
	$\overline{N}^*$		110.39	58.99	24.53	10.48	3.74	1.59	
	S		0.534	0.416	0.427	0.357	0.425		
1970	$\overline{N}$		73.25	44.61	17.98	7.86	3.03	2.75	
	SE		23.42	11.91	5.32	2.26	1.69	1.59	
	$\overline{N}^*$		71.31	32.92	13.94	6.54	2.24	2.17	
	S		0.462	0.423	0.469	0.343	0.969		
1971	$\overline{N}$		30.52	26.59	14.58	10.06	4.03	2.30	
	SE		25.24	12.88	5.74	2.44	1.82	1.72	
	$\overline{N}^*$		29.71	19.62	11.31	8.36	2.97	1.81	
	S		0.660	0.576	0.739	0.355	0.609		
1972	$\overline{N}$	557.22	124.89	58.05	22.76	8.56	5.20	3.14	0.13
	SE	79.12	17.00	8.67	3.86	1.64	1.23	1.16	0.05
	$\overline{N}^*$	1,158.95	121.58	42.83	17.65	7.19	3.84	2.47	2.07
	S	0.105	0.352	0.412	0.407	0.534	0.646	0.835	
	F								2,204.7

1972–73 were determined by averaging standing crop of these life stages over the entire year. These life stages are only present for a portion of the year and must be averaged over the whole year for comparative purposes.

An adjusted mean annual standing crop was then determined for each life stage by correcting means for the year by the development time of each stage. This is necessary since the Leslie model assumes each age or stage has the same development time. Hamilton (1969) presented the following correction for development time which was used

$$\overline{N}_i^* = \overline{N}_i(P_e/P_a) \qquad (6)$$

where $\overline{N}_i^*$ is the adjusted mean annual standing crop, $\overline{N}_i$ is the mean annual standing crop, P_e is the expected proportion of the life cycle spent at stage i ($P_e = 1/n$) under the assumption of equal development time for each life stage, P_a is the observed proportion of the life cycle spent in stage i, and n is the number of life stages.

The survivorship values (S_i) for the life tables are calculated from the adjusted standing crop of each stage. Fecundity (M_i) is estimated in the summers of 1972 and 1973. Egg capsules were weighed from about 10 females each summer. Several samples of eggs from egg capsules were removed, counted, and then weighed. The weight per egg was then

calculated and the total number of eggs per female was determined. These basic life table statistics are also the basis for the matrix model of population growth.

The value of the instantaneous rate of increase (r) of the population is estimated as the natural logarithm of the largest eigenvalue of the A matrix. The eigenvector associated with the largest eigenvalue corresponds to the stable age distribution that would develop if the population were to grow at a rate of r (Leslie 1945). The eigenvalues and vectors were extracted from the matrices by EISPACK routines (Reinsch and Wilkinson 1971).

Density dependence between life stages was tested by the Varley and Gradwell key factor analysis and the proof of density dependence test (Luck 1971, Ito 1972). Density dependence is tested for by regressing the log density of the $(i + 1)$ stage against the log density of the i stage. The independent and dependent variables are reversed and the regression run again. Density dependence between the two life stages exists if both regression lines plotted on the same scale on the same graph lie on the same side of unity ($b = 1$) and the slopes of both lines are significantly different from one.

This technique was used for nymphal sizes in the 4-yr data. Density dependence was investigated between egg and nymph, and adult to egg from data collected at McIntire, Carnahan, Mill, and Tuttle

TABLE 2. Mean annual standing crop (no./m²) ± SE of the $\bar{x}$ for eggs, nymphs, and adults collected in McIntire, Carnahan, Mill, and Tuttle coves during summer of 1973

Cove	$\bar{x} \pm$ SE		
	Eggs	Nymph	Adults
McIntire	2,177.98 ± 164.57	95.76 ± 32.08	2.07 ± 0.83
Carnahan	3,528.96 ± 162.92	95.76 ± 31.44	3.35 ± 0.92
Mill	929.06 ± 76.29	11.96 ± 3.41	0.88 ± 0.19
Tuttle	1,011.13 ± 23.11	41.90 ± 11.92	0.96 ± 0.36

coves in 1973. The relationship between potential eggs and observed egg density was also investigated.

The relationship between population growth rate and population density was determined by regressing the instantaneous growth rates against initial density. The carrying capacity was defined at the population density where growth was zero. One regression was conducted for the growth rate obtained from the eigenvalue analysis of the Leslie matrices and another for the growth rate determined by subtracting the log density between years.

A simulation of the population was conducted using the discrete time model in Eq. (1). The survivorship functions for the various sizes of nymphs were determined by regressing survivorship against nymphal density 1969–1973. Survivorship functions for the transition between egg and nymph, and adult to egg were determined by similar regression for the data collected at the four coves in 1973. The simulation program is in FORTRAN IV for an IBM™ system 360/50 digital computer, and available in Horst (1974).

RESULTS

Life tables were constructed from survey data in McIntire Cove and are presented in Table 1. Data for 1969–1972 are nymphal stage only, while 1972–1973 data include all life stages. Development times were assumed to be constant during the 4 yr and were taken from Horst (1974). The standing crop for nymphs was 209.72, 129.12, 73.78, and 195.56 nymphs/m² for 1969–70, 1970–71, 1971–72, and 1972–73, respectively. McIntire and Carnahan coves had higher standing crops for all life stages in 1973 than did Mill and Tuttle coves (Table 2).

Key factor analysis did not detect density dependence at any position in the life cycle. This may be a statistical problem since with only four data points and the observed variability, too severe a regulation would be necessary for statistical significance to be biologically plausible. A larger sample size is needed before the results of the key factor "proof of density dependence" may be accepted as indicating no density dependence.
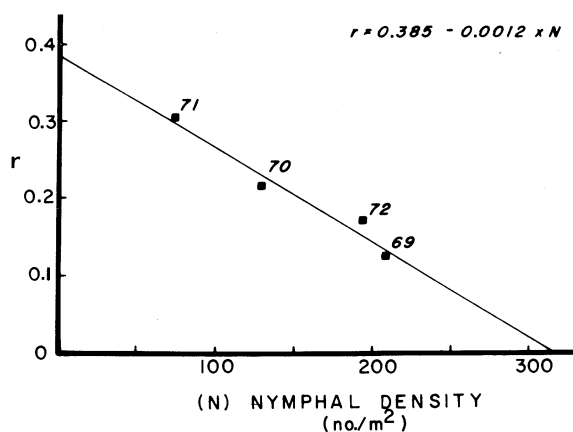

FIG. 2. Relationship between population growth rate (r) obtained from eigenvalue analysis of the Leslie matrix and the mean nymphal standing crop 1969–1972. The two variables had a correlation –0.98 and residual SD 0.012.

Eigenvalues and vectors were extracted from the four A matrices. The estimates for fecundity, egg survivorship, and survivorship of largest nymph to adult, which were only available for 1972 to 1973, were used in all four matrices. Therefore, the only difference in the A matrices was the probabilities of survivorship for the nymphal portion of the life cycle. The instantaneous growth rates or the logarithm of the largest eigenvalues were 0.12, 0.22, 0.30, and 0.17 for 1969–70, 1970–71, 1971–72, and 1972–73, respectively.

The relationship between population growth rate and mean annual standing crop of nymphs was analyzed by regression for the 4-yr data (Fig. 2). This relationship had a correlation of –0.98 which was significant at $p \leqslant 0.05$, and from the regression equation a carrying capacity of 320 nymphs/m² was extrapolated. A similar regression of the observed population growth rate between years had a cor-

TABLE 3. The survivorship (S_i) of each *Hexagenia* life stage as a function of the density of each stage (N_i), the correlation coefficient and the residual SD of the least squares regression ($S_{y \cdot \bar{x}}$)

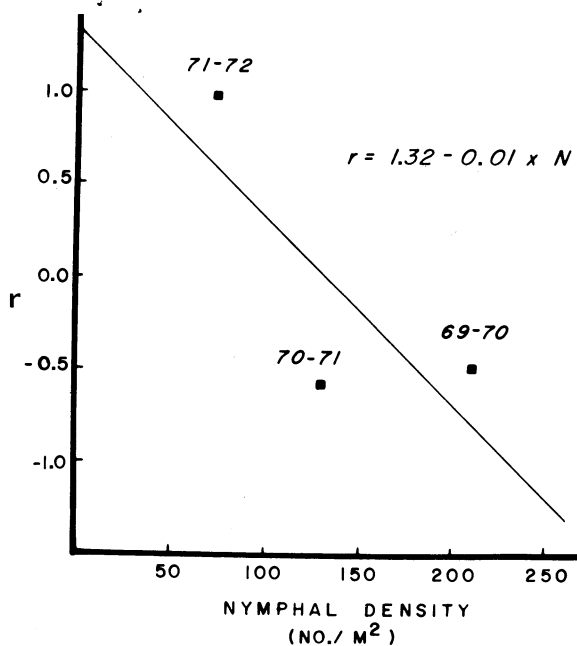| Stage	Survivorship function	Correlation (r)	$S_{y \cdot \bar{x}}$
Egg	$S_1 = 0.127 - 0.0000\ (N_1)$	0.530	0.077
Nymph (mm)			
<6	$S_2 = 0.710 - 0.0025\ (N_2)$	0.796	0.068
7–9	$S_3 = 0.600 - 0.0037\ (N_3)$	0.800	0.043
10–12	$S_4 = 0.820 - 0.0190\ (N_4)$	0.703	0.095
13–15	$S_5 = 0.530 - 0.0160\ (N_5)$	0.309	0.075
16–18	$S_6 = 1.460 - 0.0250\ (N_6)$	0.830	0.109
>18	$S_7 = 0.840$		
Subadult	$S_8 = 0.308 - 0.0000\ (N_8)$	0.515	0.122

$$r = 1.32 - 0.01 \times N$$

FIG. 3. Relationship between population growth rate (r), calculated as the difference in log densities between years, against the population density 1969–1972. The two variables had a correlation −0.78 and residual SD 0.44.

relation of −0.78 which was significant at $p \leqslant 0.50$ (Fig. 3).

Results of the survivorship against density regressions for all stages are presented in Table 3. The transition from egg to smallest nymph and from adult to egg were the only survivorships which had slopes of zero indicating that survivorship in these stages was independent of density.

The discrete time simulation utilized the functions of survivorship and density and the fecundity in Table 1 to parameterize the model presented in Eq. (5). Standing crop densities for 1969 were used as initial values for the population vector. This simulation revealed a population which initially oscillated, then converged to an equilibrium with a nymphal population of 310 nymphs/m².

DISCUSSION

The analysis of density dependence using key factor analysis does not detect density dependence in the rate of survival between any of the life stages. However, the range in population density for which data points are available and the number of data points would require quite severe density dependence before it is statistically verified.

The relationship between population growth rate, determined by eigenvalue analysis of the Leslie matrices and population density suggests that density

dependence does exist at some point within the life cycle (Fig. 2), which the key factor analysis is too weak to detect. These estimates represent long-range projected growth rates under the assumption of exponential growth.

Actual population growth rates between successive years also have a negative slope when regressed against population density (Fig. 3). Since these estimates utilize only total population density rather than specific life stage properties as the eigenvalue analysis, there is a lower correlation and a greater residual variance for the relationship. Nymphal carrying capacity should be estimated from the eigenvalue regression as it levels oscillations in the growth rate. Data for year-to-year growth rates may represent only portions of an oscillation, and therefore, produce erroneous estimates of the carrying capacity.

The density dependence observed in Fig. 2 must be due to regulation in the aquatic nymphal stage since survivorship from egg to nymph and fecundity were constant for all four matrices. The mechanism of this regulation is not presently known, but may be associated with factors such as food supply, suitable burrowing habitat or predation. Density dependence seen in Fig. 3 is consistent with that observed in Fig. 2, but could occur in any of the life stages, since it is based on the log difference between population density in successive years. Population growth of the simulated population is comparable with field estimates with negative growth between 1970–71, but positive growth from 1971 to 1972.

If the simulated population can be considered representative of the actual population, then the population appears to be regulated by density dependence only in the nymphal stage. This conclusion is also suggested in the eigenvalue analysis, since a negative linear relationship was seen between population growth rate and density. Nymphal carrying capacity extrapolated from Fig. 2 was 320 nymphs/m² while the simulated population is regulated at a density of around 310 nymphs/m².

Deductions from the theory of complex life cycles (Istock 1967) would predict more regulatory events in the aquatic stages and fewer in the terrestrial stages through evolutionary time. In the evolution of modern mayfly species the length of the terrestrial stages has been diminished to reduce regulatory events in that environment. Presently the adult is only alive for 1 or 2 days and does not feed because the mouth parts are vestigial (Needham et al. 1935). It appears this strategy has increased regulation in the aquatic nymphal stage and now the aquatic environmental carrying capacity sets the upper limit on population density.

In this study the relationships between aquatic

and terrestrial life stages are considered on a yearly basis. The dynamics of these transitions occur in much shorter time intervals and should, therefore, be considered on a daily basis. Such intensive studies may reveal additional sources and the mechanism of population regulation in the *Hexagenia* population.

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