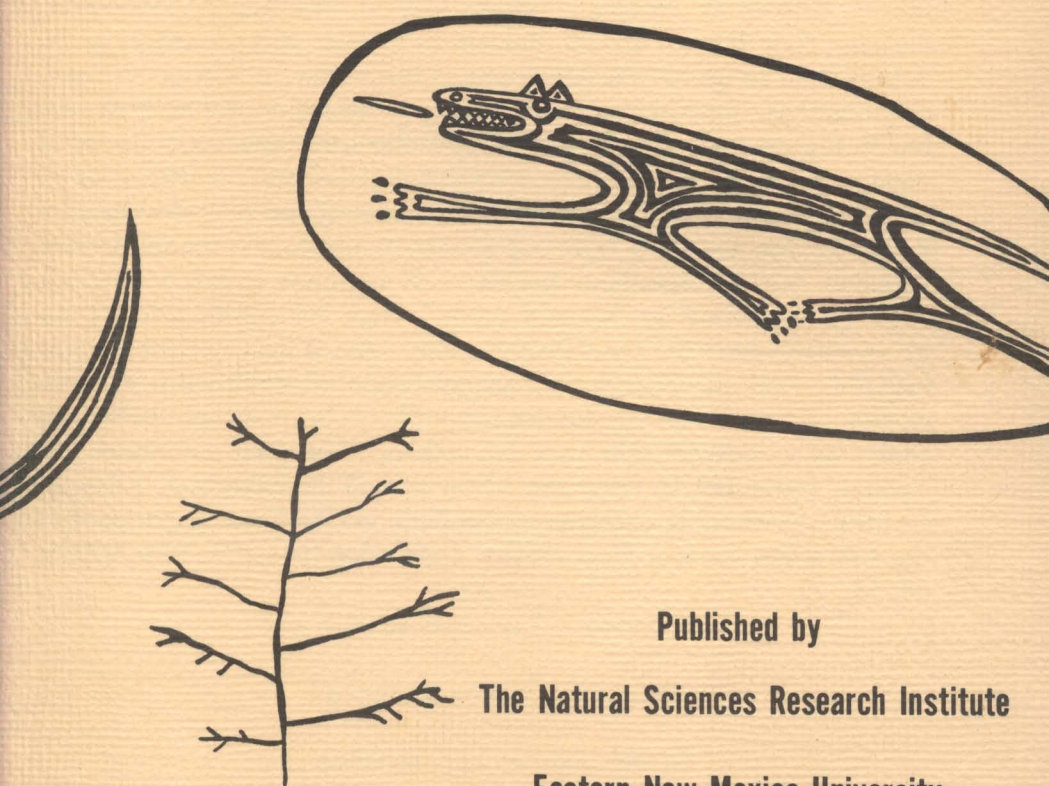


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**Production and Standing Crop
of *Hexagenia* (Ephemeroptera)
in a Large Reservoir**

by

Patrick L. Hudson and George A. Swanson

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ABSTRACT

Population dynamics of the mayflies, *Hexagenia limbata* (Serville) and *Hexagenia bilineata* (Say), were studied in Lewis and Clark Lake from 1962 to 1969. Nymphs that hatched in June and July emerged as adults in 13-14 months (titled 1-year cycle) and nymphs hatched in late August or September emerged in 22 months (titled 2-year cycle). Although an estimated 79% of the newborn nymphs begin life in the 2-year cycle group, only 53% of the emergent adults were in this group because of mortality. Standing crop was highest in the shore area, although a major migration away from the shore occurred in the spring. This migration was most intense when the population density exceeded $100/\text{m}^2$. Biomass ranged from 260 to $1070 \text{ mg}/\text{m}^2$ dry weight over the study period. Instantaneous emergence rates were higher than predatory mortality rates but were only operative from about 1 July to 15 September.

Production was estimated by two methods from extensive sampling in 1964 on a 1256 hectare section of the reservoir. The growth method yielded $1.50 \text{ gm}/\text{m}^2$ dry weight and the Hamilton method, $1.67 \text{ gm}/\text{m}^2$. The turnover ratio of 2.81 calculated from these data multiplied by the standing crop over the rest of the reservoir resulted in an average annual production of 15.6 kg/hectare for the reservoir.

The Hamilton method was applied to less extensive collections from 1964 to 1969. Maximum production occurred in 1966 at $2.41 \text{ gm}/\text{m}^2$.

Production and Standing Crop

of *Hexagenia* (Ephemeroptera)

in a Large Reservoir

by

Patrick L. Hudson and George A. Swanson¹

INTRODUCTION

Estimates of benthos production are not common because of problems associated with collecting the necessary statistics. Chapman (1967) suggested that estimation of invertebrate production should be attempted in environments where diversity is minimal. Lewis and Clark Lake, on the Missouri River, with its relatively constant depth and uniform bottom type fits this criterion. *Hexagenia limbata* (Serville) and *Hexagenia bilineata* (Say), large burrowing mayflies, account for 90% of the benthic biomass and are a significant food item for a number of fish species. The general life histories of *Hexagenia* in Lewis and Clark Lake are known (Swanson 1967).

In this paper the Allen (1949) and Ricker (1946) growth method of estimating production was applied to extensive collections of *Hexagenia* made in 1964. A production method proposed by Hynes and Coleman (1968) and modified by Hamilton (1969) was applied to the 1964 data and from 1965 to 1969 when less extensive collections were made. Also, population trends of *Hexagenia* in Lewis and Clark Lake were followed from 1962 to 1969.

1. North Central Reservoir Investigations, Bureau of Sport Fisheries and Wildlife, Yankton, South Dakota 57078.
Present address of Swanson: Northern Prairie Wildlife Research Center, Jamestown, North Dakota 58401.

Reservoir Description

Lewis and Clark Lake (Fig. 1), formed by the closure of Gavins Point Dam in 1955, is located on the boundary between South Dakota and Nebraska. It has a surface area of 113 km², a length of 34 km, an average width of 3.4 km, and an average depth of 4.9 m. Water exchange rate during the years studied varied from 4-10 days in the summer months to about 1 month in the winter.

The reservoir substrate consists of an inundated floodplain bordered by steep shale and chalk bluffs. Depth is relatively constant from the center of the reservoir to the shore margin, except in the old river channel. Bottom types are composed primarily of recently deposited silt and fine sand. The reservoir does not stratify thermally, and oxygen depletion occurs only in isolated areas of the old river channel after extended periods of calm weather.

Chironomids and *Hexagenia* comprised 98% of the weight and 87% by number of the benthic macroinvertebrate population in 1962 (Swanson 1967). Chironomids were mainly of the subfamily Tanypodinae with the genera *Procladius*, *Coelotanypus*, and *Ablabesmyia* dominant. The fingernail clam, *Musculium*, and oligochaetes were also present.

METHODS

Experimental Design

We used a systematic transect-station method and a stratified random method to sample benthos. Identical transects were used over the entire lake during 1962 and 1963 and in the central and western sections of the reservoir in 1964 (Fig. 1). Each transect was divided into stations selected to include old river channel, inundated floodplain, and shore areas. Six stations per transect were taken in 1962 and 1963 and eight in 1964.

A stratified random method was used to sample a 1256 hectare section in the eastern end of Lewis and Clark Lake from 1964 to 1969. This section was divided into four strata: shore-in (0-152 m), shore-out (152-305 m), floodplain, and channel. The area within each stratum was subdivided in squares of sufficient size (2.3 hectare for shore and channel strata and 9.3 hectare for floodplain) to be located by landmarks and depth. Squares to be sampled within each stratum were then selected, with replacement, from a table of random numbers. The percentages of total area of each stratum was shore-in and out, both 6.3; floodplain, 67.8; and channel, 19.6.

We sampled the stratified sampling area monthly from May to October in 1964, during May, July, and October in 1965 and 1966, and during May and October in 1967, 1968, and 1969. The number of samples taken within each stratum was based initially on sampling variation. A Stein's two-stage test (Steel and Torrie 1960) determined the sample size needed to estimate a mean by a confidence interval of ± 2 individuals at 90% confidence level. Results from several years indicated that variation within floodplain, channel, and shore-out strata was such that 15 samples from each would obtain the precision sought. However, the shore-in stratum had such variation that the desired sample size was physically impossible to achieve. Precision should have been based on some percent of the mean because the confidence interval achieved over 16 sampling dates averaged 28% of the mean for the shore-in, shore-out, and floodplain. The confidence interval from the channel averaged 48% of the mean. In 1968, the sampling procedure was standardized to 15 samples within each stratum for practical reasons.

A Miller plankton sampler (Miller 1961) with 0.16 mm mesh net was used to sample *Hexagenia* in the open water. Two oblique tows were taken every 3 hours over one 24-hour period each month, March through September in 1968. Sampling was limited to April in 1969 and 1970.

During May of 1965 and 1966 *Hexagenia* nymphs were collected and placed in a partially submerged rearing cage (3.7 m x 0.6 m x 0.3 m). The bottom of the cage was covered with silt and the submerged portion was covered with 0.158 mm nylon screen. The cage

was checked daily during the period of emergence and subimagos were removed. At the completion of emergence the rearing cage was removed and the remaining nymphs were counted.

Sampling and Laboratory Procedures

Samples were collected with a no. 1 orange-peel dredge in which 531 cm² (Hudson 1970) was used to convert to number per square meter. Samples were sieved through a 0.516 mm screen, preserved in 10% formalin, and bottom organisms were separated from mud and detritus in a sugar solution. *Hexagenia* nymphs were measured from the tip of the mandibles to the base of the cerci. Wet and dry weights were determined for 100 individuals per 1 mm groups ranging from 2-33 mm. Dry weights are used in this paper unless otherwise noted. These were converted to wet weight by the regression: wet weight (mg) = 6.9 dry weight (mg) + 0.1.

Essential data required for growth rate calculations were population density by dry weight and numbers and mean nymphal weight for each generation. Weight estimates for each stratum were obtained by converting monthly length-frequency plots to weight by the length-weight relationship: $\log W$ (dry weight in mg) = $-2.62416 + 2.79952 \log L$ (length in mm) with $N = 32$ and $r = 0.99$. Average weights and numbers from each stratum were then weighted by their area contribution to obtain equal representation for each stratum in each monthly mean. Mean nymphal weights for each cohort¹ were obtained by combining collections of nymphs from all strata in a given month, separating the length-frequency distributions into cohorts, and calculating an average for each cohort.

Young-of-the-year, yearling, and 2-year old nymphs were separated by length-frequency distributions. October 1965 and May 1966 show typical distributions (Fig. 2) in which the three age

1. We use the term cohort to mean a group of individuals all hatched over the entire summer.

segments can be distinguished. The distribution in the area of overlap was estimated by calculating an expected normal distribution (Dixon and Massey 1957) on the young-of-the-year and yearling distributions in October and the yearling and 2-year olds in May. They were chosen because their distributions approached a normal one. Those individuals remaining in the area of overlap were assigned to the young-of-the-year, yearling, or 2-year old group.

Production Rate

Terminology and concepts involved in using the Ricker (1946) and Allen (1949) growth model of estimating production can be found in Chapman (1967, 1968). The formula used was $P = G\bar{B}$ where P = production rate in g/m^2 day, G = instantaneous growth rate in g/g day, and \bar{B} = mean population density in g/m^2 . Instantaneous growth rate for approximately 1-month periods was calculated as the natural logarithm of the ratio of the average weight (\bar{w}) at the end of the period to that at the beginning of the period. This figure was divided by the number of days in the period to obtain G for one day. \bar{B} was the arithmetic mean of the population biomass at the beginning and end of the period.

In the Hamilton (1969) modification of the Hynes and Coleman (1968) method of estimating production, size frequency distributions obtained from sets of samples throughout the year are combined. The resulting frequency distribution was regarded as a first estimate of an "average cohort." The number of "average cohorts" was equal to the number of size classes through which the organisms grow. If growth, in terms of the size units used, is assumed to be linear, numerical differences in adjacent size classes can be attributed to mortality. Hamilton (1969) noted that if numerical differences are equated to biomass figures, multiplied by the number of length classes the species grows through, and then summed, this method of estimating production is an algebraic form of the graphical method outlined by Allen (1951).

RESULTS

Life History of *Hexagenia*

Hexagenia limbata is found throughout Lewis and Clark Lake and *H. bilineata* is found mainly in the upper half of the reservoir. Detailed accounts of the biology of *H. limbata* can be found in Hunt (1953) and of *H. bilineata* in Fremling (1960). Most of this paper pertains to *H. limbata* in the lower half of the reservoir and the life history material concerns this species.

The life history of *Hexagenia* in Lewis and Clark Lake is as follows: (1) Nymphs emerge from mid-June to the first part of October. Although nymphs emerge daily, there were five to ten periods in 1965 and 1966 when emergence was higher than adjacent dates. Fecundity was not determined in this study but Hunt (1953) found females in Michigan to carry 2,300 to 7,700 eggs, with an average of 4,000. (2) Eggs hatch within 10-21 days depending upon temperature and oxygen conditions. Upon hatching, individuals are 400 μ long. (3) Growth occurs from May to October when temperatures are above 14° C. Fremling (1967) in laboratory experiments found growth became negligible below 14° C and Hunt (1953) in field studies estimated 10° C as a cutoff point. Many of the nymphs reach the last instar (males, 22-26 mm; females, 25-33) in 13-14 months, emerging during the late summer. About 25% of the population in mid-October is over a year old (average size, 21 mm) and will overwinter and emerge in June and July as 2-year old nymphs.

The rearing cage study determined the proportion of adults completing a 1 or 2-year cycle. Similar numbers of nymphs were placed in a rearing cage in the spring of 1965 and 1966 and the percentage of surviving nymphs which had emerged by the end of the season was 46% in 1965 and 75% in 1966. The spring population consists of nymphs entering their third summer (2-year old) and those entering their second summer (yearling). Excluding natural mortality all 2-year old nymphs emerge, but only a portion of the yearlings reach

adequate size to emerge. The percentage of 1 or 2-year cycle nymphs in 1965 and 1966 was determined by subtracting the percentages of 2-year olds in May (18% in 1965, 28% in 1966, from Table 1) from the total emergent percentages in the rearing cages. The percentages were:

	1-year cycle	2-year cycle
1965	28	72
1966	47	53

The 2-year cycle is clearly dominant. An even higher percent of the nymphs are 2-year olds because they undergo an extra year of mortality.

Approximate growth patterns for *Hexagenia* with 1 and 2-year life cycles are shown in Fig. 3. The progeny of individuals emerging in June and July grow enough to emerge the following year in August and September, thus completing a 13-14 month life cycle. The progeny of nymphs taking 13-14 months obtain little fall growth because of the late emergence of their parents. Because these nymphs do not grow sufficiently the following summer, they require 22 months to complete development and emerge in June and July of their third summer. The 2-year cycle dominates because: (1) a short growing season will result in a 2-year cycle; and (2) although a long growing season with an extended emergence benefits a 1-year cycle, the offspring of this group will initiate a 2-year cycle.

Egg development is retarded at low temperature or by a combination of low temperature and anaerobic conditions (Flattum 1963; Fremling 1967). Consequently, eggs deposited in September probably overwinter as eggs. We fertilized eggs on 27 August in the laboratory, held them for 5 days to check viability, and then placed them in the reservoir on 1 September. On 15 November, at a water temperature of 8° C, the eggs were removed from the reservoir and taken to the laboratory where they were held at room temperature. The eggs began hatching the next day. We have obtained a 90% + hatch after holding eggs at 3° C for 160 days and then warming. Additional evidence for the survival of overwintering eggs was the presence of 2 mm nymphs as late as June (prior to any emergence).

Distribution and Density

The seasonal density and biomass of *Hexagenia* for the stratified area from 20 May 1964 to 21 May 1965 showed that production exceeded mortality from May to June when numbers decreased and biomass increased (Fig. 4). Emergence between the June and July estimate resulted in a decrease in both numbers and weight. Recruitment of young nymphs in August increased numbers but emergence of large individuals still kept biomass estimates on a downward trend. Emergence was minimal in September and recruitment of young nymphs and growth of the entire population increased standing crop values. The increase between October 1964 and May 1965 was not entirely due to production. Although temperatures during the period were at a level that some growth could take place, most of the increase was due to immigration into the stratified area which will be discussed later. The mean annual population biomass determined by measuring the area under the curve with a planimeter in Fig. 4 and dividing by the abscissal scale was 679 mg/m^2 .

Data from transects taken over the entire lake from May to October 1964 were in good agreement with the population trends in Fig. 4. The arithmetic mean weighted by area for the six transects and the stratified area from May to October was 579 mg/m^2 . The mean of the stratified area during approximately the same time interval was 484 mg/m^2 . Thus, the discussion of annual trends in the stratified area probably reflects the entire lake.

Population densities in the eastern stratified area from 1962 to 1969 in number and weight per square meter are given in Fig. 5. Although collections from 1962 and 1963 were not taken in the same manner as those in the following years, their location and timing allowed us to follow the buildup of *Hexagenia*. The increase in *Hexagenia* from $55/\text{m}^2$ in 1962 to $182/\text{m}^2$ in 1964 resulted from unusually warm and long growing seasons and an expanding population colonizing a benthic community without other large herbivorous species. Accumulated day degrees (10°C base level) from 1962 to 1964 were the highest values recorded from 1962 to 1969 (Table 2). As a result the majority of the nymphs completed a 1-year life cycle as

indicated by the average of only 10% of yearling nymphs in the October estimates from 1962 to 1964 (Table 1). The reproductive potential of these emerging nymphs in a partially occupied habitat resulted in large numbers of young-of-the-year. Even though the higher temperatures resulted in emergence of larger numbers it was more than compensated by recruitment of young nymphs and their increased growth.

Both number and weight decreased sharply from May to October 1965 (Fig. 5). Poor recruitment must have occurred as only 71% of the October 1965 sample was young-of-the-year as compared with 86 to 96% from 1962 to 1964 (Table 1). The ratio of young-of-the-year to yearlings and yearlings to 2-year olds established in the fall of 1965 and the spring of 1966 remained fairly constant into 1968 at an average ratio of 75:25 (Table 1). The ratio shifted in the fall of 1968 to 64:36 as a result of reduced reproductive success and reduced emergence because of cool September temperatures. Reproduction was extremely successful in 1969 and the ratio reverted back to 90:10, similar to that of the population expansion years of 1962 through 1964. These young nymphs increased number values, but their small size contributed little to biomass which was low in October (Fig. 5).

The average May biomass from the stratified area from 1963 to 1969 was 728 mg/m^2 . The average October estimate from 1964 to 1969 was 543 mg/m^2 . The average numerical densities for the May and October estimates were 134 and $114/\text{m}^2$. The maximum estimated biomass in the stratified area was $1,069 \text{ mg/m}^2$ in May 1966. The highest biomass within the four areas was $2,724 \text{ mg/m}^2$ in the shore-in during October 1965 and the lowest was 70 mg/m^2 in the channel during September 1964. The highest numerical standing crop was $1,195/\text{m}^2$ in October 1969 in the shore-in area and the lowest was $19/\text{m}^2$ in May 1963 in the floodplain.

Population estimates in October indicate the reproductive success during the past summer. Estimates the following May (minus winter mortality) should duplicate the October estimate. On the average only 7% of the day degrees when *Hexagenia* may grow occurred from October to May. There was a significant increase between the

October 1965 and the May 1966 estimate, when no reproduction occurred, and in the following two similar periods. This increase was probably due to the fact that nymphs less than 3 mm are not efficiently captured by the sieve used and to the movement of *Hexagenia* nymphs into the sampling area. Small nymphs of eggs which are not collected in October may attain enough growth by May to be captured by our gear. This is illustrated in Fig. 2 for 1965-66. Mean size of the October young-of-the-year segment increased about 1 mm during the winter; thus the 2 mm group and portions of the 3 and 4 mm groups in May were recruited to our gear. This contribution probably amounted to less than 10%.

Movement

Every year the shore-in densities in the stratified area decreased from October to May. Conversely, densities in the shore-out, floodplain, and channel increased over the winter, except for the channel and shore-out between October 1964 and May 1965. This was apparently the result of a migration of *Hexagenia* nymphs from the densely populated shore area to the center of the reservoir (Swanson 1967). This movement occurs throughout the open water period, but around 90% is believed to take place within 8 weeks after the late March and early April ice breakup.

The number of nymphs moving out of the shore-in was insufficient to explain the large increases in shore-out, floodplain, and channel. Movement from upstream (Transects E and F, Fig. 1) was probably a major source of immigrants. Although wind-produced currents may temporarily cause water masses to move in directions other than toward the outlet, the dominant current direction was towards the outlet in this reservoir with its rapid flushing rate. As a result migrating nymphs must have shifted downstream in the reservoir. Some idea of this downstream movement can be shown by the biomass captured in the discharge in the spring and early summers of 1965 and 1966 when an estimated 24 and 14 metric tons (wet weight) of nymphs

were discharged through the turbines (Cowell and Hudson 1968). This must have been replaced by nymphs from the area immediately upstream which had twice the density of *Hexagenia* as the stratified area in 1964 (Swanson 1967). Thus, the May population estimate, which was normally made after the major migration, probably included a large influx of nymphs. These nymphs, in addition to the newly recruited small nymphs, could easily make up the difference between the October and May estimates from 1964 to 1967 (Fig. 5). The October estimate was less influenced by migration and is probably the best measure of the annual production in the reservoir.

From 1965 to 1967 population density exceeded $100/\text{m}^2$ in the stratified area, and the differences between the October and May estimates were attributed to migration and redistribution. The number of nymphs discharged through the powerhouse, indicating the intensity of the migration, appeared to be very high in the spring of 1965 and 1966. Extensive towing with a Miller net in the area of the turbine intakes in 1968 and 1969 failed to yield values of this magnitude. The highest standing crop ever recorded was in the shore-in area during October 1969; this produced migrations in April of 1970 which were at least five times higher than in 1968 and comparable to those measured in 1965-66.

Mortality

Mortality rates for young-of-the-year nymphs were impossible to estimate because of continual recruitment. A seasonal total mortality rate (includes emergence) was computed for the yearling portion of the population between May and October of each year. Mortality ranged from 68 to 76% and averaged 73% from 1964 to 1967. Annual rates were closely related to the September temperature which determined how many nymphs emerged in September. Although this percentage may remain relatively constant from year to year the

ratio between those lost due to emergence and those lost due to fish predation could vary greatly. Increased predation probably would be selective on large individuals due to emerge.

The May to October yearling mortality rate in 1968 was only 59%. This resulted in a biomass increase over the summer for the first time since 1964. Numbers decreased over the summer due to low recruitment. Part of the reduced mortality rate may be attributed to a reduced emergence in September because of low temperatures, but reduced predation pressure may be responsible.

Instantaneous rates of total mortality were calculated for the yearling group for two periods in 1964 when emergence was not a factor and recruitment was adjusted. The expression used for calculating the instantaneous rate of mortality was: $N_t = N_0 e^{-it}$ where N_t equals the number of animals surviving to time t ; N_0 equals the number of animals present at the beginning of the time interval; t equals the length of the time interval in days; i equals the instantaneous rate of mortality for the time period; and e equals base of natural logarithms. The instantaneous rates from 20 May to 18 June and 8 September to 21 October were 0.0069 and 0.0081, respectively. Mortality rates were also calculated from rearing cage data in 1965 and 1966, which excluded fish predation and emergence. The instantaneous rate in the rearing cage from 8 June to 22 September 1965 at an initial density of 1,043/m² was 0.0035. The rate was 0.0031 from 21 June to 10 October 1966 at a density of 762/m². If we assume that predator and natural mortalities calculated for the yearlings in spring and fall of 1964 do not change much in July and August, and are representative of the entire population; we can estimate predator mortalities by subtracting the natural rate from the rearing cage rate. The estimate of 0.0042 for predator mortality is significant. A higher predator mortality value was probable because natural mortality may have been high due to handling and enclosing nymphs. Although instantaneous emergence rates in the enclosure were higher than both predator and natural mortalities, 0.0063 over 68 days in 1965 and 0.0093 over 86 days in 1966, the time periods for emergence was much smaller than the time periods for other mortality rates.

The above assumption can be tested by comparing the independent estimates from the field and enclosure to the seasonal total

mortality rate. The May-June estimate of 0.0069 was applied to the first half of the May-October period of 76 days and was weighted according to that figure. Similarly, the September-October figure of 0.0081 was applied to the last 79 days. The instantaneous rate of emergence of 0.0093 over 86 days for 1966 was used because it most closely approximates the 1964 temperature regimen in September which has the greatest influence on the total emergence figure. These three figures gave a weighted instantaneous rate of 0.0081. The seasonal total mortality rate for 1964 of 75% expressed as an instantaneous rate over the 155 days from May to October was 0.0088. The similarity of the two figures indicates that the extension of May-June and September-October rates into July and August is justifiable.

A crude estimate of age specific mortality was obtained by analyzing the age structure from the six sets of samples (May to October) taken in 1964 which was considered a random sample of the population. Only the shore data (in and out combined) were used because this is where most egg deposition occurs. Length frequencies were lumped into 5 mm groups and the loss at each stage was divided by the initial population to obtain a percent mortality. The mortality rate from 5-10 mm was 50%, and from 10-20 mm it averaged 32%; the mortality rate then increased to 54, 73, and 100% over the last three 5 mm groups. The rates of the smaller sizes include both predatory and natural mortality whereas rates of the larger size groups are mainly due to emergence.

Growth

Calculating growth rates requires an age structure in which groups can be separated and handled individually. In May of 1964 the majority of the population was yearlings (Table 1). Rather than separate the population into yearlings and 2-year old nymphs the entire population was taken as a cohort (Fig. 6). The difference in numbers between the May and June estimate, other than that attributable to

mortality and growth, was recruitment of small nymphs. Both the major mode and mean increased approximately 5 mm between May and June (Fig. 6), yet there were still 2-4 mm individuals present in June. The use of these recruits would underestimate the growth rate. Therefore, a segment of the June curve approximating a normal curve with a mean of 4.4 mm was removed and considered newly recruited yearling nymphs not measured in May.

The average weight of an individual from May and from the modified June estimate was used to calculate an instantaneous rate of growth (G) which was 0.0168 mg/mg day between 20 May-18 June. Because of emergence during June, July, August, and September it was not possible to obtain an estimate of G during these months. The G value of 0.0168 was used during the above periods (Table 3).

The absence of emergence from 8 September 1964 to 21 May of 1965 made it possible to estimate the instantaneous rate of growth for the yearlings (Table 3). The rate from 8 September to 22 October was 0.0130 and that from 22 October to 21 May was 0.008. Only 20% of the days between 22 October and 21 May were at a temperature level conducive to growth, but growth was expressed as a daily rate.

Transect data from 1964 taken in May and June also provided an estimate of rate of growth for the yearlings and 2-year old nymphs. Because the transects were sampled over 2-week intervals an initial and final date was obtained by weighting each date as to the number of nymphs collected on that date. An average weight of an individual (\bar{w}) was calculated for each transect, but because it was calculated from as few as two individuals to as high as 125, each estimate was also weighted to obtain a mean \bar{w} for each date. The mean weight was 3.94 on 7 May, and 7.14 on 15 June, resulting in a " G " value of 0.0152 mg/mg day. The mean weight in the stratified area from 20 May to 18 June increased from 4.68 mg to 7.10 mg giving a " G " value of 0.0168 mg/mg day. The two estimates are very close considering the early dates for the transect data and that recruitment of small nymphs were not taken into account, which would have increased the transect value. Not only does it verify the instantaneous rate of increase in weight value used, but it means that a turnover ratio

calculated from data in the stratified area could be applied to the entire lake.

The rate of growth of the young-of-the-year nymphs recruited from August through October was calculated because they could be separated from the older cohorts (Fig. 6). However, growth was underestimated as a result of recruitment. We used maximum size in the cohort to reduce this error. We assumed that the minimum (lowest point) between the young-of-the-year and the yearling groups was the maximum size for the young-of-the-year group (Fig. 6). This was probably not the maximum size, but it should indicate the relative growth between the sampling periods. The growth rates calculated in this manner differed little from those calculated by using mean size, but they were considered the best estimate. The rate was 0.0763 from 18 August to 8 September and decreased to 0.0244 from 8 September to 22 October, when temperatures decreased.

Production

Growth method

Mean population density (mg/m^2) for each period from 20 May 1964 to 21 May 1965 was taken as the arithmetic mean of the population density of the beginning and end of the period (Table 3). However, population density could not be calculated from the length-frequency data used to calculate growth rates because it was not weighted by area. The percentage that the young-of-the-year, yearling, and 2-year olds each made up in the growth data was applied to the weighted estimate for the whole stratified area to obtain \bar{B} for each cohort. Rate of growth in mg/mg day times the mean population density in mg/m^2 equaled the production rate in mg/m^2 day ($P = G\bar{B}$). Production rates from 20 May 1964 to 21 May 1965 are given in the last column in Table 3 as the production P times the number of days in the period. The production estimate was 1,143.8 and 354.7 mg/m^2 for the yearling 2-year old and young-of-the-year, respectively. This results in an annual production of 1,498 mg/m^2 in the stratified area.

Hamilton modification

Sampling in the stratified area from 1965 to 1969 was not frequent enough to estimate production by the growth method but was deemed suitable for applying Hamilton's (1969) modification of the Hynes and Coleman method (1968). This method of calculation was demonstrated for the shore-in and shore-out data for 1964-1965 which was combined into 5 mm length groups for ease of calculation (Table 4). Estimates with 1 mm groups gave similar values. Similar calculations were done for the floodplain and channel; each production estimate was weighted; the result was $2,817 \text{ mg/m}^2$. Hamilton (1969) has shown that the production estimate using a species which requires more than a year for development is overestimated by a factor approximately equal to the number of years in the animals life cycle. Therefore, this figure must then be divided by the number of years in the life cycle.

The estimation of the average length of a life cycle was done by setting up a life table (Table 5) and assuming the emergence pattern of 1966 when 53% and 47% of the emerging adults were 2 and 1-year old, respectively. Thus, for every 100, 2-year olds emerging in June, 89, 1-year olds will emerge in August. Recruitment and emergence time were assumed as in Fig. 3. A mortality rate of 20% per month, as found during the spring and fall of 1964, was applied from March to October. Winter mortality was unknown, but a figure of 2% was used from November to February. Borutsky (1939) indicated little natural mortality of the dominant invertebrates in Lake Beloie over the winter and our fish feeding studies indicated reduction in predation during the winter months. Using those mortality rates, approximately 13% of the nymphs (undergoing a 22-month cycle) in both October and May will be yearlings and 2-year olds, respectively. Actual values were variable in the buildup years from 1962 through 1964 but averaged 13% (Table 1). The above mortality and emergence rates indicated that 78.6% of all nymphs were 2-year types. The average length of the life cycle for all nymphs as calculated in Table 5 was 20.3 months or 1.69 years. The scheme is over simplified but gives an approximation of the average life cycle.

The estimated production of $2,817 \text{ mg/m}^2$ divided by 1.69 equals $1,667 \text{ mg/m}^2$ which is reasonably close to the $1,498 \text{ mg/m}^2$

estimated by the growth method. It is higher because some nymphs do not grow to the assumed maximum length used in the length frequency. This assumption, if violated, leads to an overestimate (Hamilton 1969). Male nymphs emerged at about 22 mm whereas females began to emerge around 25 mm. Less than half the population reached the 26 to 33 mm maximum lengths.

To compare the 1964-65 data with following years, the May-July-October-May and May-October-May for 1964-65 were used to estimate production by the Hamilton modification of the Hynes-Coleman method. Because the months used were periods of high standing crop with similar distributions and did not include months of low standing crop, the production estimates were high (Table 6). But they make possible relative comparisons of production from 1964-68. Because two May estimates were used in each computation, the production values followed the May standing crop (Fig. 5).

An estimate of rate of increase in weight was obtained in 1965 in the stratified area to provide a check on the Hynes-Coleman method. The G value from 20 May to 18 June was 0.0259 as compared with 0.0168 in a like period of 1964. From 3 September to 1 October 1965, a G value of 0.0414 and 0.0268 were obtained for the young-of-the-year and yearling groups, respectively. There was an increase of production from 1,804 mg/m² in 1964-65 to 2,314 in 1965-66, as estimated by the Hamilton method (Table 6).

Turnover ratios

The turnover ratio is the ratio of annual production to mean annual standing crop. The mean annual population density obtained planimetrically in 1964 was high due to a significant increase in weight over the winter. This probably resulted from immigration into the stratified area in April and May rather than production. One would assume that the population should have decreased through natural mortality or maintained the same level. Even though the May estimate was used for calculating both production (growth method) and annual population density, it affected the population density much more than the production estimate because growth during the winter was

negligible. The mean annual population density was obtained by taking the mean of the May to October estimate and substituting the October value for the following 6 months. The calculated mean annual standing crop was 573 mg/m^2 and the turnover ratio was 2.61.

Similar problems were involved in calculating mean annual density by the Hamilton method. The most realistic estimate was derived from the standing crop values actually used in calculating the production estimate (Column 5, Table 4). The annual standing crop for the seven sampling dates from May 1964 to May 1965 was 593 mg/m^2 . The production estimate of 1,667 divided by this figure resulted in a turnover ratio of 2.81 (Table 6). This agreed closely with that obtained by the growth method.

The turnover ratio was then applied to the standing crop data from transects to estimate the total production in the lake for 1964. Table 7 contains the mean standing crop from five sets of samples from May to October for transects A through F (Fig. 1) and six sets of samples for the stratified area during the same time span. The product of the mean standing crop in kg/hectare times the area represented by the transect was multiplied by the turnover ratio of 2.7 and summed to obtain a production of 176.6 metric tons of dry weight of *Hexagenia* nymphs ($P = TR \cdot \bar{B}$). The mean standing crop for the lake obtained by weighting the transects by area was 5.79 kg/hectare and the annual production was 15.6 kg/hectare.

Waters (1969) calculated an instantaneous growth rate (G) for the entire life cycle of a number of freshwater invertebrates by taking the ratio of the weight of the mature nymph to that of the smallest individual found. This should approximate the turnover ratio for a single life cycle. In applying his method to present data there is the question of whether to consider the maximum size (46.3 mg) of *Hexagenia* or the average size of the last instar (19.5 mg). By using the maximum, G is 7.7 and by using the average, G is 6.9. The annual TR (2.7), determined empirically from direct estimates of production, must be multiplied by the years in the life cycle (1.69) to give a life cycle turnover ratio of 4.6. Waters (1969) also found his life-cycle instantaneous growth rates to be somewhat higher.

DISCUSSION

Growth and Production

Temperatures, density, or possibly an unused food source must have been prime factors resulting in the population increase through 1964-65. Temperatures were the highest on record. Population density could increase without undue competition and the reproductive potential would be increased with increasing population. The possibility exists that the unoccupied sediments contained a food source which the *Hexagenia* nymphs were able to utilize over and above that which falls out of the water column.

Hunt (1953) described nymphs of *Hexagenia* to be mud eaters in that their intestinal tracts have the appearance of long, mud filled tubes. Both Neave (1932) and Hunt found diatoms and other algae, fragments of entomostraca, and large quantities of mud in their intestines. Many chironomids are filter feeders and feed mainly at the mud-water interface (Kajak and Warda 1968). They found that non-predatory chironomids selected algae. The intestinal tract of these chironomids had some detritus and very little mineral matter. Allochthonous material deposited in the reservoir after 5 to 6 years of impoundment and not utilized by chironomids could be effectively used by *Hexagenia*, resulting in the large population in 1964-65.

In 1965 and 1966, production rates increased while population density decreased. The relationship between population density and production rate is a function of the growth rate which is influenced mainly by temperature, food, and population density. Although temperatures decreased sharply in 1966 and probably slowed the growth rate, there was an increased food supply. Phytoplankton populations increased twofold from 1964 to 1967 (North Central Reservoir Investigation, unpublished data).² Similarly, discharge rates increased 21% over the period resulting in more planktonic food coming into Lewis and Clark Lake. Jonasson and Kristiansen (1967) found that the chief factors controlling growth in *Chironomus*

2. Bureau of Sport Fisheries and Wildlife, Yankton, South Dakota 57078.

anthracinus were oxygen and food. The oxygen supply in Lewis and Clark is rarely deficient. Finally, the high population density generated in 1964-65 would at least maintain production even with a slightly reduced growth rate.

An apparent relationship between the discharge (flushing rate) and *Hexagenia* food was evident in 1969. The increase in the young-of-the-year in 1969 could have been the result of suitable weather during emergence resulting in better adult survival and conditions for egg laying. The significance of weather over a 2-1/2 month emergence period is questionable, and temperature appears not to be a factor. Discharge rates from July through October when this cohort was developing were 40% higher than in 1968. This may have brought in more allochthonous food per unit time and the population responded by a significant increase.

A description by Warren and Davis (1967) of the dynamics of yearling sculpins in a laboratory stream fits the population dynamics of *Hexagenia* in Lewis and Clark Lake. They found that production, being a function of both growth rate and biomass, increased with increasing biomass to a point at which the decline in food resources and increased utilization of food for maintaining the sculpins (*Hexagenia*) reduced the growth rate sufficiently for production to decline. This point appears to have been reached in 1967 for *Hexagenia* in Lewis and Clark Lake and subsequently modified in 1969 by increased discharge rates.

Migration, Predation, and Mortality

High densities in 1964-65 resulted in a migration phenomenon similar to the drift hypothesis of Waters (1966). Population density may have reached or exceeded the carrying capacity of the reservoir bottom, and competition and stress resulted in increased migration as a means of removal and population control. This migration was extensive in 1964, 1965, 1966, and 1970 when densities were

above $100/\text{m}^2$ in the stratified area and resulted in the high May populations through 1967 even though densities were decreasing. Each spring the population must have shifted downstream bringing in recruits from the middle of the reservoir. Even though densities in that section of the reservoir were declining, they were at such a high level they continued to maintain the stratified area until densities were reduced in the middle section and migration declined.

Predation by fish at *Hexagenia* levels above $100/\text{m}^2$ was probably very efficient and resulted in their increased growth and abundance which in turn caused a steady decline in *Hexagenia* numbers through 1968. Availability may have been enhanced during those years with a large migration. Swedberg (1968) concluded that increased growth and abundance of freshwater drum (*Aplodinotus grunniens*) in Lewis and Clark Lake was possibly caused by the 1962-66 increase in *Hexagenia* abundance. Siefert (1969) related improved growth of white crappie (*Pomoxis annularis*) with the increased population of *Hexagenia*. White bass (*Roccus chrysops*), which became an important fish species in Lewis and Clark Lake in 1963, also feed on *Hexagenia* and their growth and abundance increased through 1966 (Ruelle 1971). Food habit studies of fish in the tailwater of Lewis and Clark Lake indicated that *Hexagenia* was the major food item for seven of nine species collected during the peak spring migration (Walburg, *et al.* 1971). The May to October decrease of *Hexagenia* from 1965 to 1968 may be the result of fish predation. *Hexagenia* growth rates were maintained or even increased, but mortality rates were higher and the standing crop decreased.

Instantaneous rates of emergence and natural mortality from the enclosure, compared with instantaneous rates of total mortality from the lake, indicated that fish predation was important. It is obvious that emergence and predation may be compensatory in the yearling segment. Larger nymphs are probably selected by fish, thereby reducing the emergence loss. Emergence could not be a factor in the young-of-the-year segment and any increase in predation would cause a decrease in numbers. Because of recruitment no estimates of mortality rates were possible.

Age specific mortality calculated from the average age

structure offered some insight on differential mortality. The increase from 29% at 15-20 mm to 54% at 20-25 mm included some emergence but must reflect increased fish predation on larger individuals. The 50% mortality rate for the 5 to 10 mm group could be due to predation by the predatory chironomids. The 10-20 mm range is too large a prey for the chironomids and relatively small for fish and as a result has only a 32% mortality rate.

Turnover Ratio and G/Z Ratio

The low calculated annual turnover ratio of 2.7 appears to be realistic. Long-lived species usually have a small annual turnover ratio (Waters 1969). Mann (1967) suggested that animals taking 2 years to complete their life histories may have a ratio of about 2, annuals 5, and those completing more than one generation per year, about 10. The theoretical turnover ratio considered as equal to the life cycle instantaneous growth rate of around seven was higher than the calculated 4.6. This is expected according to Waters (1969) because of the long drawn out emergence of *Hexagenia* and the fact that the emergent population was calculated to be 0.1% of the initial.

Neess and Dugdale (1959) were interested in the number of natural populations showing a constant G/Z ratio in which G was the instantaneous growth rate and Z was the instantaneous rate of mortality. Simultaneous estimates of the two values were possible in the yearling segment in May-June and September-October of 1964. Although the ratios were different, 2.42 in May-June and 1.61 in September-October, their mean was near the ratio of two obtained by Dugdale (1955) for *Chironomus plumosus* in Lake Mendota. Chapman (1967) saw no reason for the G/Z to remain constant for more than short periods. However, the average value may be similar for closely related species.

Sources of Error

Chapman (1968) stated that the major inaccuracy in production calculations is the large error associated with population estimation. The error associated with growth is frequently small if sampling is adequate. The fact that the 95% confidence interval around the no./m² was on the average, over the years studied, only 21% of the mean indicates good precision in the estimates. Because a large number of nymphs (200-1,000) were used, growth estimates should also be precise. Also, the weighting of habitat areas such as the shore, floodplain, and channel, and the weighting of entire reservoir from the headwater to the face of the dam contributed to the reliability of the estimate. Two sources of error in collecting *Hexagenia* made the standing crop and production rate estimates minimal. The seive did not collect nymphs below 3 mm in length and the orange-peel did not sample as efficiently as a Ponar dredge (Hudson 1970). The Ponar collected more *Hexagenia* numbers and biomass by a factor of 1.4 than did the orange-peel. Additional testing showed a consistent difference of 1.3, but the differences were significant in only two of four of the independent tests due to sampling variation. Inherent to the argument is that the Ponar is 100% efficient, which it probably is not.

The contribution to the production estimate of *Hexagenia* nymphs 3 mm or less can be estimated. Teal (1957) and Borotsky (1939) estimated mortality rates of 87 to 96% for chironomids from the egg stage to the young larvae stage. If we assume a 95% mortality rate from hatching to 3 mm and increase the 3 to 4 mm rate from 36 to 50%, we would only increase the production estimate by 10%.

The daily instantaneous rate of growth of 0.0168 for the 20 May to 18 June period had to be used for summer months because emergence caused calculated growth rates to be reduced or even negative. Temperatures were much higher in July and August, although Hargrave (1970) found that the growth of *Hyaella* were more affected by epibenthic primary production than temperature. Relating the major modes at 12 and 16 mm in June with 15 to 20 mm modes in July (Fig. 6) results in a G value of 0.0190 which is higher than 0.0168.

There are five assumptions underlying the Hynes-Coleman method which would lead to less accurate estimates (Hamilton 1969). Two were mentioned in the result section and two others are applicable. First, samples should be arranged or weighted so that all seasons of the year are equally represented. Because months of only high standing crop dominated after 1964 (May and October) and the May value was influenced by immigration, the increase in production may only reflect the high standing crop values. Because the data used cover so few months it may not be sensitive enough to show changes in growth or mortality. However, it appears to be a suitable method for the more extensive 1964 collections. Secondly, an assumption is that all individuals should require the same amount of time to grow through each length class. In many insects growth is rapid in the early instars and slows down in later instars. If the growth pattern is known it can be used to give a better estimate of the average cohort (Hamilton 1969). There is no published information on *Hexagenia* growth patterns. Only the data from September to October of 1964 (Fig. 6) lend themselves to this problem. By using the mode to eliminate recruitment, the young-of-the-year mode shifted approximately 4 mm over the period, whereas the mean length of the 1 + year old nymphs increased 3.8 mm. Therefore, no correction was made.

Comparison with Other Bodies of Water

Hexagenia nymphs are found in most large river systems but do not become abundant unless large areas of suitable substrate become available as may develop by impoundment (Swanson 1967). Standing crop of benthos is scant in the unimpounded Missouri River (1.1 kg/hectare) but *Hexagenia* can be found along the mud banks and main channel portion of the river (Morris, *et al.* 1968). Densities as high as 170/m² have been found in an isolated remnant of the former channel above Lewis and Clark Lake. A small population of *Hexagenia* nymphs was probably present in 1955 to colonize the newly created

reservoir when conditions became suitable. The colonization of *Hexagenia* nymphs must await the covering of the original bottom of field soil and sand bars with soft flocculent silt and detritus into which the nymphs can burrow readily. The new reservoir was probably dominated by chironomids because of their intensive reproduction (several generations a year) and planktonic habits during the early stages of development. This situation occurred in Russian reservoirs (Ioffe 1961). Gersbacher (1937) estimated that it took 10 years for the *Hexagenia* community to replace the *Chironomus plumosus* community in reservoirs in central Illinois. Chironomids were numerically and volumetrically the most important organism in Lewis and Clark Lake in 1960. Although Schmulbach and Sandholm (1962) did not sample depths exceeding 3 m, they found an average of 2.2 *Hexagenia* per m² from June to August. In 1962, our sampling over the entire reservoir showed 14/m² during the same time interval. Chironomids dominated numerically but *Hexagenia* dominated the total mass (Swanson 1967). Thus, it took 6-7 years for *Hexagenia* to dominate the bottom fauna community.

The standing crop of *Hexagenia* in the reservoir in 1964 was 40 kg/hectare (wet weight). If we assume that the stratified area represents the whole reservoir, then there was a standing crop of 54 kg/hectare in 1965. If the chironomids and other elements of the fauna constituted approximately 10% of the benthic fauna by weight, there was a standing crop of 44 and 60 kg/hectare present in Lewis and Clark Lake in 1964 and 1965. Lewis and Clark is classified as a reservoir of medium (30-60 kg/hectare) productivity according to Ioffe's (1961) classification of Russian reservoirs based on benthos standing crop.

Production rate values are rare for benthic invertebrates. Waters' (1966) estimate of 126 kg/hectare for a small stream dealt with a species which comprised only a small portion of the fauna. Estimated production of *Tanytarsus* [= *Tribelos*] *jucundus* by Anderson and Hooper (1956), corrected by Neess and Dugdale (1959) to 106 kg/hectare, included only the littoral area of the lake. Production values for crayfish (Momot 1967) of 207 kg/hectare and *Corixa* (Crisp 1962) of 1,300 kg/hectare are based on the littoral area which usually comprises a small portion of the lake and normally has the highest

standing crop and production. The production value for *Hexagenia*, contributing 90% of the benthic biomass of Lewis and Clark Lake, covered the entire reservoir. The annual production of 108 kg/hectare for the entire lake in 1964 was the best estimate and the maximum figure was 166 kg/hectare for the stratified area in 1966.

The high standing crops in the shore area and middle sections of Lewis and Clark Lake point to the possible importance of allochthonous material to *Hexagenia* production. Mordukhai-Boltovskoi (1963a) discussed these processes for the Volga Reservoir and suggested that the main pathway to this production is through organic detritus formed as a result of decomposing shoreline vegetation and that brought in by the river. This vegetation may be terrestrial or aquatic. The material brought in by the river is usually deposited where current velocity drops off (Fillion 1967; Mordukhai-Boltovskoi 1963b). In Lewis and Clark Lake this deposit is in the middle section of the reservoir. Maximum numbers of *Hexagenia* were found at the 5-7 m depth interval (Swanson 1967). This suggests that narrow and relatively shallow reservoirs with a fairly rapid water exchange rate may be conducive to the development of a high benthic biomass.

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Table 1. Age groups of *Hexagenia* nymphs in May and October, 1962-1969. Expressed as percent of total population.

Year	May Yearling	October Young-of-year	May 2-year olds	October Yearling
1962	...	86	...	14
1963	70	96	30	04
1964	95	88	05	12
1965	82	71	18	29
1966	72	76	28	24
1967	82	71	18	29
1968	78	64	22	36
1969	69	90	31	10

Table 2. Monthly accumulated water temperature in day degrees above 10° C, Lewis and Clark Lake, 1962 to 1969

Month	1962	1963	1964	1965	1966	1967	1968	1969
April	31.1	18.0	14.2	16.3	0.0	9.0	28.8	21.1
May	269.1	170.5	219.1	207.1	94.9	102.7	157.6	147.1
June	362.2	361.8	341.2	340.2	310.9	269.5	379.7	270.7
July	483.7	499.4	517.9	477.9	473.7	421.4	457.0	423.2
August	467.9	480.1	429.8	475.6	404.8	441.3	430.8	477.7
September	323.0	375.9	319.0	251.4	311.6	315.6	283.4	352.4
October	212.9	296.0	100.4	135.5	119.4	135.7	128.5	113.6
November	11.5	31.4	14.7	22.0	2.1	0.0	1.1	0.0
Total	2161.6	2233.1	1956.3	1926.0	1717.4	1695.2	1866.9	1805.8

Table 3. Production rate of *Hexagenia* by the growth method from 20 May 1964 to 21 May 1965 (dry weight).

Period	Days	G mg/mg day	\bar{B} mg/mg ²	Production rate-P for day mg/m ² day	Production rate-P for period mg/m ²
Yearling-two					
year old nymphs					
20 May-18 June	29	0.0168	602.2	10.1	292.9
18 June-21 July	33	0.0168	533.8	9.0	297.0
21 July-18 Aug.	28	0.0168	322.9	5.4	151.2
18 Aug.-8 Sept.	21	0.0168	302.6	5.1	107.1
8 Sept.-22 Oct.	44	0.0130	372.2	4.8	211.2
22 Oct.-21 May	211	0.0008	541.2	0.4	84.4
Total					1143.8
Young-of-the-year					
18 Aug.-8 Sept.	21	0.0763	38.2	2.9	60.9
8 Sept.-22 Oct.	44	0.0244	153.8	3.8	167.2
22 Oct.-21 May	211	0.0023	264.6	0.6	126.6
Total					354.7
Total annual production					
				1498.5 mg/m ² dry weight	
				10.340 g/m ² wet weight (92 lbs/acre)	

Table 4. Hamilton method of calculating production using the total number of *Hexagenia* nymphs collected from 5.58 m² from 7 sets of samples in the shore sections of the stratified area of Lewis and Clark Lake from May 1964 to May 1965.

Size group (mm)	Number of nymphs	Loss at each stage	Average weight of the mm group (mg)	Standing crop (mg)	Average weight between mm groups (mg)	Loss X average weight between mm groups (mg)	Number of times loss occurs (l)	Production in dry weight (mg)
3-7	931		0.21	195.51				
		461			0.78	359.58	6	2,157.48
8-12	470		1.35	634.50				
		164			2.91	477.24	6	2,863.44
13-17	306		4.47	1,367.82				
		90			7.84	705.60	6	4,233.60
18-22	216		11.21	2,421.36				
		116			15.35	1,780.60	6	10,683.60
23-27	100		19.49	1,949.00				
		73			26.87	1,961.51	6	11,769.06
28-32	27		34.25	924.75				
		27			39.49	1,066.23	6	6,397.38
			44.74					
Standing crop = 1,343 mg/m ²				7,492.94	Production = 6,829 mg/m ²			
					38,104.56			

Table 5. Hypothetical table illustrating the relative number of nymphs in a 1-year (14 month) and 2-year (22 month) cycle over a 2-year period (August of year 1 to August of year 3). Starting points were at the point of emergence in June and August based on a ratio of emerging adults of 53% and 47%, 2 and 1-year old, respectively. A 20% per month mortality rate is applied from March until October and 2% during the winter months..

Month	22 month nymphs		14 month nymphs		Total 22 month	Total all nymphs
August	1,772*	336	472	89†	2,108	2,669
September	1,418	269	378		1,687	2,065
October	1,134	215	302		1,349	1,651
November	1,111	211	296		1,322	1,618
December	1,089	207	290		1,296	1,586
January	1,067	203	284		1,270	1,554
February	1,046	199	278		1,245	1,523
March	1,025	195	272		1,220	1,492
April	820	156	218		976	1,194
May	656	125	174		781	955
June	525	100†	139		625	764
July	420		111	590*	420	1,121
August	336	1,772*	89†	472	14,299	18,192
September	269	1,418		378		
October	215	1,134		302		
November	211	1,111		296		
December	207	1,089		290		
January	203	1,067		284		
February	199	1,046		278		
March	195	1,025		272		
April	156	820		218		
May	125	656		174		
June	100†	525		139		
July		420		111		
August		336		89†		
					Percent 22 month = 78.6	
					$78.6 \cdot 22 + 21.4 \cdot 14 = 20.3$	
					100	
					$\frac{20.3}{12} = 1.69$ years = Average	
					length of life cycle	

*—Recently hatched

†—About to emerge

Table 6. Annual production rates and turnover ratios for *Hexagenia* in the 1,256-hectare stratified area by the growth and modified Hynes-Coleman method from 1964 to 1969.

Months and Years	Mean annual population density mg/m ²	Annual production mg/m ²	Turnover ratio
May, June, July, August, September, October, 1964; May, 1965*	573	1,498	2.61
May, June, July, August, September, October, 1964; May, 1965†	593	1,667	2.81
May, July, October, 1964; May, 1965†	649	1,804	2.78
May, October, 1964; May, 1965†	727	2,028	2.79
May, July, October, 1965; May, 1966†	906	2,314	2.55
May, October, 1965; May, 1966†	938	2,398	2.56
May, July, October, 1966; May, 1967†	794	2,113	2.66
May, October, 1966; May, 1967†	920	2,407	2.62
May, October, 1967; May, 1968†	702	1,844	2.63
May, October, 1968; May, 1969†	639	1,525	2.39

*—Growth method $P = G\bar{B}$

†—Hamilton modification of Hynes-Coleman method; estimated production divided by 1.69 the number of years in the life cycle.

Table 7. Annual production of *Hexagenia* in Lewis and Clark Lake from May to October 1964 obtained by multiplying mean standing crop times a turnover ratio of 2.7.

Transect	Mean standing crop (kg/hectare)	Area (hectare)	Standing crop in area (kg)	Production standing crop X turnover ratio (2.7)
A	0.32	1,165	373	1,007
B	1.93	1,380	2,663	7,190
C	4.41	1,787	7,881	21,279
D	7.04	1,516	10,673	28,817
E	9.48	2,039	19,330	52,191
F	8.99	1,935	17,396	46,969
Stratified area	4.84	1,465	7,091	19,146
11,300 hectare				176,600 kg
Weighted mean standing crop 5.79 kg/hectare				
Production for lake 15.6 kg/hectare				

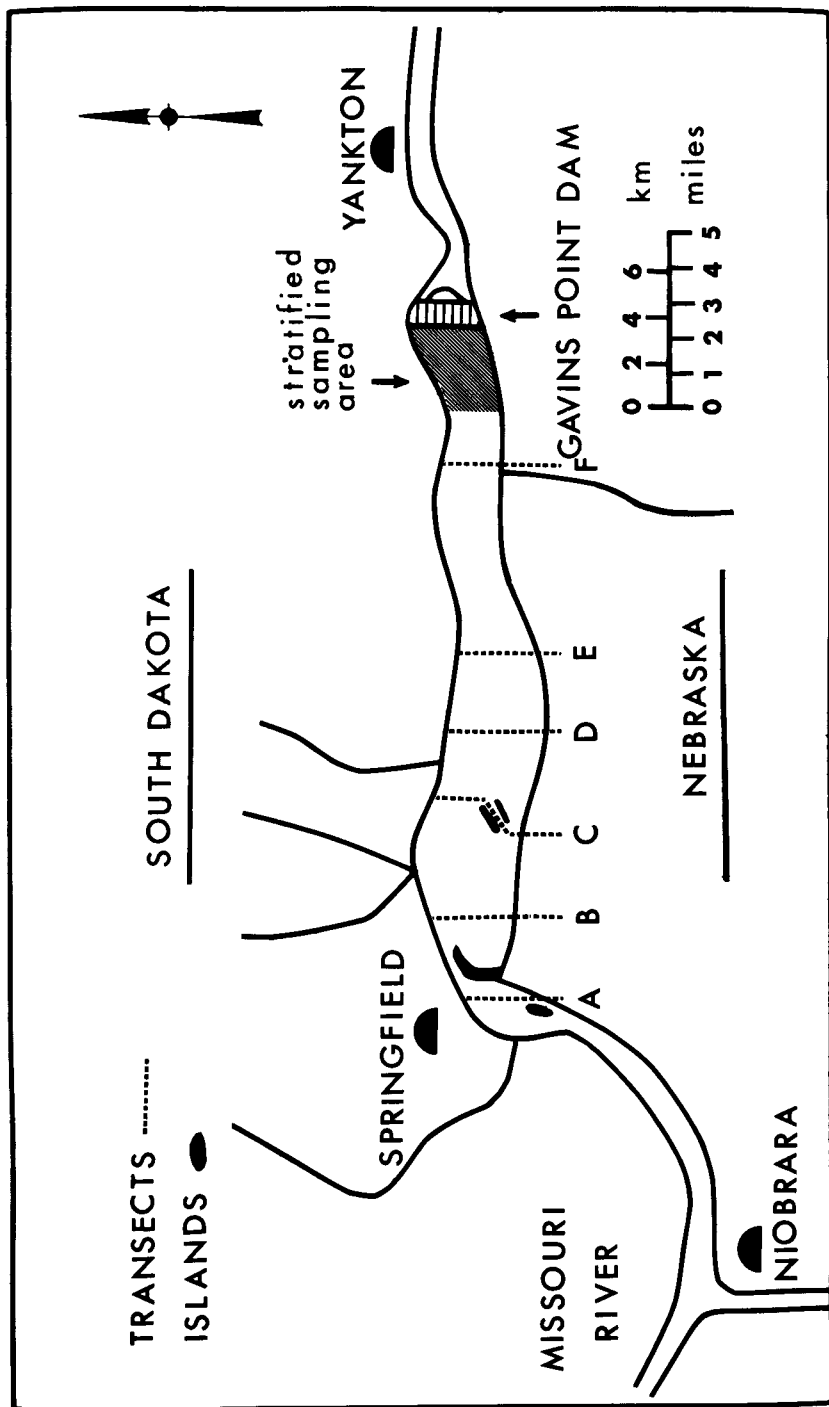


Fig. 1. Lewis and Clark Lake showing the sampling sites.

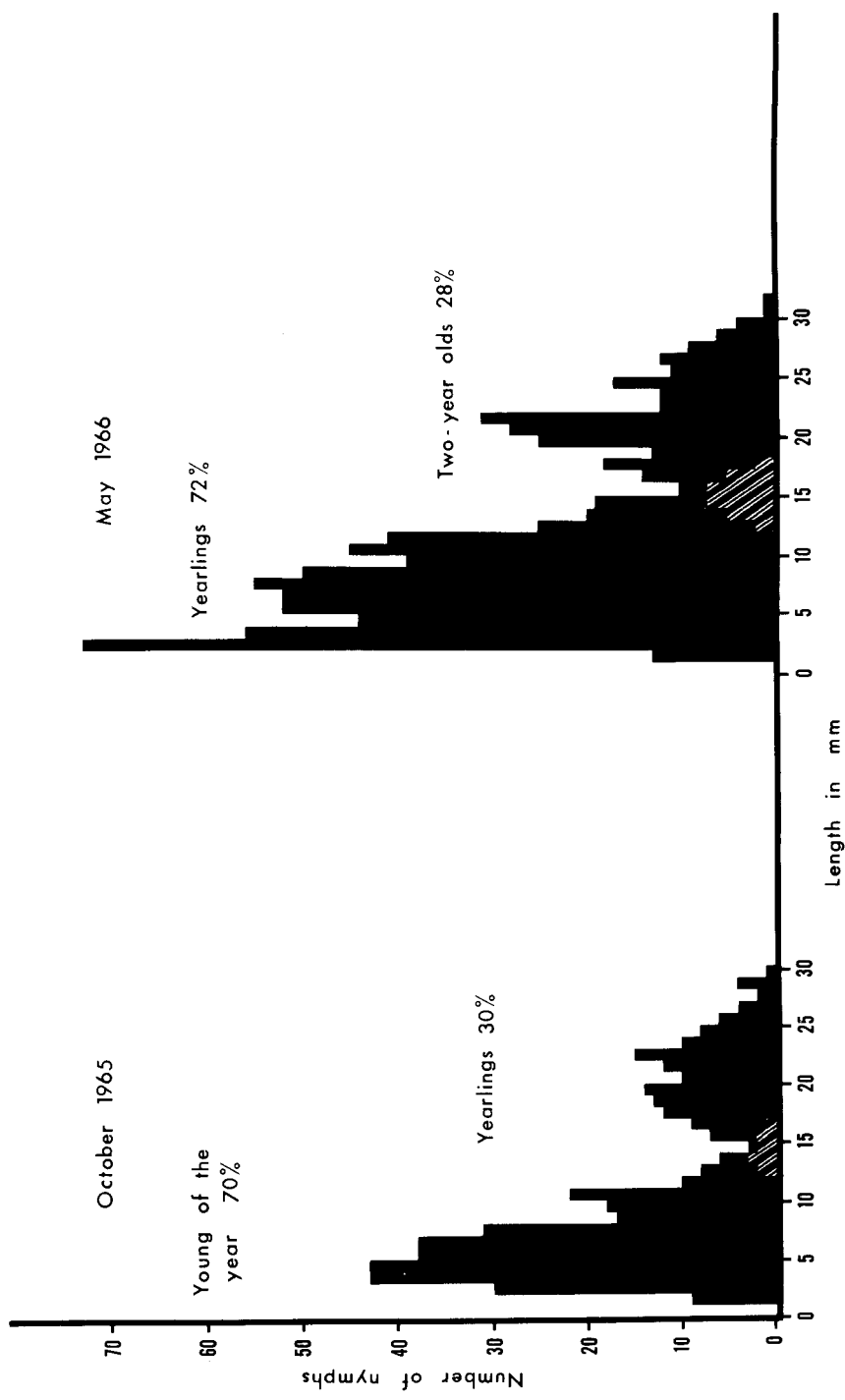


Fig. 2. Length-frequency plots for October 1965 and May 1966 partitioned into young-of-the-year, yearling, and 2-year old segments. Cross hatching shows area of overlap.

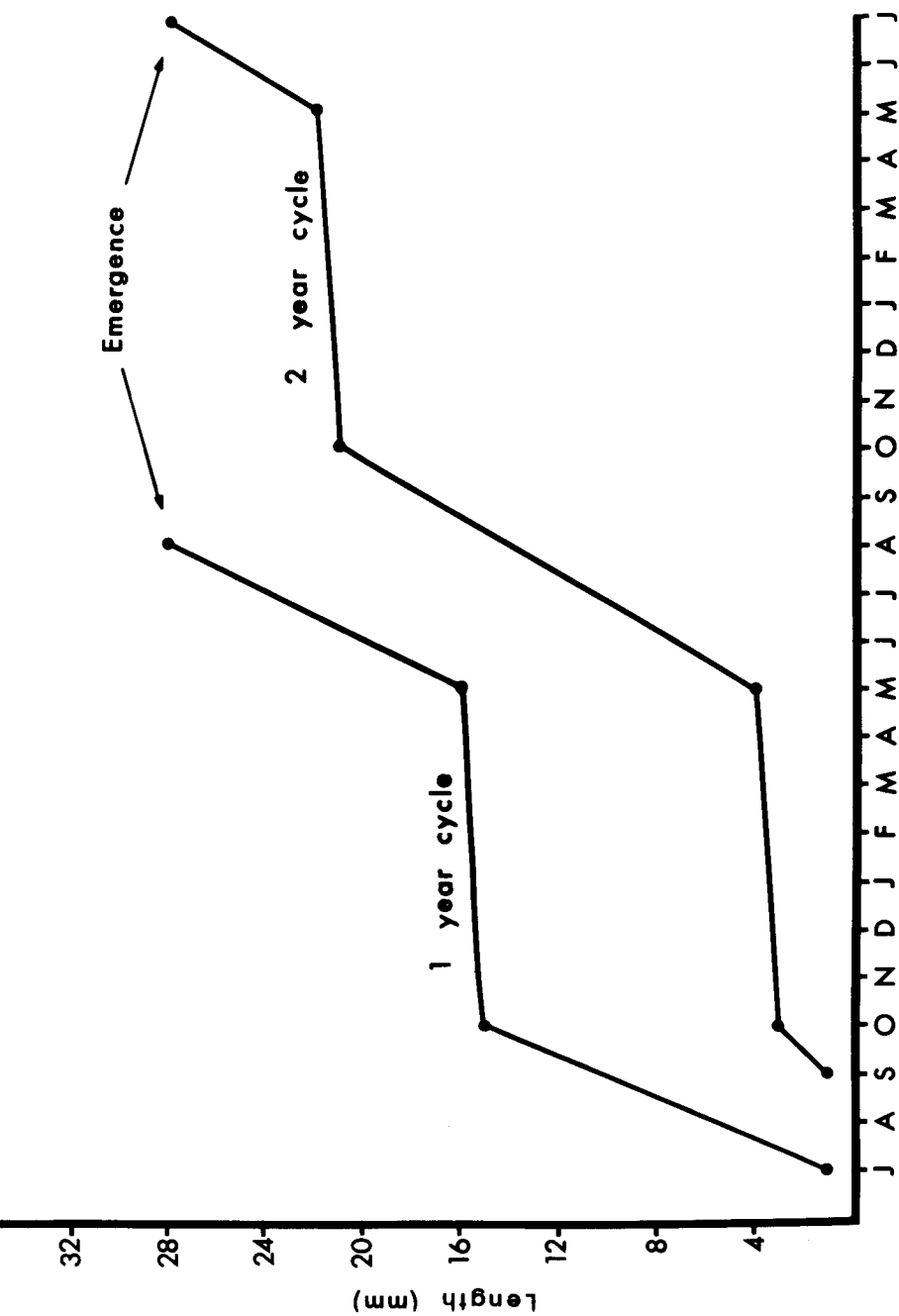


Fig. 3. Approximate growth patterns of *Hexagenia* nymphs taking 1 year and 2 years to complete life cycle.

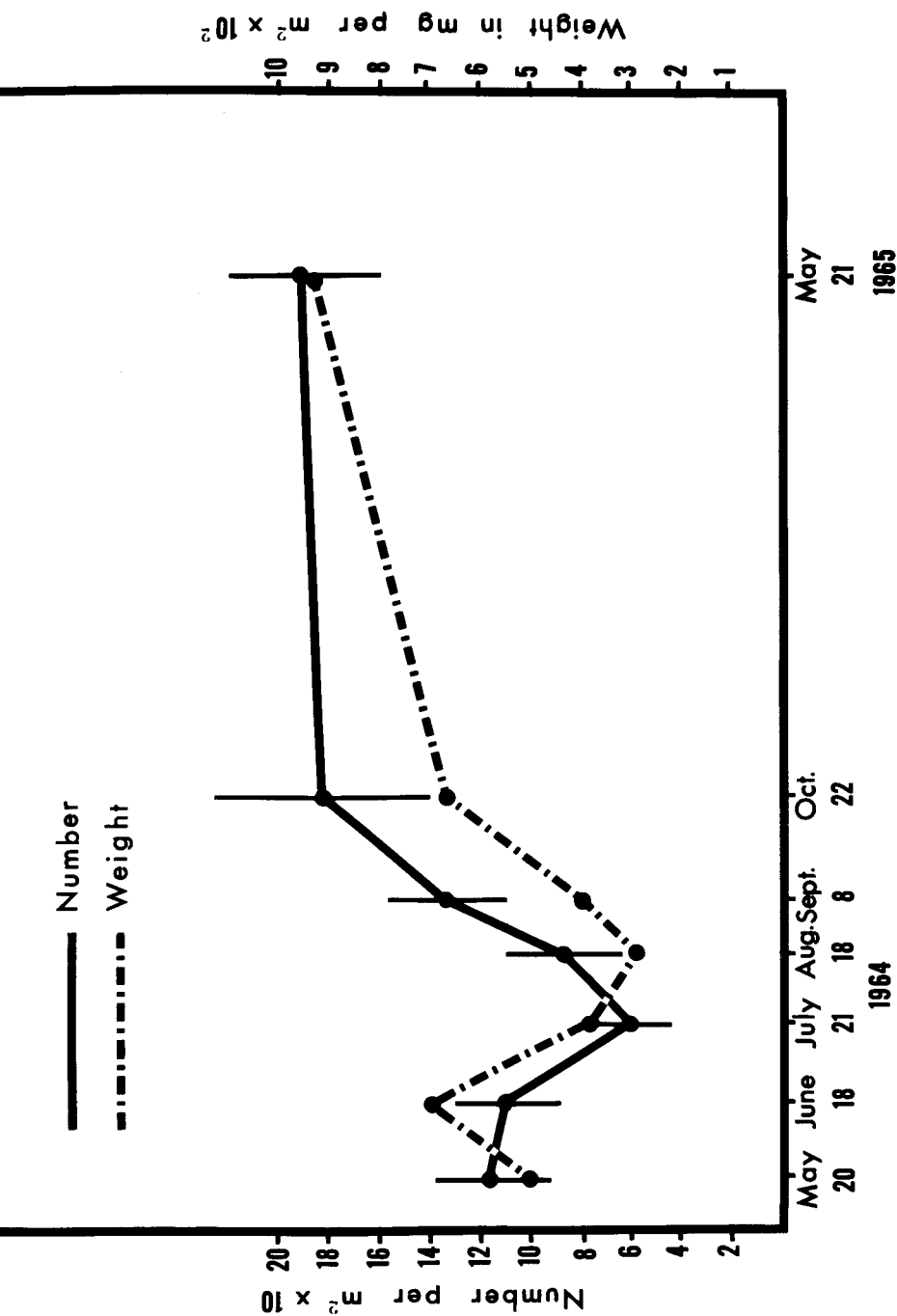


Fig. 4. Density of *Hexagenia* in stratified area of Lewis and Clark Lake in no./m² and mg/m² dry weight from May 1964 to May 1965. Vertical lines represent 95% confidence limits.

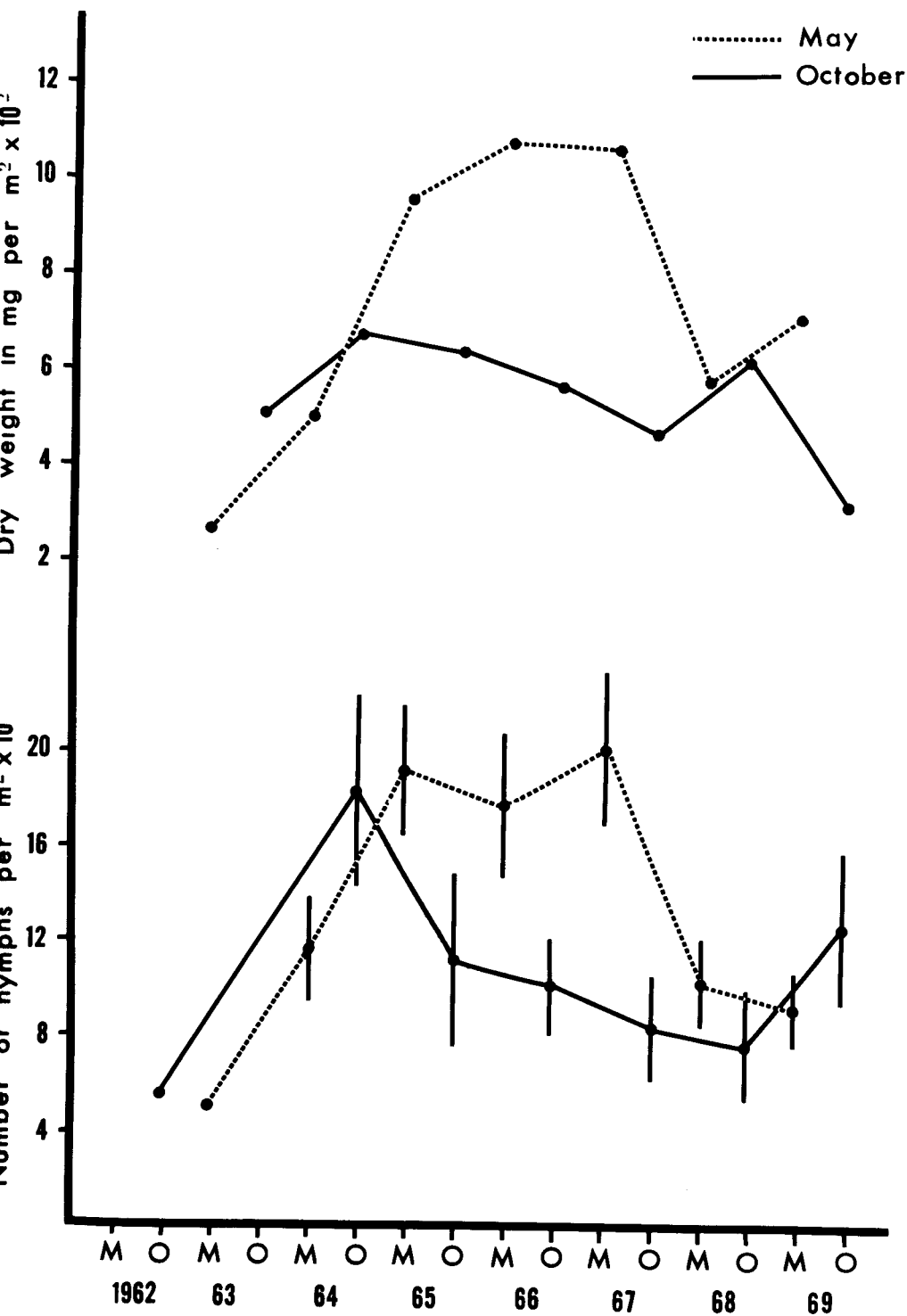


Fig. 5. Population density of *Hexagenia* nymphs in the eastern stratified area of Lewis and Clark Lake in May and October from 1962 to 1969 expressed in mg/m² and no./m². Vertical lines represent 95% confidence limits.

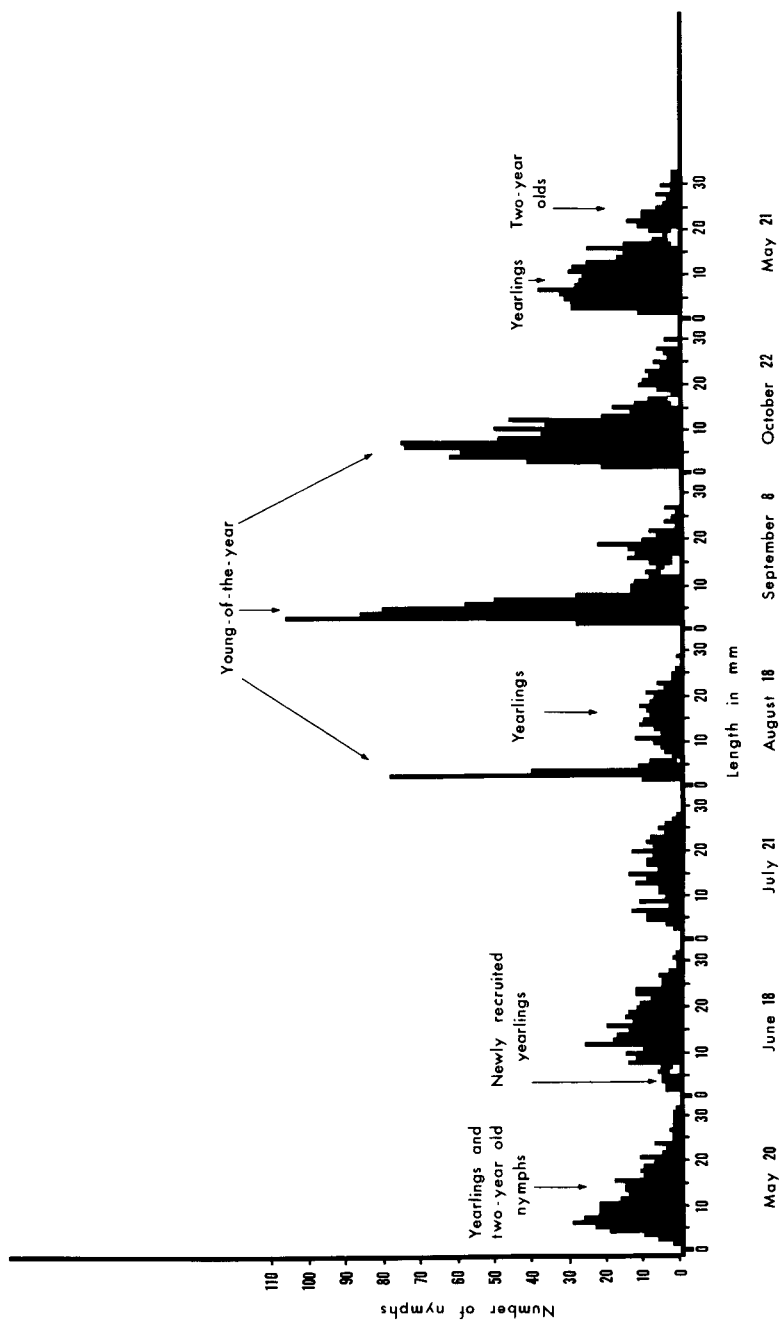


Fig. 6. Length-frequency distribution of *Hexagenia* nymphs from Lewis and Clark Lake from 20 May 1964 to 21 May 1965. Distributions partitioned into young-of-the-year, newly recruited yearlings, yearlings, and 2-year old nymphs.

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