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FACTORS INFLUENCING THE DISTRIBUTION AND ABUNDANCE OF *HEXAGENIA* NYMPHS (EPHEMEROPTERA) IN A MISSOURI RIVER RESERVOIR

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Abstract. Abundance of bottom organisms in Lewis and Clark Lake was measured by transect-station and randomly-stratified sampling methods. Samples were collected with modified orange-peel and Ekman dredges, and cores were used to delineate bottom types. *Hexagenia* nymphs have reached an abundance on the inundated flood plain comparable to populations in natural lakes with suitable habitat. Length frequencies of nymphs, plotted at monthly intervals throughout the summer, suggest a 2-yr life cycle for the major portion of the populations.

Concentrations of the fall progeny (1–10 mm) indicate that the early distribution of nymphs is a function of imago activity during oviposition. Distribution of the overwintering nymphs differs considerably from that of the previous fall. Evidence of migration from densely populated shore areas was observed. An interaction of depth, wind, current, and bottom type is influential in redistributing the population.

Introduction

A study of the bottom fauna of Lewis and Clark Lake was initiated in 1962 as a part of the fisheries research program of North Central Reservoir Investigations, Bureau of Sport Fisheries and Wildlife. The purpose of the study was to determine the environmental conditions limiting the distribution and abundance of benthic invertebrates. This paper is devoted to the burrowing mayflies which dominate the mass of macroinvertebrates inhabiting the reservoir substrates.

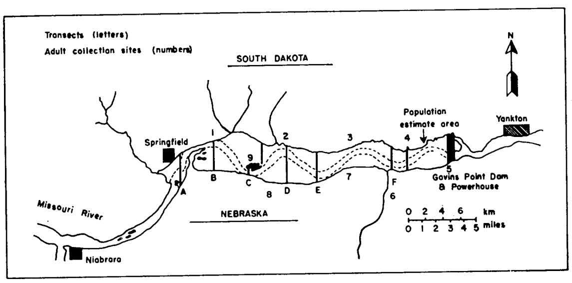

Fig. 1. Map of Lewis and Clark Lake showing the 1964 sampling sites.

Reservoir description

Lewis and Clark Lake (Fig. 1), formed by the closure of Gavins Point Dam on 31 July 1955, is the smallest of six main-stem Missouri River reservoirs constructed by the U.S. Army, Corps of Engineers. It is located on the boundary between South Dakota and Nebraska, 45 miles (72.4 km) below the tailwaters of Lake Francis Case (Fort Randall Reservoir) and serves primarily to regulate releases from the latter and to maintain downstream navigation.

The Niobrara River, with a mean flow of 1,750 c.f.s. (49.6 m^3/sec), enters the Missouri River approximately 9 miles (14.5 km) above the reservoir. The Niobrara carries a load of sand, silt, and organic debris that is deposited in the upper end of the reservoir. Six intermittent creeks also enter the reservoir.

Pool elevation is normally maintained between 1,204 and 1,208 ft msl (367.0–368.2 m) and weekly fluctuations rarely exceed 1 ft (0.3 m). Discharges vary from a winter minimum of 5,000 c.f.s. (141.6 m^3/sec) to a summer maximum of 30,000 c.f.s. (849.6 m^3/sec). The water exchange rate (flushing time) is 8–10 days from March to November and approximately 30 days during the winter. Hydrographic, physical, and chemical characteristics of the reservoir are presented in Table 1.

The reservoir normally does not stratify thermally, and oxygen depletion occurs only in isolated, deep areas after extended periods of calm weather. Wind velocities of 30–50 mph (48.3–80.5 km/hr) occur frequently during the spring, early summer, and late fall. The resulting wave action on the soft bluffs and shallow silted areas produces high turbidity, especially in the upper end of the reservoir. The reservoir basin, essentially subrectangular-elongate, is surrounded by steep bluffs composed of Niobrara chalk and Carlisle shale. The substrate is the original river channel and the flood plain, which is covered by a layer of recently deposited silt. Vascular plants are restricted to a few small beds of smartweed (*Polygonum* spp.). A narrow band of periphyton

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TABLE 1. Hydrographic, physical, and chemical characteristics of Lewis and Clark Lake. All hydrographic data are based on 1,208 ft mean sea level. Physical-chemical measurements represent annual ranges

Hydrographic features	
Length (km)	34.1
Avg width (km)	3.4
Max depth (m)	17.7
Avg depth (m)	4.9
Shoreline length (km)	80.4
Shoreline development (D_L)	2.1
Area (ha)	11,331
Storage capacity (m^3)	555×10^6
Physical-chemical features	
Temperature (°C)	0–28
Conductivity (micromhos/cm at 25 C)	650–840
Secchi disc (cm)	8–183
Turbidity (ppm)	10–675
pH	7.8–8.4
Bicarbonate alkalinity (ppm)	140–180
Dissolved oxygen (ppm)	1.2–14.0

is attached to the shale base of the eroded bluffs and to stands of inundated trees.

METHODS

Experimental design

The systematic transect-station method was used during the summers of 1962, 1963, and in the central and western sections of the reservoir, in 1964. Transects were divided into stations selected to include the old river channel, inundated flood plain, and shore areas (Fig. 2). Individual

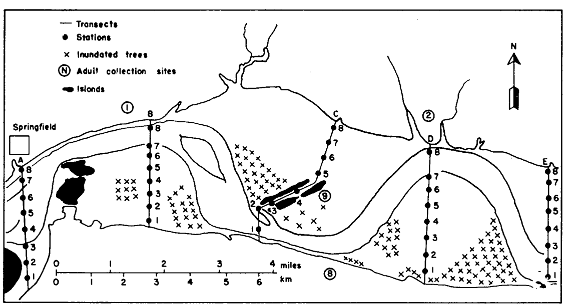

FIG. 2. Detail map of the western half of Lewis and Clark Lake showing the 1964 sampling stations in relation to the preimpoundment river channel, islands, and stands of partly inundated trees.

transects were oriented north to south, perpendicular to the shoreline.

A stratified-random method of sampling was used in 1964 on a 3,103-acre (1,255.7 ha) section of the reservoir. This procedure permitted the use of analysis of variance and *t* comparisons between the flood plain, channel, and shore. It reduced variability and increased accuracy of estimates and interpretation of population trends. Since the small size of individual sampling units ($669\ cm^2$) made it impossible to locate sample sites completely at random, the strata (shore, channel and flood plain) were divided into areas of sufficient size to be located by landmarks and depth. Areas to be sampled were then selected from a table of random numbers, with replacement, and individual sample units were assumed to have been taken at random over the entire stratum. The factors which influence normal sampling procedures were sufficient to prevent bias within areas.

The number of samples required to obtain desired confidence intervals was determined with Stein's two-stage sampling procedure (Steel and Torrie 1960). Square root transformations ($\sqrt{x+1}$) were used to avoid the effects of a Poisson distribution (Snedecor 1956).

Sampling procedures

Samples were collected with a no. 1 orange-peel dredge with an estimated surface area of 0.72 ft^2 (Henson 1954) and with an Ekman dredge of 0.56 ft^2. Both dredges were modified to reduce loss of interface organisms in flocculent substrates. A no. 00 nylon screen was attached to the canvas cover below the flaps of the orange-peel, and a stainless steel screen of comparable size was attached to the top of the Ekman dredge. Comparisons between the two dredges showed no significant differences between catches of *Hexagenia,* but the orange-peel was used because of its mechanical superiority.

Samples were screened through 30- and 60-mesh-per-inch screens (11.8 and 23.6 mesh per cm). Use of the smaller mesh screen more than doubled the effort required to process samples. A comparison between the two screen sizes showed a significant loss of chironomid larvae with the larger mesh but not of the large *Hexagenia* nymphs. Consequently all estimates of the *Hexagenia* population were based on the 30-mesh screen. The increased efficiency allowed more samples to be processed and provided better estimates of the population. Organisms were preserved in 10% formalin.

Core samples of the bottom sediments were collected with a Phleger corer at all sampling stations during 1964. These cores were sealed in plastic tubes and frozen until analyzed.

Adults were collected four times at nine sites along the reservoir (Fig. 1). Two light traps were also used at the extreme eastern and western ends of the reservoir.

Dissolved oxygen, total alkalinity, turbidity, water temperature, conductivity and pH were measured at 2-week intervals on 10 stations during the period of open water. Except for total alkalinity, a monitoring system located in the powerhouse provided this information during the winter months. Oxygen concentrations at the mud-water interface were obtained through use of the polyethylene-bag method described by Fremling and Evans (1963).

Laboratory procedures

Bottom organisms were separated from detritus by flotation in a sugar solution of 1.12 specific gravity (Anderson 1959). The organisms were separated into taxonomic groups, counted, measured, and weighed.

Hexagenia nymphs were measured from the tip of the mandibles to the base of the cerci, sorted into 1-mm size groups of about 100 organisms each, and weighed. Wet, centrifuged, and dry weights were determined to permit comparisons with various weights in the literature. Individual groups were placed in a stainless steel screen (0.14 mm aperture), and the excess moisture was removed by blotting. The organisms were centrifuged for 2 min at 3,200 rpm and weighed (centrifuged weight). The moisture removed from the nymphs by centrifuging was weighed and added to centrifuge weight to obtain wet weight. Finally each group was dried in an oven for 24 hr at 60°C (Lovegrove 1962). Subsequent estimates of weight were calculated from nymph length frequencies.

Five series of core samples were collected to describe sediments. The length of each layer of sediment was measured and grossly classified as sand, silt, clay, or loam. The pipette method recommended by the International Society of Soil Science (Barnes 1959) was used for the October series. This technique is based on the Atterberg scale of particle-size classification and separates sediments into fractions of stone, coarse sand, fine sand, silt, and clay. Analyses were performed only on the top 3 in. (7.6 cm) of sediment because laboratory studies conducted by Hunt (1953) showed that most *Hexagenia* burrows were less than 4 in. deep.

Species Structure

Thirty-six invertebrate species have been identified from 874 samples collected in the reservoir. Most of these species are rare and are limited to the shore areas. Chironomids (Diptera) and *Hexagenia* (Ephemeroptera) comprised 98% by weight and 87% by number in 1962, and 96% by weight and 90% by number in 1963. Chironomid larvae were more abundant than *Hexagenia* nymphs but did not contribute significantly to the total mass. *Hexagenia* nymphs accounted for 91% (1962) and 85% (1963) of the macroinvertebrate mass.

Three species of adult burrowing mayflies (*Hexagenia limbata, H. bilineata* and *Pentagenia vittigera*) were collected from 30 June to 24 August 1964. Adults of *H. limbata* dominated the collections and were most abundant in July. *H. bilineata* adults, found only during August, accounted for only 8% of the adult population; more than 84% of these were collected at site no. 2 on the northwestern section of the reservoir (Fig. 2). A single adult of *Pentagenia vittigera* was collected. *H. bilineata* nymphs were never observed but the structure of the nymph population was assumed to approach that of the adults. Identifications were made with the key prepared by Hamilton (1959).

Life History

The life history of *Hexagenia limbata* has been described by Hunt (1953). Nymphs generally inhabit silted areas of large, slow-flowing rivers and relatively shallow lakes with soft substrates and little aquatic vegetation. Both 1- and 2-yr life cycles have been reported for *H. limbata* and *H. bilineata* (Lyman 1942; Hunt 1953). Temperature appears to be the major factor controlling the duration of the life cycle because 2 yr are required in northern, and only 1 yr in southern waters. The bimodal nymph population present after completion of emergence in August indicates a 2-yr life cycle for most of the population in Lewis and Clark Lake (Fig. 3). Those nymphs hatching in early July may attain sufficient size to mature in a single year.

The emergence of adult mayflies on Lewis and Clark Lake started in late June, reached a peak in July, and ended in late August. The major emergence occurred during early summer (21 June to 22 July) and was reflected in the monthly variations of number and mass (Fig. 4). Last instar nymphs with dark, opaque wing pads were found only during June, July, and August. Young-of-the-year nymphs appeared in August, and the hatch continued throughout the fall. Small (2 mm) nymphs were found as late as 11 June during the following spring, so overwintering of viable eggs may occur. Eggs artificially fertilized and incubated in the laboratory at 25°C (simulating lake temperature) began hatching in 10 days and continued to hatch for a period of 11 days.

Population Density

The *Hexagenia* population of Lewis and Clark Lake increased yearly from 1963 to 1965 (Table

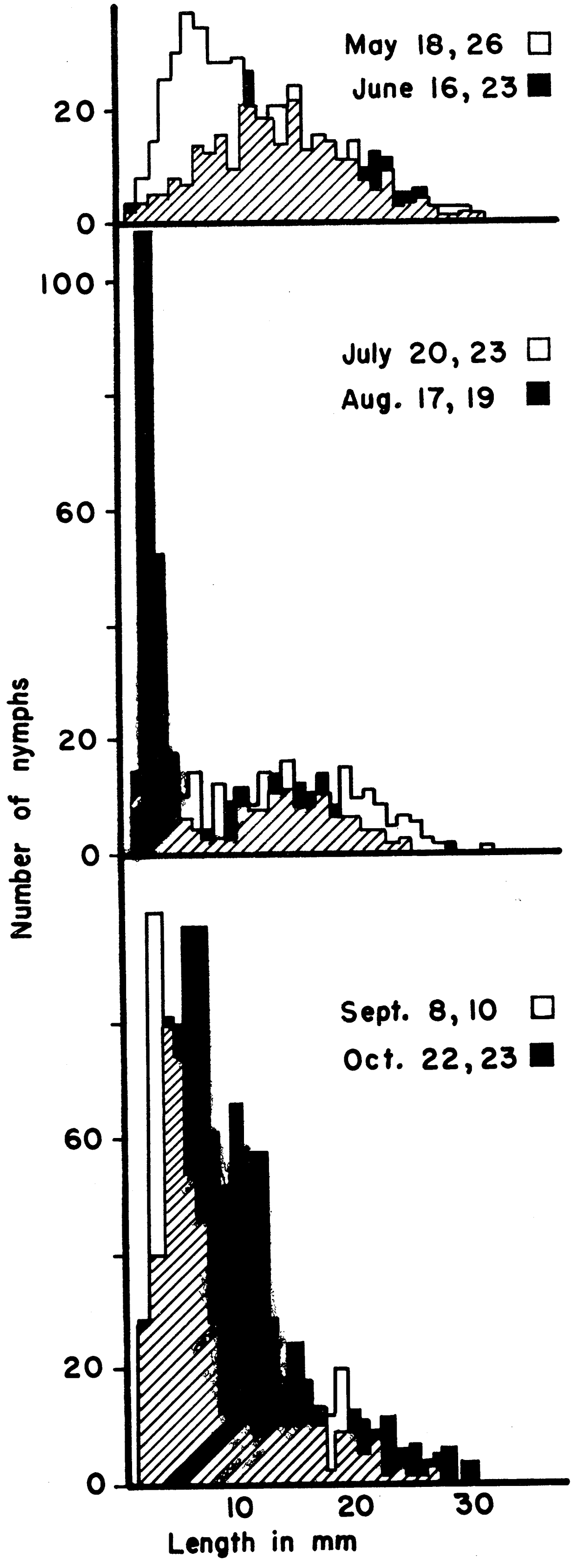

FIG. 3. Monthly plots of the length frequencies of *Hexagenia* nymphs collected during 1964.

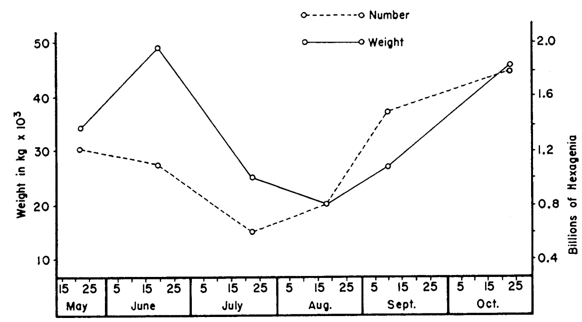

FIG. 4. Monthly variation in the number and mass of *Hexagenia* nymphs collected on the eastern section of Lewis and Clark Lake.

TABLE 2. Spring populations of *Hexagenia* nymphs in a 1,256-ha section of Lewis and Clark Lake in 1963, 1964, and 1965

Date	Area	Mean no. per m²	Estimated no. in area (millions)
April 23-June 11, 1963	shore[a]	142.0	224
	flood plain	30.1	256
	channel	15.1	37
	Total	41.2	517
May 19-May 26, 1964	shore (in)[a]	261.5	207
	shore (out)[a]	128.5	102
	flood plain	76.2	648
	channel	79.2	194
	Total	91.6	1,151
May 17-May 28, 1965	shore (in)[a]	364.6	288
	shore (out)[a]	210.7	167
	flood plain	134.5	1,150
	channel	127.0	312
	Total	152.6	1,917

[a]Shore (in) 0-500 ft, shore (out) 500-1000 ft, shore 0-1000 ft.

2). Comparisons among years were made for May to avoid the influences of recruitment and emergence. The 1963 estimate was based on three eastern transects, which included most of the area sampled in the population estimates of 1964 and 1965. Spring samples for 1962 are not available, but the low population encountered during the summer and fall indicates that the spring population was low. By the spring of 1965 densities of the nymphs approached those of lakes which are known to contain large populations.

Only limited information is available on Lewis and Clark bottom fauna for the period preceding this investigation. Schmulbach and Sandholm (1962) sampled three areas of the reservoir during June, July, and August of 1960 and found an average of 2.2 *Hexagenia* per m². They observed but one emergence in late July. The relatively low number of nymphs during this period may be attributed in part to the sampling procedure because samples were not taken at depths exceeding 3 m.

Comparisons of *Hexagenia* populations among different bodies of water are complicated by lack of a common basis for comparison. Nymphs may inhabit the entire lake bottom, as in Lewis and Clark Lake, or may be limited to the lake margin by thermal stratification and reduced oxygen. Maximum figures may represent only a small portion of the habitat occupied by nymphs.

Several investigators give estimates of mean number per unit area. Using Tables 2 and 3, one

TABLE 3. Spring populations of *Hexagenia* nymphs in established populations in Iowa, Michigan, and Ohio

Location	Sample date	Mean number of nymphs per m²
West Gun Lake, southern Michigan, Plot 1	5/20/47	240
	5/ 6/48	218
Plot 2	5/20/47	285
	5/ 6/48	273
Island area of western Lake Erie	6/17/52	388
	6/23/53	300
Mississippi River at Keokuk, Iowa	7/ 9/58	353

can compare the spring populations in the eastern end of Lewis and Clark Lake with those of West Gun Lake in southern Michigan (Hunt 1953), the island section of western Lake Erie preceding the population decrease of September 1953 (Britt 1955b), and the Mississippi River at Keokuk, Iowa (Fremling 1960). These figures indicate that a spring population of approximately 300 nymphs/m^2 represents a relatively large population. The shore area of Lewis and Clark Lake, which represents an area equivalent to the littoral area of many stratified lakes, contains a comparatively dense *Hexagenia* population.

General distribution

The reservoir can be divided into two general areas for analyses of the distribution of *Hexagenia* nymphs. The upper or western half of the reservoir (transects A–E, Fig. 1) is a transition zone where current velocity decreases as depth increases, and where river conditions change to lake conditions. The lower or eastern half of the reservoir (east of transect E) is more lakelike.

Hexagenia nymphs were distributed over the entire reservoir substrate, but showed marked variations in densities. The population increased downstream from transect A to E with each subsequent transect. This downstream increase was noted during all 3 yr of the investigation and between months within individual sampling seasons

TABLE 4. Monthly downstream distribution of *Hexagenia* nymphs during the summer of 1964 (mean number m^2)

Month	Transect A	B	C	D	E	F
May	5	42	99	135	233	142
June	9	46	43	103	159	133
July	2	17	45	58	105	84
August	14	12	36	81	178	112
October	38	72	139	126	333	208
Avg.	14	38	72	101	202	136

(Table 4). Maximum abundance occurred near the center of the reservoir (transect E) in 1964. This midreservoir peak was less apparent in preceding years.

Progeny distributions

Plots of length frequencies, at monthly intervals, demonstrated that individuals from two different generations dominated fall and spring nymph populations (Fig. 3). The spring population included nymphs entering their third summer (those which will emerge) and 1-yr-old nymphs. The fall population is comprised of the latter group plus young-of-the-year nymphs, which first appeared in August and dominated the population by October, accounting for 90% by number but only 41% of the total mass. Differences in distributions between spring and fall populations occurred at individual stations on western transects B and C. Sheltered stations (1–2B, 2–4C) accounted for 81% of the nymphs collected from 29 April to 27 July. The same stations accounted for only 36% from 3 August to 12 October. Young-of-the-year nymphs were more evenly distributed across transects than the overwintering generations. This difference is most likely the result of prolonged exposure to the less favorable conditions in the western section of the reservoir.

FACTORS INFLUENCING DISTRIBUTION

Ovipositing imagoes

Hunt (1953) observed the activities of mature females on three southern Michigan lakes and reported, in each case, a tendency for the ovipositing imagoes to deposit eggs on shoal areas close to shore. Analyses of the 1962 collections suggested that shore stations supported the greatest number of *Hexagenia* nymphs. This was especially true in the eastern half of the reservoir, where 82% of the nymphs were collected at shore stations. Eastern shore stations sampled in 1963 comprised only 1/3 of the samples but accounted for 72% of the nymphs. Central and western

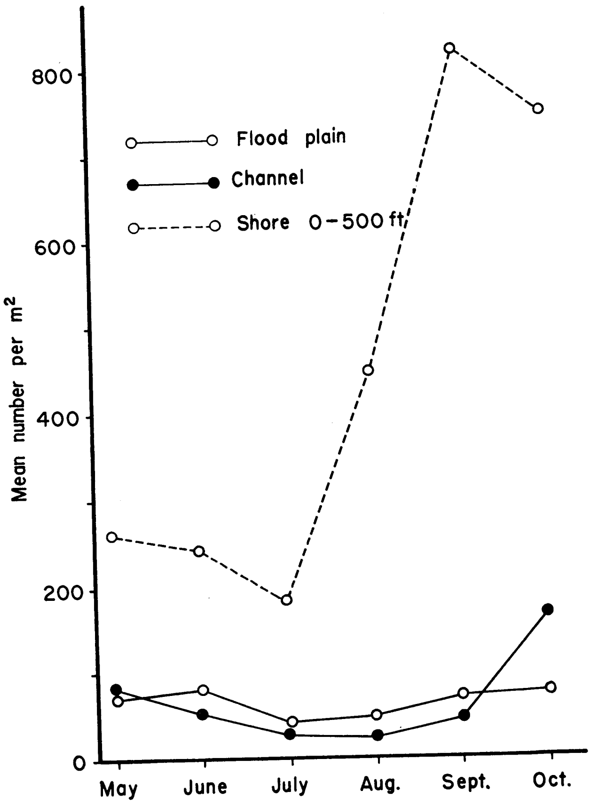

FIG. 5. Monthly variation in the standing crop of *Hexagenia* nymphs occupying the eastern flood plain, channel, and shore during 1964.

shore areas accounted for 56% and 49% respectively.

Statistical comparisons among areas on the stratified eastern section, sampled during 1964, showed that the shore strata contained a significantly greater population (.01 level of significance) than did the flood plain or channel (Fig. 5). This difference persisted throughout the summer and reached a maximum in September following the midsummer hatch.

Comparisons among individual stations on transect F also demonstrate this shore influence (Fig. 6). The difference was less apparent on western transects because islands and stands of dead trees provide locations for molting and subsequent mating flights.

Depth

Mean depth increased downstream toward the dam, as did the nymph population as far as 5.7 m at transect E (Fig. 7). Comparisons of the average number of nymphs at stations exposed to wind action (all stations north and east of station C–4) demonstrated a maximum at the 5–7 m interval (Table 5).

Sublette (1957) also located the maximum con-

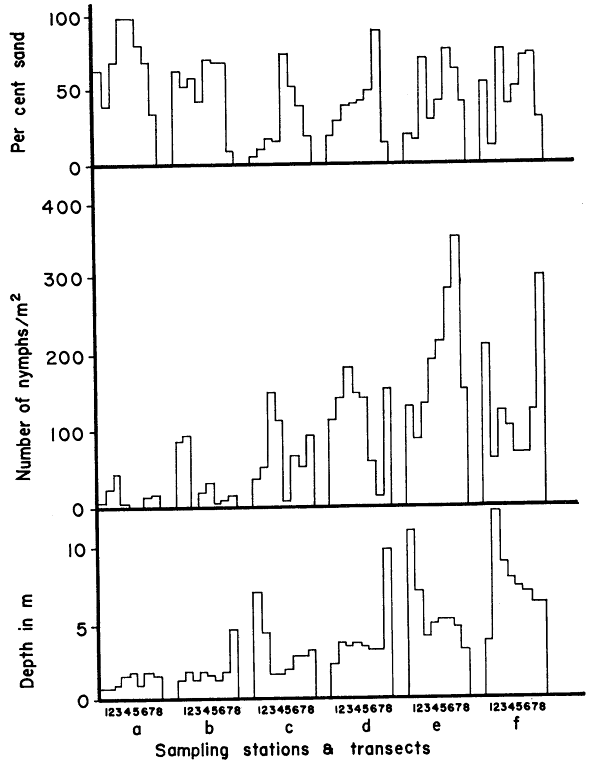

FIG. 6. Comparisons of mean number of *Hexagenia* nymphs with per cent sand and mean depth on individual stations during 1964.

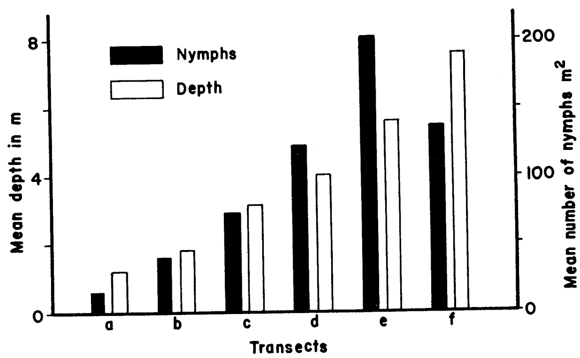

FIG. 7. A comparison of the mean number of nymphs collected on individual transects with mean transect depth during the 1964 sampling season.

centration of *H. limbata* nymphs at a depth of 6 m in Lake Texoma (Denison Reservoir), Oklahoma and Texas. Hunt (1953) reported that nymphs have been located at a depth of 21 m. Within the range encountered in Lewis and Clark Lake (0–17.7 m), depth alone is not a limiting factor to population growth, although it is limiting when combined with other environmental factors.

Depth and oxygen

Depths exceeding 11 m were confined to the old river channel and a dredged area in the east-

TABLE 5. The depth distribution of *Hexagenia* nymphs at stations exposed to wave action in Lewis and Clark Lake during the 1964 sampling season

Depth in meters	Mean number of *Hexagenia* per m²
1.0- 2.9	16
3.0- 4.9	187
5.0- 6.9	259
7.0- 8.9	175
9.0-10.9	117
11.0-12.9	54
13.0-14.9	57
15.0-16.9	30

TABLE 6. Monthly comparisons of the mean number of *Hexagenia* nymphs collected in the flood plain and channel on transects C-F in 1964

Period	Mean no. of *Hexagenia* per m²	
	Flood plain	Channel
May	153	150
June	114	74
July	82	13
August	107	4
October	223	246

ern end of the reservoir. The number of nymphs in the river channel was below the number in the flood plain during July and August 1964 (Table 6). A similar reduction was noted on the eastern strata where the number of nymphs in the channel exceeded that in the flood plain during early spring and late fall (Fig. 5).

Statistical comparisons between the flood plain and channel demonstrated a significant difference ($P < 0.05$) during August. A series of chemical and physical measurements were taken on 14 August 1963 following a period of unusually calm weather. The channel station, which was 12.8 m deep, showed a reduction in dissolved oxygen (6.0–1.6 ppm) and an increase in turbidity (17–105 ppm) between the 9 and 12 m sampling depths. Such changes did not occur at flood plain stations.

The shallow nature of the reservoir, the silt introduced by the Missouri River, and constant agitation by wind generally hold concentrations of suspended materials and dissolved oxygen at high levels throughout the open-water season (April to December). During calm periods suspended materials concentrate near the bottom, and, when accompanied by high midsummer temperatures, oxygen levels are reduced in the deep, isolated channel.

A drastic reduction in oxygen is known to stimulate activity and cause mortality of nymphs. Hunt (1953), in laboratory experiments, described the reaction of *Hexagenia limbata* nymphs to reduced oxygen as an attempt to escape to a better-aerated environment. Britt (1955a) attributed a late-summer kill (1–4 September 1953) of *Hexagenia* nymphs in western Lake Erie to a short-termed reduction in oxygen, accompanied by relatively high temperatures and unusually calm conditions. *Hexagenia limbata* nymphs lose their ability to compensate for reduced oxygen at concentrations approaching 1.2 ppm, and with subsequent reductions they exhibit a response suggesting anoxia (Eriksen 1964).

Depth and molar action

Hexagenia nymphs are unable to burrow in the hard substrates produced by the constant eroding effects of river currents and waves. Nymphs were absent on transect A, where current velocities were sufficient to produce shifting sand (stations 5A and 6A), but they were found in backwater areas with reduced velocities (Figs. 2 and 6).

The shallow area located east of transect A and extending to transect D is influenced by heavy wave action. Following the spring ice break-up in early April and preceding the summer hatch, sheltered areas showed high concentrations (stations 1–2B, 3–4C). Areas of equivalent depth, but exposed to wave action, supported minimum numbers (stations 3–7B, 5C). As depth increased, wave action was reduced, silt was deposited and the nymph population increased (Fig. 7). Substrates located at intermediate depths (stations 6–8C) contained flocculent deposits, periodically influenced by changes in the pool elevation, wind velocity, and wind direction. Hunt (1953) stated that burrows cannot be maintained in flocculent bottoms. He further noted that wave action eliminated nymphs from shoal areas in southern Michigan lakes. Wave action was confined to shore areas in the area east of transect D in Lewis and Clark Lake.

Bottom type

The reservoir substrate, with the exception of isolated areas of sand, is suitable for habitation by *Hexagenia* nymphs. Nymphal abundance decreased with increase in percentage of sand in the upper 76 mm of substrate (stations 4–5A, 5C, and 7D; Fig. 6). This influence was less apparent east of transect D, where silt accumulations above preimpoundment sand deposits remained undisturbed and were inhabited by nymphs.

Major concentrations of sand were located in three areas of the reservoir. The upper transition zone contained deposits transported by the Missouri River (stations 4–5A). Additional concentrations were previously deposited on the inner curve of the original channel as it meandered down the flood plain (stations 5C, 7D, 3E and 3F). The third area was formed by wave action on shore areas.

Water levels

Fluctuations in water level of the magnitude normally encountered in Lewis and Clark Lake do not influence substrates inhabited by *Hexagenia* nymphs, except in a few protected embayments and backwater areas. Elevation from May 1962 to September 1964 showed a range of 1.5 m (1,204–1,209 ft). The maximum monthly range (June 1964) was only 1 m.

Hexagenia nymphs may respond to a drawdown by migrating. When a guard gate was raised to the surface at Lock 19, Keokuk, Iowa, nymphs abandoned their burrows in the silt of the subfloor of the gate and crawled upon the soft mud surface (Fremling 1960).

A similar response was observed in rearing ponds at the Gavins Point National Fish Hatchery, where many nymphs inhabit the clay substrate of the ponds. Periodically when the ponds are drained to recover fish, nymphs crawl in the seepage toward the catch basin at the lower end of the pond. Many nymphs are probably able to survive small drawdowns by reacting in this manner. The major limiting effect of a normal drop in reservoir elevation in Lewis and Clark Lake would be to expose more of the reservoir substrate to wave action.

Migration

Evidence of redistribution through migration has been restricted to movements in response to stagnation or unsuitable substrates. Hunt (1953) reported young-of-the-year nymphs migrating from shallow shoal areas to deeper water and to softer bottoms. This movement was attributed to growth and a demand for more extensive silt accumulations.

A movement from the densely populated shore to the center of the reservoir occurred east of transect E in Lewis and Clark Lake. Shore stations attained maximum densities following the midsummer hatch. Although shore strata remained consistently higher, the magnitude of the difference declined following the hatch. A comparison of the eastern shore and flood plain demonstrated this response (Fig. 5).

During the winter of 1965, screens (.592-mm aperture) were installed in the powerhouse of Gavins Point Dam to monitor the loss of aquatic insects through the turbines. The screens collect a weekly composite sample from a constant flow of 8 liter/min (80,640 liter/week). During the 14-week period of ice cover (10 December to 12 April) a total of 4 nymphs were collected, but the 1-week sample of 8–15 April, which included the first 3 days of open water, contained a total of 122 nymphs. The period of high activity, initiated during the spring break-up, extended to the end of May and averaged 47 nymphs per week. The mean daily discharge from the powerhouse during May 1965 was 6×10^{10} liters, and this discharge carried an estimated 35 million nymphs each day, weighing 1,190 kg. The May standing crop of the eastern stratified section of the reservoir was estimated at 1.5 million nymphs per ha (Table 7).

TABLE 7. Wet weights of the 1965 population of *Hexagenia* nymphs in a 1,256-ha section of Lewis and Clark Lake

Area	millions/ha	kg/ha	Area mass in kg
Shore (in)	3.65	107	8,419
Shore (out)	2.11	85	6,692
Flood plain	1.35	48	41,093
Channel	1.27	37	9,126
Total	1.53	52	65,330

If this figure represents the mean distribution throughout the reservoir, then the total loss during the month of May would not exceed 6% of the nymph population. During June and July the weekly collections averaged three nymphs, which represented a 98% decrease from the peak period of April.

In May, meter nets were placed in the tailwaters of Fort Randall Reservoir and 10 miles (16.1 km) upstream from Lewis and Clark Lake to follow the downstream movement of larval fish. *Hexagenia* nymphs were found only in the latter. Burrowing nymphs inhabit the isolated backwater areas in this section of the river, and it is likely that the nymphs that were collected came from this source. It appears that the loss of nymphs from Lewis and Clark Lake far exceeds the import.

Because information is not available on the *Hexagenia* population inhabiting Fort Randall Reservoir, it cannot be determined why nymphs do not appear in the discharge. However, the turbine intakes are located at a depth of 30 m, which exceeds by 15 m those of Gavins Point Dam. This factor alone could limit emigration.

During May 1964, meter nets were placed immediately above the intakes to the turbines of Gavins Point Dam to compare day and night catches. The major loss took place during the night. Additional information on nightly migra-

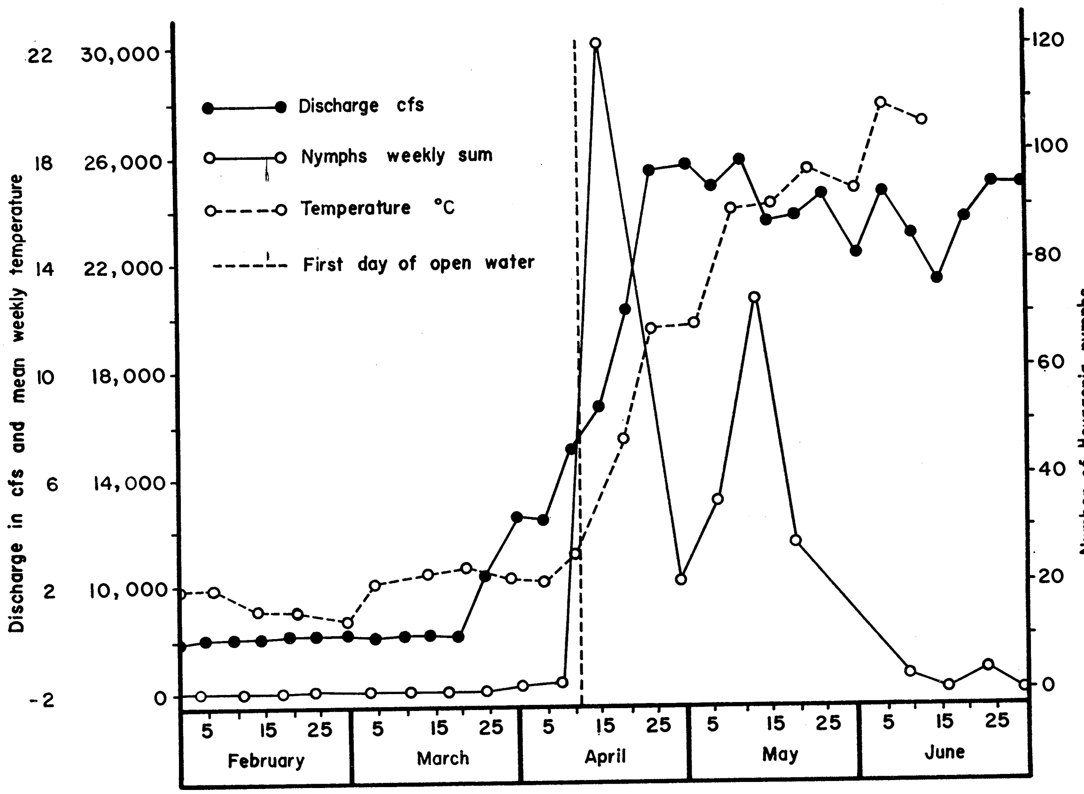

FIG. 8. Comparisons of discharge rates, water temperatures and the loss of *Hexagenia* nymphs in reservoir discharge before and after the spring ice breakup of 1965.

tion was obtained in July 1965; meter nets were periodically examined during a 24-hr period and the nymphs removed. The migration, 100% in this case, occurred between sunset and sunrise following a pattern similar to that described for *Baetis vagans* by Waters (1962).

The period that followed the spring breakup and the initiation of a migration was also accompanied by a resumption of wave action and an increase in discharge (Fig. 8). These factors may have influenced the substrate immediately above the powerhouse intakes, but the number of nymphs involved and the restriction of the loss to night hours suggests that this movement is a normal response and not a forced migration. The increase in discharge rate that preceded the spring breakup did not produce a subsequent increase in the loss of nymphs.

Temperature did increase over this period. It is likely that the increased loss reflects a period of high activity associated with an increase in temperature; at this time a redistribution of the population must take place. The presence of nymphs in most fish stomachs during this period provided additional evidence of nymphal activity. Dorris and Copeland (1962) observed a downstream movement of *Hexagenia* nymphs between April and June in the Mississippi River near Quincy, Illinois.

CONCLUSIONS

Small, relatively shallow impoundments located on silt-laden river systems appear to provide excellent habitat for burrowing mayflies. Fremling (1960) stated impoundments that have been formed along the Mississippi River have undoubtedly increased the habitat for *Hexagenia* nymphs. Surber (1954) sampled three Mississippi backwater areas and found an increase in *Hexagenia* nymphs following impoundment. He noted that this increase was associated with a decrease in the quantity of plant material. Lyman (1942), upon completion of a preimpoundment study of Watts Bar Reservoir, also concluded that *Hexagenia* nymphs would not only survive impoundment but would reach greater production under the new conditions. Impoundments in central and southern Illinois that have characteristics of a large, slow river produce flights of *Hexagenia bilineata* or *limbata* (Burks 1953).

The *Hexagenia* population of Lewis and Clark Lake has increased since impoundment in 1955 and is not yet stabilized. The major portion of the population is concentrated in the eastern half of the reservoir and attains maximum abundance near shore at depths exceeding 2 m. The population is limited in the shallow western section of the reservoir primarily by the effects of wave action, and in the old river channel by reduced oxygen.

The continuous deposit of coarse sediments transported by the Missouri River will undoubtedly reduce the amount of suitable habitat, although at present the extent of such deposits is relatively small.

Oxygen depletion appears to reduce established *Hexagenia* populations. The probability of this occurring will no doubt increase as more extensive accumulations of organic material are deposited by the Missouri River.

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EFFECT OF LIGHT INTENSITY ON THE DRIFT OF STREAM INVERTEBRATES[1]

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Abstract. Various experiments were conducted in a small Minnesota stream to determine the effect of light intensity on the circadian rhythms in drift of two aquatic invertebrates, the nymph of the mayfly *Baetis vagans* McDunnough and the amphipod *Gammarus pseudolimnaeus* Bousfield. Experiments included 1) artificial light in an exclosure which insured that experimental conditions were applied only to the organisms on the stream bottom area in the exclosure, 2) artificial light in the open stream, and 3) artificially produced darkness in an exclosure. A threshold of light intensity which, decreasing, initiated high drift rates and which, increasing, caused cessation of drift, was about 0.1 ft-c (1 lux) for both species. Continuous artificial light above the threshold level for an entire night period, and also for 4 consecutive days, depressed the normal high nocturnal drift rates in the exclosure to near