Reprinted from
Reservoir Fishery Resources Symposium
Athens, Georgia, April 5-7, 1967
Published November 1968

SOME ENVIRONMENTAL FACTORS INFLUENCING BENTHIC INVERTEBRATES IN TWO MISSOURI RIVER RESERVOIRS

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Abstract

Variations in morphometry and water management practices are responsible for differences in the benthic invertebrate populations of the Missouri River reservoirs. In Lewis and Clark Lake, a relatively shallow impoundment, water temperature, behavior of the ovipositing females, and depth-related factors regulate the distribution and abundance of *Hexagenia* nymphs which dominate the biomass. Water-level fluctuations and the accompanying wind and wave action on the bottom are responsible for small *Hexagenia* populations in Lake Francis Case. Despite the complete exposure of the littoral zone, chironomids are 3-fold more abundant in Lake Francis Case than in Lewis and Clark Lake.

Evidence of migration of *Hexagenia* nymphs and chironomid larvae was observed. *Hexagenia* nymphs migrate in response to water temperature and population density, and chironomids migrate with water-level fluctuations. Migration in the Missouri River reservoirs which are characterized by high water discharge rates can produce a significant loss of benthic invertebrates through the turbines. In 1964 we estimated the loss from Lewis and Clark Lake as 44 metric tons: 24 tons of *Hexagenia* nymphs and 20 tons of chironomid and ceratopogonid larvae.

High populations of benthic invertebrates were found on periphyton substrates of submerged trees and higher aquatic plants. The density of these organisms on submerged trees was correlated with pigment concentration.

Introduction

CONSTRUCTION of the main stem Missouri River reservoirs has greatly increased the amount of habitat suitable for development of benthic invertebrate populations. Standing crop values in the unimpounded portions of the Missouri River average less than 1 kg/ha (Berner, 1951; Russell, 1965), but values as high as 70 kg/ha are found in the reservoirs. However, marked differences in morphometry and water management practices produce large variations among the reservoirs. This paper compares the effects of some environmental factors upon the benthic invertebrate populations of two of the reservoirs, Lewis and Clark Lake and Lake Francis Case.

We wish to acknowledge George A. Swanson, a former staff member of North Central Reservoir Investigations, who participated in the collection and analyses of some of the data (See Swanson, 1967).

General Features of the Reservoirs

The U. S. Army Corps of Engineers has constructed six multipurpose reservoirs on the main stem of the Missouri River. Lewis and Clark Lake, formed by the closure of Gavins Point Dam in July 1955, is the smallest and farthest downstream of the six reservoirs. It is located on the boundary between South Dakota and Nebraska, and serves primarily to re-regulate releases from Lake Francis Case and to maintain flow for downstream navigation. Lake Francis Case, 71 km (44 miles) above Lewis and Clark Lake, was formed by the closure of Fort Randall Dam in July 1952. It is used principally for flood control and generation of hydro-electric power.

The two reservoirs differ markedly in morphometry and other hydrographic features (Table 1). Lewis and Clark Lake is comparatively small and shallow, the water exchange rate (flushing time) is fairly rapid, and water-level fluctuations are small. Surface elevation of Lewis and Clark Lake normally is maintained between 367.2 and 368.4 m (1204 and 1208 ft) mean sea level, and weekly fluctuations rarely exceed 0.3 m (1 ft). In contrast, Lake Francis Case is large and deep, the water exchange rate is longer, and water-level fluctuations are large. Surface elevation of Lake Francis Case fluctuates between summer maxima of 414.8 ± 1.5 m (1360 ± 5 ft) and winter minima of 401.1 ± 1.5 m (1315 ± 5 ft) mean sea level; daily fluctuations of 0.3 m (1 ft) are common. These fluctuations have pronounced effects on the hydrographical features of the reservoir, and large areas which are inundated during the summer months may be exposed in winter.

The reservoirs also differ in the composition of the surrounding geologic formations. Lewis and Clark Lake is surrounded by steep bluffs of Carlisle shale and Niobrara chalk whereas Lake Francis Case is surrounded by moderate to steeply-sloped hills of clay and clay loam. Bottom types of both reservoirs are composed primarily of recently deposited silt and fine sand, except in areas of extreme water-level fluctuation or heavy wave action. Water-level fluctuations in Lake Francis Case expose silt deposits to the atmosphere and the subsequent drying and freezing produces clay chips which may remain in solid form following inundation of the area. Wave action on glacial rock outcroppings and exposed slopes, in Lake Francis Case, produces small, gravel-rubble beaches and gravel-sand bottom areas. Heavy wave action in the shallow upper end of Lewis and Clark Lake produces flocculent bottom types.

Physical-chemical conditions in the two reservoirs do not differ significantly. Lewis and Clark Lake does not stratify thermally during the summer and oxygen depletion occurs only in isolated areas of the old river channel after extended periods of calm weather. Temporary stratifications of temperature and dissolved oxygen occur in Lake Francis Case, but are destroyed easily by wind; velocities of 50-80 km/hr are common in the spring, late summer, and fall. High winds

Table 1. Hydrographic features of Lewis and Clark Lake and Lake Francis Case. Data are based upon pool elevations of 368.4 m (1208 ft) and 414.8 m (1360 ft) mean sea level, respectively.

Hydrographic features	Reservoir: Lewis and Clark Lake		Reservoir: Lake Francis Case	
Length	34 km	(21 mile)	161 km	(100 mile)
Average width	3.4 km	(2.1 mile)	2.1 km	(1.3 mile)
Maximum depth	17.7 m	(58 ft)	45.8 m	(150 ft)
Average depth	4.9 m	(16 ft)	15.2 m	(50 ft)
Shoreline length	80.4 km	(50 mile)	804.5 km	(500 mile)
Shoreline development (D L)	2.1		11.7	
Surface area	113 km^2	(28,000 acre)	377 km^2	(93,000 acre)
			202 km^2	(50,000 acre)[1]
Volume	$55.5 \times 10^7 m^3$	(450,000 acre-ft)	$573.6 \times 10^7 m^3$	(4,650,000 acre-ft)
			$228.2 \times 10^7 m^3$	(1,850,000 acre-ft)[1]
Water exchange rate				
March-November	8-10 days		3 months	
December-April	1 month		9 months	

[1]At elevation 402.6 m (1,320 ft) mean sea level.

and the resultant wave action on the steep bluffs and shallow bottom of Lewis and Clark Lake produce high turbidity (up to 675 ppm), especially in the upper end of the reservoir. Turbidity is low throughout Lake Francis Case except along the shore and in bays.

The rapid rate of water exchange in Lewis and Clarke Lake insures that the characteristics of the water mass closely resemble those of waters released from Lake Francis Case. Alkalinity, pH, conductivity, and chemical constituents are similar (Benson, 1967). The species composition and quantitative characteristics of the plankton in the two reservoirs also are quite similar (Cowell, 1967; and unpublished data, North Central Reservoir Investigations).

Methods

Two sampling procedures were employed in the limnetic portions of the reservoirs. A systematic transect-station method was used in the central and western sections of Lewis and Clark Lake and in Lake Francis Case. In Lewis and Clark Lake six transects were sampled; each contained eight stations selected to include the old river channel, inundated flood plain, and shore areas. In Lake Francis Case transects were located in bays with stations at 1.5 or 3 m depth intervals. Additional samples were taken in the inundated flood plain and old river channel of the reservoir.

A stratified-random method was used to sample a 1,256 ha section in the eastern end of Lewis and Clark Lake. This section was divided into three strata: shore, flood plain, and channel. The area within each stratum was subdivided into squares of sufficient size 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 factors which influence normal sampling procedures were sufficient to prevent bias within squares.

Bottom samples were collected in the limnetic area with a no. 1 orange-peel dredge with an estimate surface area of 669 cm^2 and in the smartweeds, trees, and littoral area with an Ekman dredge of 520 cm^2. Samples were screened through 30 and 60 mesh-per-inch screens (11.8 and 23.6 mesh per cm). The 30 screen was sufficient for sampling *Hexagenia* as there was no significant loss, but a 60 screen was necessary for chironomids.

Aufwuchs samples were obtained by removing branches from inundated trees, smartweeds, and portions of stakes placed in the reservoir. The substrate material was measured to calculate the surface area.

A screening system (0.592 mm aperture) was installed in the powerhouse of Gavins Point Dam to monitor the loss of aquatic insects through the turbines. This system filters a constant flow of water (8 liters/min) tapped from the turbine cooling system. The filtration rate, related to mean daily discharge rates supplied by the U. S. Army Corps of Engineers, was used to estimate loss from the reservoir. Sampling of migrating insects in the reservoir was done with a high-speed Miller sampler (Miller, 1961) with a net of 0.158 mm aperture.

Bottom organisms were separated from detritus by flotation in a sugar solution of 1.12 specific gravity (Anderson, 1959). Organisms were preserved in 10% formalin.

During May *Hexagenia* nymphs were collected and placed in a partially submerged rearing cage (12 ft x 2 ft x 1 ft) located in a sheltered boat basin. The bottom of the cage was covered with silt and the submerged portion was covered with 0.158 mm nylon screen. Water circulated through the screen but nymphs were contained effectively. The rearing cage was checked daily during the period of emergence and subimagoes were removed from the top of the cage which extended above the water level. At the completion of emergence the rearing cage was removed and the remaining nymphs were counted.

Composition of the Benthic Fauna

The benthic fauna of the limnetic region of Lewis and Clark Lake is dominated by Chironomidae (Diptera) larvae and *Hexagenia* (Ephemeroptera) nymphs. These organisms compose 90% by number, and 95% by mass of the total population. Chironomids are more abundant but are comparatively insignificant in terms of total biomass; *Hexagenia* nymphs account for 85-90% of the mass. Oligochaetes, fingernail clams (*Musculium*), and Ceratopogonidae (Diptera) are found occasionally in limnetic samples.

In Lake Francis Case, chironomids and oligochaetes are the most abundant benthic invertebrates. Chironomids are numerically dominant in all areas except the old river channel in the lower half of the reservoir where oligochaetes are more abundant; chironomids compose 93% of the fauna and oligochaetes constitute 6%. *Hexagenia,* Ceratopogonidae and *Chaoborus* (Diptera: Culicidae) occur in low densities.

The littoral fauna of both reservoirs is fairly large and diversified. Shorelines, inundated trees, and smartweeds (*Polygonum* spp.) serve as substrates for periphyton growth and subsequent colonization by Aufwuchs fauna. The species structure of the two reservoirs is comparatively similar. The abundant species of chironomids, oligochaetes, and mayflies (*Hexagenia limbata* and *H. bilineata*) are found in both reservoirs.

Factors Influencing Benthic Invertebrate Populations

Temperature and emergence

Temperature is the major factor controlling the duration of the life cycle of *Hexagenia limbata* in Lewis and Clark Lake. Nymphs hatching in early July may attain sufficient size to emerge the following year, but most of the population has a 2-yr life cycle. The emergence of adult mayflies begins in late June or early July, and continues into September or October, depending upon the water temperature. Mean temperature was almost 3 C greater in September 1966 than in September 1965 (19.4 vs. 16.6), and comparisons of the weekly emergence of *Hexagenia* subimagoes from our rearing cage showed that emergence was extended during the fall of 1966 (Fig. 1). Mean water temperatures were comparable during June, July, and August of both years.

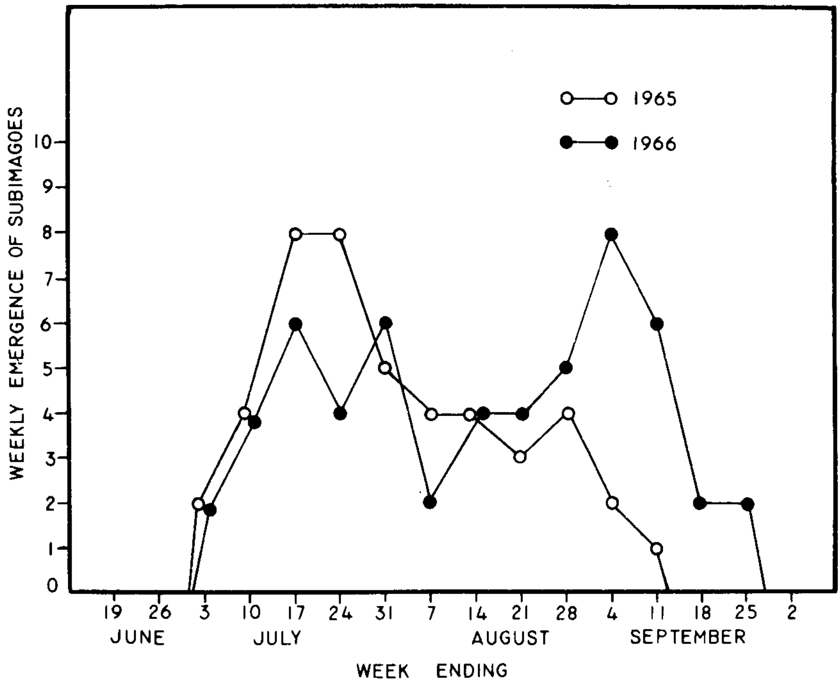

FIGURE 1. The number of **Hexagenia** subimagoes emerging from a rearing cage placed in Lewis and Clark Lake during 1965 and 1966.

The extended fall emergence produced marked differences between the 1965 and 1966 estimates of the per cent emergence of the population. Similar numbers of nymphs were placed in the rearing cage each spring and the mortality was comparable between years, 31.2 and 29.1%, respectively. However, the percentages of the surviving nymphs which emerged were 46.4% in 1965, and 75.3% in 1966. Such differences can be of great significance when between-year comparisons of population densities or estimates of production are made.

Shore influence on ovipositing females

The tendency for females to deposit eggs close to shore is the major factor influencing the distribution of *Hexagenia* nymphs in Lewis and Clark Lake. In 1964, 82% of the nymphs collected in the lower half of the reservoir were obtained from shore stations. Moreover, statistical comparisons among strata (flood plain, channel, and shore) of the eastern section showed that the population density was significantly greater in the shore area throughout the summer. The differences were greatest in September, after the midsummer hatch, when the mean density of the shore stratum was 8-fold greater than either the flood plain or channel. The shore influence is less apparent in the upper half of the reservoir because islands and stands of partially inundated trees also serve as sites for molting and subsequent mating flights.

Bottom type

The reservoir substrates, unless modified by physical factors, are suitable for development of bottom fauna populations except in areas composed of coarse sediments. Sand appears to be the only substrate in Lewis and Clark Lake which is not utilized by benthic invertebrates. The abundance of *Hexagenia* nymphs and chironomid larvae is inversely related to the per cent of sand in the substrate. However, such deposits are not extensive and recent silt deposition has covered much of the sand of the original Missouri River channel. In Lake Francis Case bottom type is a limiting factor when modified by water-level fluctuations, but below the level of maximum drawdown the substrate is suitable for habitation by benthic invertebrates.

Depth distribution

The distribution of benthic invertebrates in many reservoirs is related to the depth of the water. In Lewis and Clark Lake, mean depth increases progressively as sampling transects approach the dam. The density of *Hexagenia* nymphs increases with depth up to a mean transect depth of 5.7 m; slight decreases occur on deeper transects. Similar comparisons of chironomid densities showed increases with depth over the entire range of transect depths (1.2 to 7.6 m). The average number of *Hexagenia* nymphs and chironomid larvae at stations exposed to wind action was greatest at the 5-7 m and 7-11 m intervals, respectively (Table 2). Samples from depths of less than 3 m and from depths greater than 11 m contained significantly lower numbers of *Hexagenia* nymphs. The chironomids showed similar trends but the magnitude of the differences was not as great (Table 2). Comparisons of the depth distribution of benthic invertebrates in Lake Francis Case are futile because of the large fluctuations in water levels (approximately 9-11 m per year).

Table 2. Depth distribution of *Hexagenia* nymphs and Chironomidae larvae at stations exposed to wave action, Lewis and Clark Lake, 1964.

Depth	Mean number of organisms per m^2	
in meters	*Hexagenia*	Chironomidae
1.0 - 2.9	16	111
3.0 - 4.9	187	122
5.0 - 6.9	259	186
7.0 - 8.9	175	207
9.0 - 10.9	117	214
11.0 - 12.9	54	167
13.0 - 14.9	57	168
15.0 - 16.9	30	164

Within the ranges encountered in Lewis and Clark Lake and Lake Francis Case, depth is not a limiting factor to population growth or abundance. Depth becomes limiting only when combined with other environmental factors.

Depth and oxygen

The comparatively low densities of *Hexagenia* nymphs found at depths below 11 m (Table 2) have been correlated with reduced oxygen concentrations at the mudwater interface. Depths exceeding 11 m are confined to the old river channel in the lower end of Lewis and Clark Lake. *Hexagenia* populations in the channel were comparable to those in the adjacent flood plain during May and October, but summer densities were considerably lower. The maximum difference occurred in August when the mean numbers of nymphs in the flood plain and channel were 107 and 4 per m^2, respectively. This difference was significant at the 5% level.

Experiments conducted in August 1965 with the polyethylene bag technique of measuring oxygen at the mudwater interface (Fremling and Evans, 1963) showed reduced oxygen concentrations in the channel following extended periods of calm weather. Concentrations as low as 1.2 ppm were recorded in the channel at this time. Reductions of this magnitude did not occur in the more shallow flood plain. The *Hexagenia* nymphs undoubtedly migrate from the channel during periods of low oxygen. Eriksen (1964) and Hunt (1953) both reported that *Hexagenia* nymphs leave their burrows in response to low oxygen stress.

Depth and molar action

Densities of *Hexagenia* nymphs and Chironomidae larvae are lowest in Lewis and Clark Lake at depths of less than 3 m (Table 2) where river currents or wind-generated waves produce shifting or flocculent bottom types. River currents produce shifting-sand bottom types in the headwaters and *Hexagenia* nymphs are absent, except in protected backwaters. Chironomid densities are lowest in this area also. Heavy wave action in the shallow upper half of the reservoir produces unstable bottom types except in areas protected by islands or inundated trees. *Hexagenia* and chironomid densities are significantly higher in the protected areas.

In the lower half of Lewis and Clark Lake, depth increases and the effect of wave action on the bottom is reduced considerably. Silt deposits accumulate and densities of benthic invertebrates increase. Effects of wave action in this part of the reservoir are confined to shorelines in water less than 3 m deep.

In Lake Francis Case, effects of wave action on bottom soils are confined primarily to shorelines subject to extreme water-level fluctuations. Wave action mechanically sorts the sediments into various size groups. Small terraces of coarse material (sand, gravel, and clay pebbles) are found at the upper end of the slope and silt is deposited near the lower limits of drawdown (Fig. 2). Distribution of benthic invertebrates in these areas is regulated by water-level fluctuations and bottom type requirements of individual species.

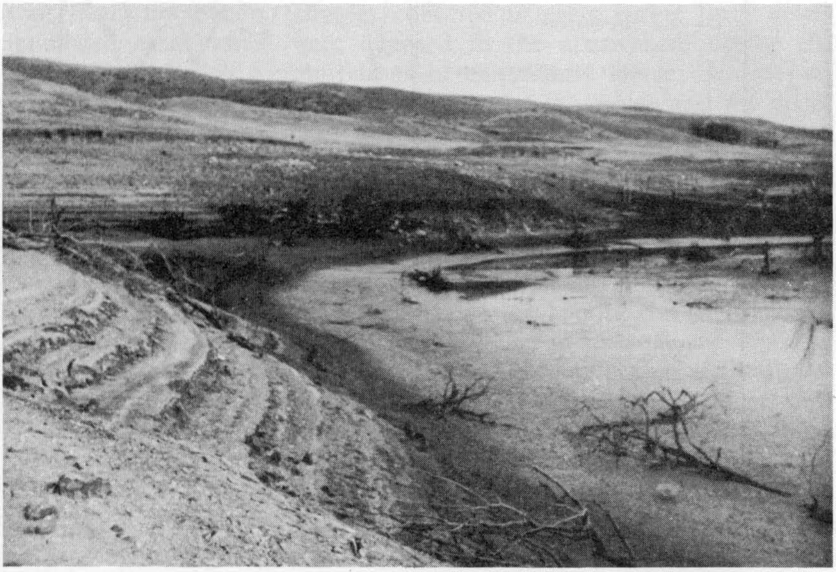

FIGURE 2. An exposed slope in Lake Francis Case illustrating mechanical sorting of sediments by wave action during reservoir drawdown of approximately 11 meters.

Migration

Redistribution of larval insects through migration is a significant factor in the dynamics of benthos in reservoirs. In the Missouri River reservoirs which are characterized by high water discharge rates, migration by benthic invertebrates can produce a significant loss of biomass through the turbines during the spring and summer. This may have an important effect on the standing crop if there is no import from upstream. Migration in response to water-level fluctuations also influences the distribution and abundance of benthic invertebrates.

In Lewis and Clark Lake migration of *Hexagenia* nymphs and chironomid larvae and pupae has been observed throughout the open-water period (April-December). Migration by *Hexagenia* nymphs is strictly nocturnal, and although chironomid larvae and pupae are most active at night, some remain in the water column during daylight hours. Densities of chironomids in the water are relatively constant throughout the season, but *Hexagenia* nymphs are most active immediately after the ice breakup. More than 85% of the nymphs monitored in the discharge during 1964 were collected within 8 weeks of ice breakup (Fig. 3).

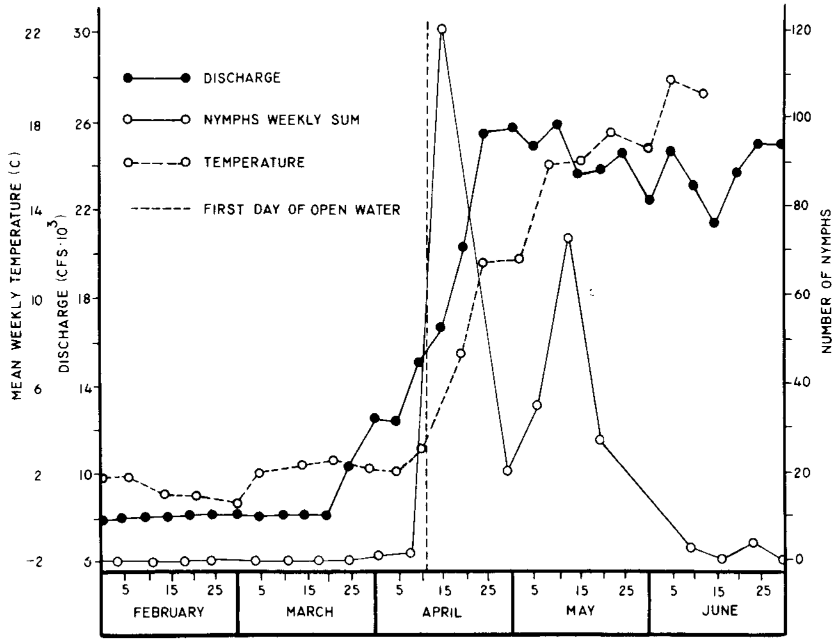

FIGURE 3. Comparisons of discharge rates, water temperatures, and the loss of **Hexagenia** nymphs from the reservoir, spring 1965 (Swanson, 1967).

Water temperature and population density appear to be the factors which initiate migration of *Hexagenia* nymphs in Lewis and Clark Lake. Increased wave action and discharge of water following ice breakup cannot be significant factors since migration is strictly nocturnal and occurs throughout the reservoir instead of in the immediate vicinity of the dam. Increasing temperature apparently stimulates nymphal activity (see Fig. 3) and subsequent migration from shore areas. In May of each year, densities of nymphs in the shore stratum are approximately one-half of the October values for the preceding years; flood plain and channel densities increase considerably over the same period.

Although densities of benthic invertebrates in the water during periods of migration are comparatively small, 0.5 to 8.0 per m^3, they become significant when the loss attributable to water discharge from the reservoir is calculated. During the period of *Hexagenia* migration in 1965, 12 April to 1 July, the loss in the discharge (460 x 107 m^3) was estimated to be 17 x 10^8 nymphs or 24.1 metric tons. Since there is no import of *Hexagenia* into Lewis and Clark Lake from upstream, the loss amounts to 7-10% of the spring standing crop. Similarly, by projecting estimates of the planktonic abundance of chironomids and ceratopogonids in the discharge, we obtained an estimate of the annual loss which, in 1965, amounted to 20 metric tons. However, this loss is partially balanced by import from Lake Francis Case. Sufficient data are not available to relate the loss of these dipterans to the standing crops.

In Lake Francis Case migration is most evident in the zone of water-level fluctuation. Samples collected in early spring from newly inundated areas which were exposed to the atmosphere during the winter showed high concentrations of chironomid larvae; densities as high as 1,600/m^2 were recorded. The size of the larvae and the water temperatures on these dates suggest that the presence of larvae can only be explained by migration. In some cases, migration in the zone of water-level fluctuation involves distances of 1 km or more. Migration in response to receding water levels was evident from samples collected near shore in November when the water level was near its lowest level; densities as high as 60,620/m^2 were recorded at this time.

A study of stranding and migration of benthic invertebrates as related to water-level fluctuation was initiated in Lake Francis Case in the summer of 1966. Samples were collected on either side of the shoreline, one in 5-15 cm of water, and another in moist ground immediately above the waterline. A third sample was collected in damp soil above the most recent watermark produced by wave action; the distance of this sample from the shoreline varied from 1 to 15 m depending upon the magnitude of the water-level fluctuation and the slope of the bottom. Further references to these samples will be designated as wet, moist, and dry, respectively.

Stranding of benthic invertebrates was evident at Transect C on all sampling dates, especially on 4 August when 6,146 chironomids/m^2 were found about 4 m above the shoreline at the C-dry sampling station (Table 3). Survival of stranded chironomids appears to be negligible since few living larvae were found at the same depth contour on 19 August. Concentration of chironomid larvae which migrated with receding water also was evident at Transect C. On both 22 July and 4 August, the density at the C-wet sampling station was considerably higher than at C-moist (Table 3). These samples were taken in such close proximity, less than 2 m apart, that only water levels could account for the differences.

Wave action and the slope of the bottom have significant effects on migration and stranding of organisms at some stations in Lake Francis Case. Prevailing winds in the summer are from the southeast and the length of the fetch at Transect B is 5-fold greater than at Transect C. The accompanying wave action reduces the chironomid population considerably in the shallow areas of Transect B. Furthermore, the slope of the bottom at Transect B is steep compared with Transect C, and stranding is reduced (Table 3).

Aufwuchs communities of inundated trees and higher aquatic plants

The inundated trees and higher aquatic plants, found in the Missouri River reservoirs, serve as substrates for the development of periphyton

Table 3. Densities of chironomid larvae and pupae at two transects in the zone of water level fluctuation, Lake Francis Case, 1966. Position of samples is described in the text.

	Water level fluctuation between sample dates	Density in number per m^2					
		Transect C			Transect B		
Date	(cm)	Dry	Moist	Wet	Dry	Moist	Wet
July 22			409	1,808			
Aug. 4	-58	6,146	1,636	2,820	97	43	151
Aug. 12	-23	603	8,461	8,073	0	78	538
Aug. 19	+28	43	54	495	0	19	39

communities which subsequently are colonized by benthic invertebrates. Growth of periphyton on inundated trees in Lewis and Clark Lake begins immediately after the spring ice breakup (March or April); in Lake Francis Case spring inundation initiates growth. Periphyton growth on smartweed (*Polygonum*) stems occurs in Lewis and Clark Lake in late May or early June, when the plants first emerge. Higher aquatic plants are found rarely in Lake Francis Case.

Benthic invertebrates appear on the trees and aquatic plants immediately after the onset of periphyton growth. Moreover, densities of most of these organisms are considerably higher on the periphyton subtrates than on the reservoir bottom in adjacent areas. In the summer of 1964, the mean density of chironomids on the trees in Lewis and Clark Lake was 11-fold greater than the mean density on the bottom, and in Lake Francis Case the difference was 4-fold. Comparisons between densities of benthic invertebrates on smartweed stems and in bottom samples showed differences of similar magnitude (Table 4). Oligochaetes, chironomids, and miscellaneous insect groups were 7- to 30-fold more abundant on the periphyton substrates, and snails (*Ferrissia*)

Table 4. Mean densities of benthic invertebrates on smartweed (*Polygonum*) stems, in adjacent bottom areas, and in control areas not protected by smartweed, Lewis and Clark Lake, 4 September 1964.

	Mean density (no. per m^2)		
Organism	Smartweed stems	Smartweed area	Control area
Chironomidae			
Larvae	7,427	988	695
Pupae	517	62	8
Hexagenia	0	310	164
Oligochaeta	10,000[1]	699	352
Gasteropoda			
Ferrissia	560	0	0
Miscellaneous insects[2]	369	19	39
Total	18,873	2,078	1,258

[1]Density estimated visually
[2]Miscellaneous insects include: Trichoptera, Ephemeroptera, Diptera, and Odonata

were found only on these substrates. Burrowing mayflies (*Hexagenia*) were not found on the smartweeds, although they were present in bottom samples.

Densities of benthic invertebrates were 2-fold greater in bottom samples collected in the smartweeds than in samples from a control area of similar depth and bottom type which was devoid of smartweeds (Table 4). This difference is significant at the 1% level. Water depth in the vicinity of the smartweed beds ranges from 1-3 m and bottom types usually are flocculent silt or shifting sand. Apparently the root systems of the smartweeds produce a more stable bottom type for bottom fauna.

Although the trees and higher aquatic plants undoubtedly serve as emergence sites for chironomids and other insects, the high densities of immature stages are apparently related to the abundance of periphyton on the substrates. Fluctuations of chironomid populations on submerged trees in Lewis and Clark Lake, and Lake Francis Case have been correlated positively with fluctuations in the total pigment concentration of the periphyton (Fig. 4). However, the ratio of chironomid density to pigment concentration is inverse between the reservoirs (Fig. 4). This discrepancy is attributable to two factors: (1) periphyton growth on trees in Lake Francis Case is destroyed by winter drawdown of the reservoir whereas trees in Lewis and Clark Lake are constantly inundated; and (2) chironomid densities in Lake Francis Case are approximately 3-fold greater than in Lewis and Clark Lake.

Conclusions

Interactions of environmental factors produce distinct differences between the benthic invertebrate populations of the Missouri River reservoirs. In Lewis and Clark Lake, a relatively shallow impoundment, almost all of the bottom area is suitable habitat for *Hexagenia* nymphs, and population densities have attained levels comparable to those found in other eutrophic bodies of water (Swanson, 1967). However, in Lake Francis Case *Hexagenia* populations are exceptionally small because water-level fluctuations destroy much of the habitat. Bottom types below the zone of water-level fluctuation, approximately 11 m below summer pool level, are suitable for nymphs, but depth or some related factor apparently inhibits population development. Despite the complete exposure of the littoral zone, the most productive area of most bodies of water, chironomids are approximately 3-fold more abundant in Lake Francis Case than in Lewis and Clark Lake. Lack of competition with *Hexagenia* nymphs for space and food may be the cause of this difference, although our data are not conclusive at present.

However, the high turnover ratio (i.e., the number of times the population replaces itself in one year) of Chironomidae is more significant to benthic population dynamics than standing crop measurements. Our calculations of the biomass discharged from Lewis and

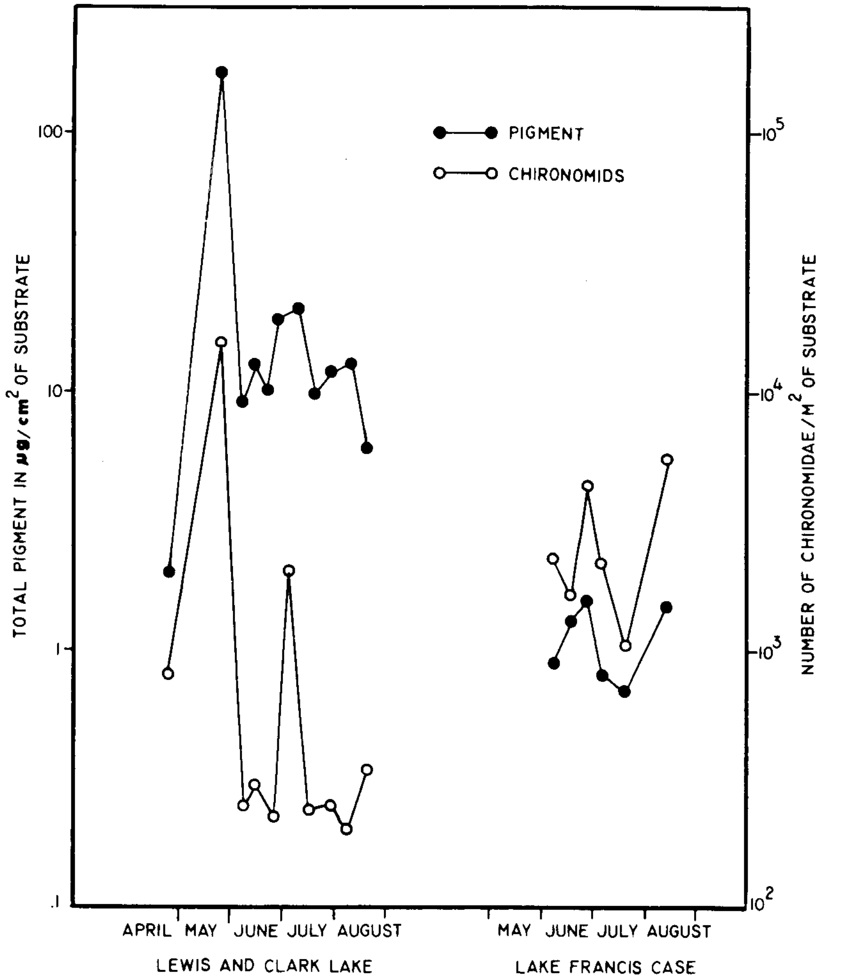

FIGURE 4. The relationship between the total pigment concentration of the periphyton and density of Chironomidae on submerged trees in two Missouri River reservoirs (plotted from data obtained by Claflin, 1966).

Clark Lake in the spring and summer of 1965 showed that the loss of chironomid larvae was almost equivalent to the loss of *Hexagenia* nymphs, even though the biomass ratio in the standing crop was only 1:9. Studies of life cycles and turnover ratios of chironomid species are currently being conducted in both reservoirs.

The large discrepancy observed between the 1964 and 1965 estimates of the per cent emergence of *Hexagenia* subimagoes suggests that future sampling of benthic invertebrates should be correlated with water temperature if between-year comparisons are to be made.

Swanson (1967) presented evidence that *Hexagenia* eggs may over-winter and hatch in the spring as water temperature increases. Between-year temperature differences undoubtedly produce differential hatching of these eggs and differential growth rates which affect estimates of standing crop and calculations of production. In future estimates of the standing crop of benthic invertebrates in Lewis and Clark Lake, we intend to use the day-degree method of sampling instead of sampling on the same dates each year. A base temperature of 10 C will be used in the determination of sampling time since Hunt (1953) indicated that growth of *Hexagenia* nymphs is greatly retarded or ceases completely at lower temperatures.

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