

Carlson

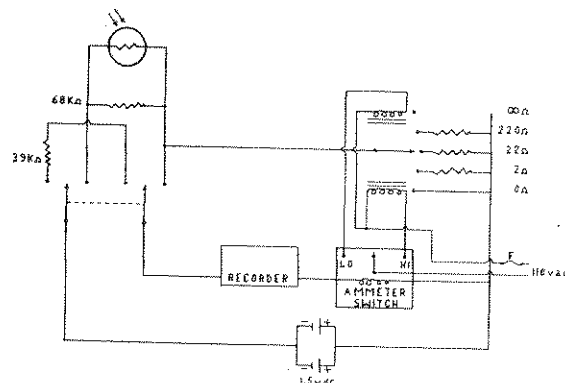


FIG. 1. Schematic diagram of recording photometer (all resistors 5%).

was needed, and to make the correct change, a 0-50 μ a high-low switching microammeter (Api optical meter relay, model 503-LD) was used to activate an add-and-subtract stepping relay (Guardian, Model IR-RAS) on which resistances were mounted.

The switching microammeter has high and low set points which close their own appropriate circuits. The low set point was used to energize the low side of the stepping relay, to increase the resistance in the parallel loop. The high set point was used to energize the high side of the stepping relay to decrease the resistance in the parallel loop.

The unit was equipped with a battery testing circuit that is operated by an on-off-on 3 position DPDT toggle switch. When the switch is in the operate position, the photocell is placed in series with the microammeter, recorder and their parallel loop. When the switch is in test position, a 39K ohm resistor is placed in series with the microammeter, leaving the photocell and parallel loop circuit open. In addition to the battery testing circuit, the photometer was equipped with a 68K ohm resistor and a slow blowing fuse (MDL $\frac{1}{8}$ amp 250-volt) to prevent accidental damage to the stepping relay switch when light intensities suddenly change or fall below .10 foot-candle. The photocell was protected from rain or accidental damage by a plexiglass shield.

The recorder does not indicate which range or relay position is being recorded. The ranges can easily be determined by following any sequence of change as from sunrise to sunset.

Figure 2 (A) is the equivalent μ a values taken from the strip chart recording (Fig. 2, B) plotted at 15-min intervals against time. Ranges of the photometer and

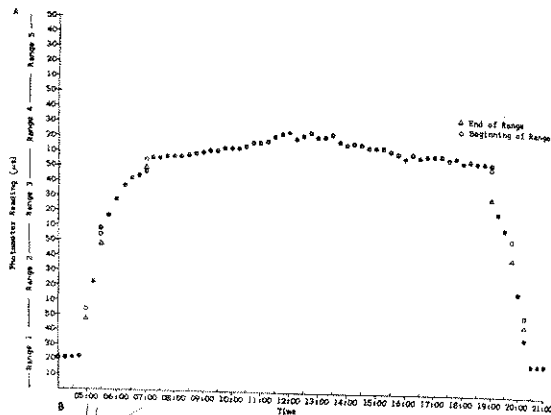


FIG. 2. (A) microampere values taken from strip chart recording (B) plotted against time.

equivalent μ a values for periods when the photometer switched ranges are shown by a triangle and circle. The triangle represents the end of one range and the circle, the beginning of the next range. To prevent oscillation of the microammeter switch, the low set point was set at 2 and the high set point at 48.

Comparative readings were taken in sunlight with a Weston photometer (Model 756, quartz filter) to determine foot-candle and μ a equivalents. That the photocell response is not linear results in a nonlinear relationship between ranges of the photometer. Therefore, each range should be calibrated separately with a standard photometer.

ACKNOWLEDGMENTS

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SUMMER BOTTOM FAUNA OF THE MISSISSIPPI RIVER, ABOVE DAM 19, KEOKUK, IOWA¹

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Abstract. Over 1400 benthos collections were made from eight sampling areas near the Illinois shore of the Mississippi River above Dam 19 in the summers of 1960 and 1961. No significant difference was found in numbers of macroscopic organisms collected after sifting Ekman dredge contents through 20- and 40-mesh screens. *Sphaerium transversum* was the most abundant organism and was the only organism collected at every sampling plot on each

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collection date. *Hexagenia* naiads were the most abundant insects at all sampling areas in 1960. *Coelotanytus*, *Tendipes plumosus*, *Stenochironomus*, oligochaetes, *Campeloma*, and *Lioplax subcarinata* were also abundant and frequently collected. *Somatogyrus depressus* and *Oecetis* sp. b were abundant during certain time intervals. *Tendipes plumosus* became the most abundant insect in 1961 at the part of the study area nearest Dam 19. Several organisms were more abundant in 1961, when mayfly population densities were low, than in 1960. As the most abundant insects emerged during each summer, other elements of the benthos increased in abundance. An average of 2,924 organisms/m² was collected in the study area. Major elements of the benthos seem to have changed little in the last 30 years. The study area had a climax community characteristic of mature streams and showed no evidence of serious pollution.

INTRODUCTION

With development of large metropolitan areas along the Upper Mississippi River, the river has received increasingly large amounts of organic pollutants. Certain areas of the Upper Mississippi have been considered seriously polluted for some time, and a recent study of the distribution of burrowing mayflies indicates particularly serious pollution in areas down river from Minneapolis-St. Paul and from St. Louis (Fremling 1964). Bottom fauna data collected during 1960 and 1961 near Keokuk, Iowa, are herein presented as an indicator of the biological conditions in the portion of the Mississippi between southeastern Iowa and western Illinois.

Bottom fauna collections were made as part of a study of the advisability and practicability of local control of nuisance species of mayflies and caddisflies in the Keokuk area (Fremling 1960a and 1960b, Hoopes 1960, Carlson 1966). Several possible methods of reducing numbers of nuisance insect species were considered, including the local removal of benthic immature stages by application of insecticides to the river. The present paper records the bottom fauna of the relatively shallow silted areas above Dam 19 at Keokuk prior to any control measures which may be attempted.

MATERIALS AND METHODS

Eight sampling areas (Table 1) were established in early June, 1960, on the Illinois (eastern) side of the navigation channel above Dam 19 at Keokuk, Iowa. Each sampling area included two stations, 20 m² and 20 m apart. The bottom sediments at all areas were classified as silt-loam rich in organic matter. Current was negligible except at area C, where a moderate current existed. Collections were made at each sampling area once each week from June 14 to August 17, 1960. Eight dredge hauls were taken with a 15.5 × 15.5 cm Ekman dredge within each station each time an area was sampled. Four samples were washed in a screened pail (Fremling 1961) containing 20-mesh wire screen. The other four were washed in a screened pail containing 40-mesh screen. The numbers of macroscopic organisms collected from the two screens were not different. Three areas were selected at random, and the numbers of *Hexagenia* and

combined numbers of leeches, chironomids, and oligochaetes collected with the two pails were compared in tests of differences (Snedecor 1956). All six tests for significance resulted in "t" values that were nonsignificant at the 95% level, indicating no reason to assume that the two pails would yield different results. Data resulting from use of the two pails in 1960 were, therefore, combined to provide single estimates of the number of organisms. In 1961, only the 20-mesh pail was used, and four Ekman dredge samples were taken from each station in June, in July, and in August. The total number of individually-preserved Ekman dredge samples was 1280 in 1960 and 192 in 1961.

During the analysis of collections, specimens were identified at least to the generic level in almost all cases. Because of the large numbers of *Sphaerium transversum* collected, their numbers were estimated after several counts had been made. *Sphaerium* from 55 collections selected at random and representing all 16 plots and both years were counted, and their total volume after air drying was measured. An average of 38.5 *Sphaerium*/cm³ was calculated. Thereafter, in collections containing more than a few *Sphaerium*, only the volume of the air-dried clams was measured. Their number was later estimated by multiplying their volume in cc by 38.5.

To ensure accurate identification of chironomid larvae, it was necessary to prepare slide mounts, as described by Curry (1961), of the larvae and their severed heads. Several mounting media were employed, but the use of "Euparal" as described by Johannsen (1937) for mounting of Nematocera was most efficient.

Representatives of each genus of chironomids were sent to Dr. LaVerne L. Curry of Central Michigan University for confirmation of determinations. Gastropoda and Sphaeriidae were sent to Dr. Henry van der Schalie of the University of Michigan Museum of Zoology for confirmation. The oligochaetes encountered above Dam 19 fragmented excessively in alcohol and could not be positively identified by the author. Representatives were sent to Dr. Ralph O. Brinkhurst of the University of Toronto for identification. Many Ephemeroptera and Trichoptera had been previously identified by Dr. H. H. Ross of the Illinois Natural History Survey, Mr. Thomas Thew of the Davenport Public Museum, and Dr. C. R. Fremling. All other organisms were identified only by the author with existing keys and other descriptive literature.

Annotated List

In the following list of organisms, an asterisk indicates those collected only rarely. Numbers taken at each station and dates are given in the thesis on file in the Iowa State University library (Carlson 1963).

Platyhelminthes

Turbellaria

Planariidae* only 1960. Most specimens probably passed through screen.

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TABLE 1. Approximate location of sampling areas and ranges of water depths encountered

Sampling area	Approximate mile number on the Upper Mississippi	Approximate distance above Dam 19	Approximate distance from eastern bank of the river	Ranges of water depths encountered
A.....	364.5	0.40Km	275m	1.2-1.5m
B.....	365.0	0.80	550	1.1-1.4
C.....	365.2	1.13	30	2.0-2.3
D.....	365.3	1.29	550	1.1-1.4
E.....	365.8	2.09	135	1.4-1.8
F.....	366.4	4.35	275	1.4-1.7
G.....	366.6	4.67	275	1.2-1.5
H.....	366.8	4.99	135	1.4-1.7

Annelida

Oligochaeta

Tubificidae relatively abundant all stations. The maximum was 398 oligochaetes m² at one station in Area B in July 1960.

Branchiura sowerbyi Beddard. This species fragments in alcohol, making counts and identification difficult.

Limnodrilus hoffmeisteri Claparede

Unidentified species*

Hirudinea

Glossiphoniidae

Helobdella stagnalis (Linne)

H. nepheloidea (Graf)

Glossiphonia complanata (Linne) only 1960.

Placobdella montifera Moore*

Erpobdellidae

Erpobdella punctata (Leidy)

Unidentified species*

Arthropoda

Insecta

Plecoptera

Perlodidae*

Ephemeroptera

Ephemeridae

Hexagenia spp.

Pentagenia vittigera (Walsh)* only 1960.

Caenidae

Caenis sp. only 1961.

Baetidae

Isonychia sp.* only 1960.

Odonata

Gomphidae

Gomphus sp.

Coenagrionidae

Ischnura sp.* only 1961.

Hemiptera

Corixidae only 1961.

Megaloptera

Sialidae

Sialis sp. infrequently collected by dredging, but abundant near the river bank.

Trichoptera

Leptoceridae

Oecetis sp. b (of Ross 1944), larvae and pupae were collected only in July and August 1961. Because it seems unlikely that these were suddenly introduced into the area after June 1961, the author believes *Oecetis* may have been erroneously overlooked during previous sampling periods. The portable cases of *Oecetis* could have been mistaken for small bits of hollow plant stems. It is also unlikely

that *Oecetis* could have been as abundant in 1960 as in 1961 and gone unnoticed throughout the summer.

Hydropsychidae

Potamyia flava (Hagen)* only 1960.

Cheumatopsyche campyla Ross* only 1960.

Psychomyiidae

Neureclipsis sp.* only 1960.

Coleoptera

Elmidae

Stenelmis sp.

Diptera

Chironomidae

Pelopiinae

Coelotanypus sp.

Pentaneura sp.

Procladius sp.

Pelopia sp. only 1961.

Chironominae

Tendipes plumosus (Linne)

Cryptochironomus sp.

C. digitatus (Malloch)

Stenochironomus sp.

Polypedilum sp.

Microtendipes sp.* only 1960.

Tanytarsus sp.

Unidentified species*

Culicidae

Chaoborus sp.*

Ceratopogonidae

Palpomyia sp.

Tabanidae

Chrysops sp.

Crustacea

Amphipoda

Hyallela azteca (Saussure) only 1961.

Isopoda

Asellus brevicaudus Forbes only 1960.

Decapoda

Orconectes virilis (Hagen), not taken by dredging but in fish traps in the area.

Mollusca

Gastropoda

Viviparidae

Campeloma sp. (probably *C. decisum* young)

C. decisum Say

Lioplax subcarinata Say

Viviparus intertextus Say

Amnicolidae

Somatogyrus depressus Tryon, most abundant in August 1960 when 291/m² were collected at one station in area H. Much less abundant in 1961.

TABLE 2. Average numbers of organisms/m² in each area, by months

	A	B	C	D	E	F	G	H	Over-all
<i>Hexogenia</i>									
June 1960	520	395	582	364	418	628	884	844	579
1961	48	27	1114	81	32	183	457	318	282
July 1960	209	257	377	219	267	310	497	544	335
1961	5	0	38	0	0	27	97	48	27
Aug. 1960	61	80	128	60	87	59	142	119	92
1961	0	5	0	16	5	5	0	5	5
<i>Tendipes</i>									
June 1960	0	0	0	0	0	0	0	0	0
1961	2427	140	3052	0	0	5	0	0	703
July 1960	1	0	0	0	0	1	0	0	0
1961	135	16	264	0	0	0	0	0	52
Aug. 1960	3	1	0	1	0	0	0	0	1
1961	70	32	16	11	0	0	0	0	16
<i>Coelotanypus</i>									
June 1960	76	51	4	30	9	32	62	26	36
1961	102	86	59	38	81	54	86	16	65
July 1960	8	17	4	19	6	10	30	10	13
1961	0	5	5	11	32	5	11	5	9
Aug. 1960	6	20	8	22	6	72	19	18	21
1961	43	11	16	43	11	32	38	16	26
Leeches									
June 1960	4	2	8	3	9	5	0	0	4
1961	11	11	22	05	54	0	43	27	29
July 1960	7	1	12	4	22	8	5	12	9
1961	0	38	124	27	38	0	11	0	30
Aug. 1960	13	12	25	13	46	17	20	28	22
1961	91	27	22	59	59	16	11	32	40
<i>Sphaerium transversum</i>									
June 1960	339	1536	412	2030	1814	507	4099	2513	1657
1961	2734	2153	237	1173	608	2858	2212	2040	1752
July 1960	249	1622	582	2384	1363	1274	3707	4242	1927
1961	4704	3461	877	1539	2223	3988	2320	4381	2937
Aug. 1960	332	3950	1184	4862	2516	4140	4766	7570	3677
1961	1792	1243	231	823	1582	1981	2476	2088	1527
<i>Campelema</i>									
June 1960	36	26	80	22	60	17	50	34	41
1961	43	27	248	38	86	59	59	54	77
July 1960	13	28	93	15	50	20	53	40	39
1961	48	59	194	75	86	38	118	48	83
Aug. 1960	11	55	80	24	45	46	81	25	46
1961	38	43	102	65	91	32	161	43	72
Other									
Chironomids									
June 1960	9	14	5	27	6	28	9	4	13
1961	86	5	178	5	0	27	43	22	46
July 1960	32	45	14	48	28	64	79	82	46
1961	27	11	32	5	0	86	22	22	26
Aug. 1960	15	45	13	50	15	38	65	39	35
1961	231	11	129	43	48	48	124	124	95
Oreocetes									
June 1961	0	5	0	0	0	0	0	0	1
July 1961	188	54	16	161	75	48	113	118	97
Aug. 1961	16	5	0	5	5	0	0	5	5
Other									
Arthropods									
June 1960	1	3	0	2	1	3	2	3	2
1961	11	0	11	0	0	0	0	0	0
July 1960	1	1	4	2	3	1	3	5	3
1961	27	5	5	5	11	0	0	5	3
Aug. 1960	1	0	2	0	1	0	2	2	7
1961	5	0	5	0	0	5	0	5	2

TABLE 2. (continued)

	A	B	C	D	E	F	G	H	Over-all
<i>Oligochaetes</i>									
June 1960	104	166	36	129	56	109	75	32	88
1961	118	113	38	145	91	135	86	113	105
July 1960	90	240	41	164	30	106	62	36	95
1961	38	70	59	38	59	59	32	81	55
Aug. 1960	129	237	48	184	69	94	103	60	115
1961	54	27	43	43	43	97	48	70	53
Other									
Mollusks									
June 1960	12	17	14	16	93	29	36	29	31
1961	38	22	43	38	16	22	86	48	39
July 1960	3	17	18	12	70	31	36	35	28
1961	113	54	54	81	54	38	48	54	62
Aug. 1960	21	68	57	62	179	170	219	197	122
1961	86	97	135	178	264	124	124	183	149
All Organisms									
June 1960	1101	2210	1141	2623	2465	1356	5216	3493	2451
1961	5619	2589	5000	1582	969	3342	3073	2637	3101
July 1960	612	2227	1145	2868	1840	1819	4472	5004	2498
1961	5285	3773	1668	1943	2578	4289	2772	4763	3383
Aug. 1960	592	4468	1545	5278	2964	4636	5418	8060	4120
1961	2427	1502	700	1286	2110	2341	2982	2573	1990
Overall	2606	2795	1866	2596	2154	2964	3989	4421	2924

S. subglobosus Say (*Birgella* of Baker 1928a)
Amnicola binneyana Hannibal

Physidae
Physa sp.
 Pleuroceridae
Pleurocera sp.

Pelecypoda
Sphaeriidae

Sphaerium transversum (Say), the most numerous organism and the only one collected at every station on every collection date. A maximum of 12,131/m² was estimated at one station in area H in August 1960.

S. striatinum (Lamarck)

Unionidae
Quadrula sp.
Q. quadrula Rafinesque
Actinonaias sp.
Anodonta sp.

A. imbecillis Say (Utterbackia of Baker 1928b)* only 1960.

Lampsilis sp.* only 1961.
Amblema sp.* only 1960.
Lasmigona sp.* only 1961.
Leptodea sp.* only 1961.
Truncilla sp.* only 1960.

Seasonal and Area Variation in Abundance

Although the sampling areas were similar in most environmental conditions, the benthic communities differed somewhat in species composition and in total numbers (Table 2, Fig. 1). Populations were usually highest in areas H, G and F, the three farthest upstream. Dense populations of *Sphaerium transversum* were responsible for much of this, but *Hexagenia* were also usually more abundant in areas F to H than in the other areas.

Area C, which had the lowest population of *Sphaerium*, had the greatest variety of molluscan species. This area

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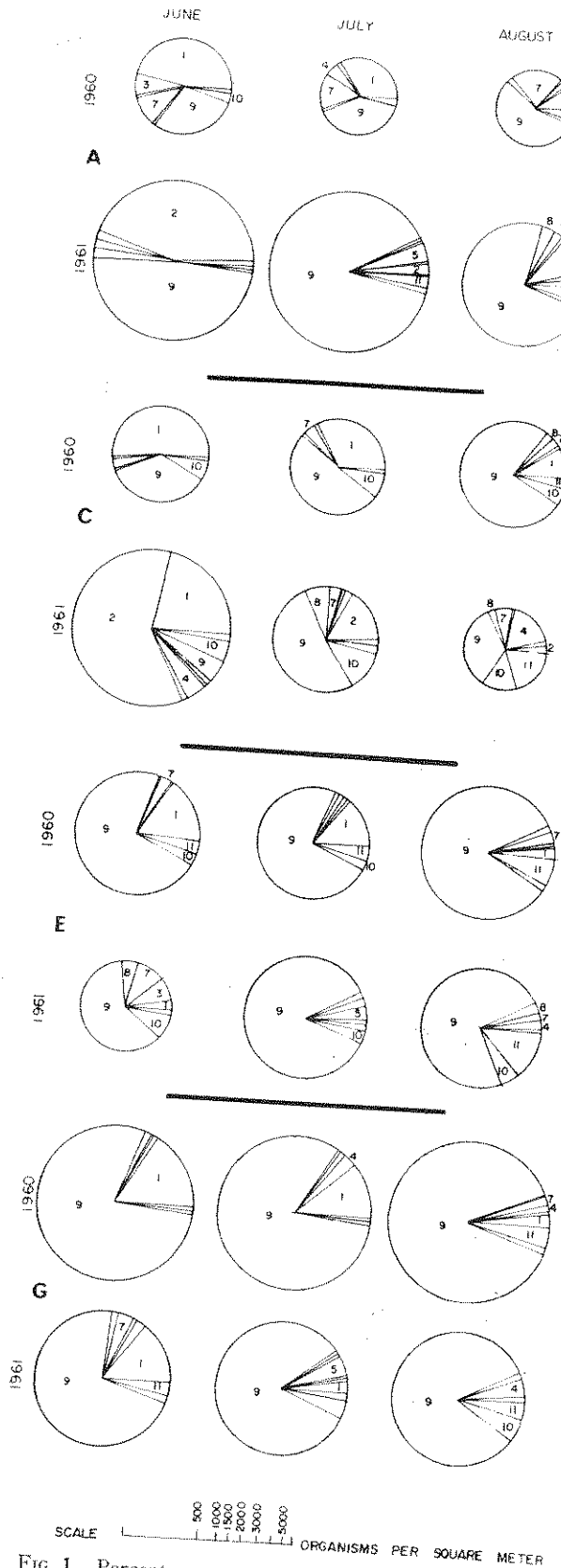


Fig. 1. Percentage composition of the benthos at areas

was near the mouth of a small tributary stream and had a bit more current than the other areas.

Insect populations, which declined during the summer months, generally controlled the abundance of all organisms at areas A through C. At areas farther from the dam, molluscan populations dominated the benthos and maintained their abundance throughout the summers, serving to provide more stable populations.

Hexagenia naiads were generally much more abundant in 1960 than in 1961 throughout the study area. *Hexagenia* were more abundant in 1960 and 1962 in Pool 19 than in 1959, 1961, or 1963 (Carlander, Carlson, Gooch and Wenke 1967). It was estimated that the entire pool had 18.7 billion naiads in June 1960 compared to 6.7 billion in 1961. Naiads were, however, more numerous in June of 1961 than in June 1960, at area C. The decline in *Hexagenia* in June 1961, as compared with early 1960, was more pronounced at sampling areas near Dam 19 than at the part of the study area farthest from the dam (areas G and H). In both 1960 and 1961, a decrease in *Hexagenia* populations through the summer was observed at all sampling areas, the result of emergences throughout the summer months. There was a notable paucity of naiads in August 1961.

In 1961, when *Hexagenia* populations were lower, populations of chironomids and some other benthic organisms generally were higher. *Tendipes plumosus*, rarely found in 1960, became the most abundant organism at areas A through C. Although *Tendipes* appeared to be filling in where *Hexagenia* were absent, large numbers of both *Hexagenia* and *Tendipes* were found in area C in June 1961. At areas above C, *Tendipes* was seldom collected, and there was an increase in numbers of other chironomids in 1961. *Coelotanypus* and *Stenochironomus* were the dominant chironomids at areas above C in 1960 and 1961.

The caddisfly, *Oecetis*, was relatively abundant in 1961 but was scarce, if not absent, in 1960. *Physa* was collected frequently in 1961 but only once in 1960.

Several chironomids (*Stenochironomus*, *Cryptochironomus*, *Procladius*, *Pentamura* and *Pelopia*) were more numerous in July and August than in June before the *Hexagenia*, *Tendipes* and *Coelotanypus* emerged. Leeches (*Helobdella*) and snails (*Somatogyrus*, *Physa* and *Lio-plax*) were also more abundant in July and August. These increases as other forms emerged may indicate efficient use of the available habitat.

DISCUSSION

A limited study of Lake Keokuk (= lower Pool 19) was made in 1930 by Ellis (1931). The bottom fauna in silted areas of the main portion of the lake consisted primarily of:

"... sludge worms, bloodworms, corethra, a few snails of the pulmonate group, tiny bivalves of the genus *Musculium*, and several species of leeches..." (p. 8).

"At a few stations in the lake the larvae of the large May fly, *Hexagenia*" (sic) "were taken, although this species was very much more abundant upriver than in the lake proper."

"Summarizing the bottom fauna of the lake as a whole as shown by a large number of hauls, dredg-

A, C, E and G in June, July and August, 1960 and 1961.
 1. *Hexagenia*, 2. *Tendipes*, 3. *Coelotanypus*, 4. other chironomids, 5. *Oecetis*, 6. other arthropods, 7. oligochaetes, 8. leeches, 9. *Sphaerium transversum*, 10. *Campeloma*, 11. other mollusks.

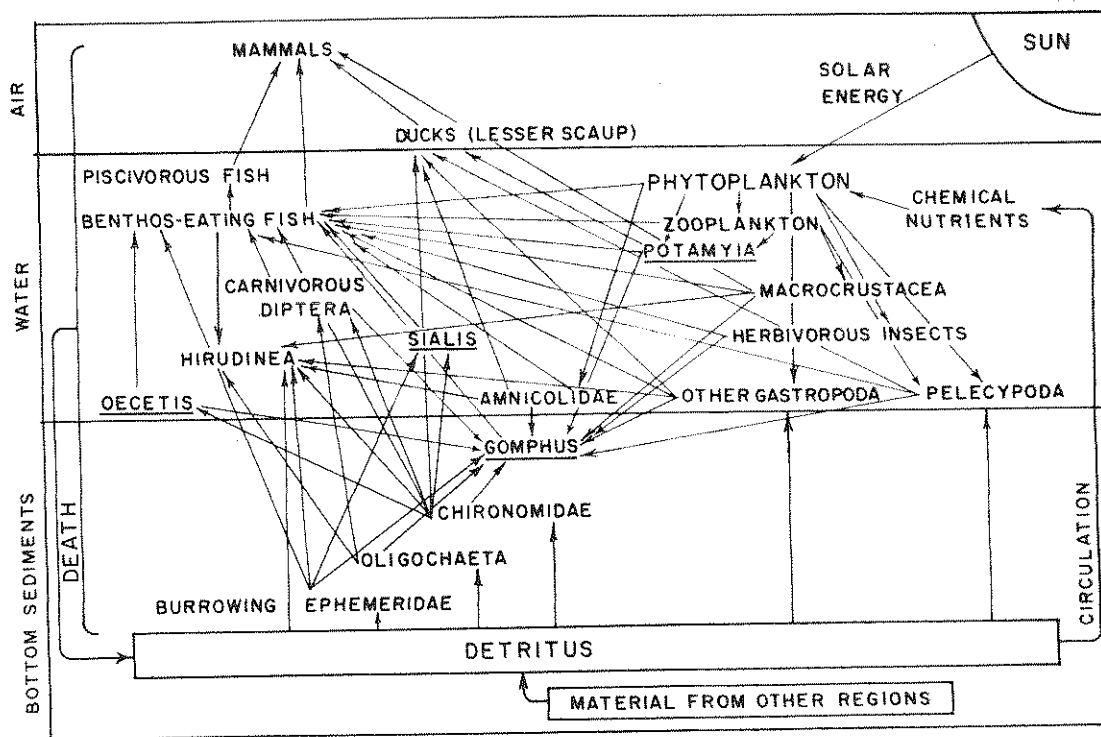


FIG. 2. Diagrammatic representation of the probable nutrient and energy flow in the biological community of mud flats along the eastern shore of the Mississippi River above Dam 19, Keokuk, Iowa.

ings, and samplings during the month of July, 1930, the fauna was found to consist almost entirely of those forms tolerant of low oxygen conditions and, therefore, forms which have come to be regarded as indices of a polluted or biologically unfavorable body of water. The once abundant beds of fresh-water mussels which were worked commercially in the region now covered by Lake Keokuk before the rection of the dam have all disappeared."

The major elements in the benthos show little change from 1930 to 1960-61. Since the 1930 samples were taken only in July, *Hexagenia* may have already emerged and thus been underestimated.

The benthic community in Pool 19 corresponds closely to that defined by Gersbacher (1937) as the *Hexagenia-Musculium-Viviparus* community characteristic of the climax in large rivers.

On the basis of food habits described in the literature and observations in the study area, the principal channels in nutrient and energy flow are tentatively diagrammed (Fig. 2). With the exception of *Tendipes* sp., all of the most abundant organisms collected were detritus-feeders. In general, strictly herbivorous, omnivorous and carnivorous organisms were less abundant. The number of genera classified as consumers of detritus also greatly exceeded those otherwise classified. Detritus seems to be the major source of basic food of this benthic community, indicating the community probably depends heavily on imported material.

The benthos does not indicate pollution damage as severe as some other areas of the Upper Mississippi (Fremling 1964). Among the dominant benthic organisms collected at Keokuk were the following considered by Richardson (1928) as pollutional: *Limnodrilus hoffmeisteri* and *Tendipes plumosus*; as subpollutional, *Sphae-*

rium transversum; and as clean water species, *Hexagenia bilineata*. Other less abundant organisms taken at Keokuk are representative of conditions from subpollutional to clean water.

Studies of benthos of the Mississippi just below Minneapolis-St. Paul (Wiebe 1927) and in Lake Pepin (Johnson 1929, Johnson and Munger 1930) indicated significant pollution before 1930. *Tendipes*, tubificids and sphaeriid mussels had become quite abundant, and mayflies were scarce or absent. Collections taken above Minneapolis and below Lake Pepin (Wiebe 1927) were more similar to those taken above Dam 19. In lakes adjacent to the Mississippi near Quincy, Illinois, Dorris (1958) found benthic communities quite different from those encountered in the study area near Keokuk. The lakes yielded far greater numbers of organisms per unit area than the study area.

Few studies of benthos of other large, lowland rivers are available for comparison with the study area. Mississippi bottom fauna above Dam 19 resembled that of comparable regions of the Illinois River, before it began to receive increased sewage pollution (Richardson 1921b). The study area was more productive (on the basis of total number of organisms collected per unit area) than all lake, channel and shallow-water areas studied by Richardson, with the exception of the region between Liverpool and Havana. With the advent of increased sewage pollution in the Illinois after 1915, similarity to the study area declined as mollusks and most arthropods decreased in abundance, and tolerant oligochaetes and chironomids became more numerous (Richardson 1921a). Richardson's final tabulated data show numbers of organisms per unit area at many collection sites on the Illinois far surpassed those collected at the study area, and that they were largely composed of tubificids and sphaeriids (Richard-

son 1928). Evidence of slight improvement in water quality in the Illinois in 1925 was reported by Richardson (1928). Paloumpis and Starrett (1960) reported, after study of organisms collected in some of the same flood-plain lakes studied by Richardson, that conditions had further improved since 1925. Most of the organisms collected at the study area were also taken in these lakes adjacent to the Illinois, but the latter contained far greater densities of oligochaetes and more organisms per unit area.

Berner (1951) found that the lower Missouri River harbored very little benthos and attributed this to high turbidity and current velocity. Dipterous larvae (mainly chironomids), trichopterous larvae and aquatic annelids were the only important constituents of the benthos. Only 750 organisms were collected in 130 Petersen dredge-hauls between April and October 1945.

Few quantitative studies of benthos of large lowland rivers of Europe are available for comparison with the impounded Upper Mississippi. Behning (1928) reported that mud sediments of the Volga River in Russia contained at least 300 organisms/m², far below the average (2924) collected/m² near Keokuk. Bays and side-channels of the Volga had thicker mud deposits and harbored an average of 400 individuals/m². Taxonomic composition of the benthos above Dam 19 was more similar to that of the bays and side-channels of the Volga than to that of mud sediments of the river. Mikulski (1961) collected up to 1650 individuals/m² of sediments from habitats behind regulating dams on the Vistula River in Poland. Chironomidae (including *Tendipes plumosus*), oligochaetes and mollusks were the most abundant groups collected.

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GLUCONEOGENESIS IN THE ORIENTAL HORNET *VESPA ORIENTALIS*¹ F.

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Abstract. Adults and larvae of the Oriental Hornet (*Vespa orientalis* F.) have been fed on C¹⁴-labeled protein, derived from Chlorella, in order to determine to what extent such protein may be converted into carbohydrates. Only larvae were found capable of converting the labeled protein. Products of this conversion were the sugars glucose, fructose and sucrose, and also tri- and tetrasaccharides as yet unidentified. It is suggested that this ability of the larvae to carry out gluconeogenesis and the subsequent transfer of the formed sugars to the adults (in saliva droplets) may play an important part in the adult-larva interrelations of various insect societies.

INTRODUCTION

It is a well known fact that the intact body of animals is capable of converting a great variety of compounds into glycogen. Fructose, mannose, galactose and glycerol are among the active precursors in such reactions. That the ingestion of proteins by vertebrates results in increased glycogen content of the liver, a subject of controversy in the early part of this century, is now generally accepted (Krebs 1964). It is also now recognized that gluconeogenesis from protein is dependent on the gluconeogenic properties of the individual amino acids which make up the protein molecule.

The ability of the insect fat body to interconvert metabolites is well demonstrated by the works of Clements (1959) and Hines and Smith (1963) in which locust fat body was incubated with labeled glycine, leucine, acetate, glucose or succinate, leading to the formation of a wide range of labeled products, including Krebs-cycle acids, amino acids, sugars and fats. It has been observed by Bursell (1963) that in flying diptera, e.g., tsetse flies, proline is rapidly removed from the circulation, thus suggesting conversion of the amino acid to carbohydrate. Furthermore, Lipke *et al.* (1965) have proved that a high rate of conversion of proline to trehalose characterizes the intermolt period in *Periplaneta americana*.

The present communication is intended to contribute to an understanding of gluconeogenesis in insects. We considered it of interest to determine whether there were differences in this respect between the adult and larval stages, especially in insects in which these stages maintain constant food-exchange relationships (trophallaxis). Such exchange of food materials is known to exist among hornets. It has been shown by Wheeler (1928) that adults feeding the larvae obtain from them a drop of

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saliva in return. A similar phenomenon exists also among ants, where the adults constantly lick the bodies of the larvae, as well as among termites.

Brian and Brian (1952) who studied trophallaxis in colonies of *Vespula sylvestris*, maintain that "larvae do secrete sugar, notably glucose, but in such dilute concentrations that the solution in itself is not attractive to adults." They therefore conclude that "the glucose appears to have no social significance. It may be a vestige of an earlier stage in social evolution, or perhaps a co-enzyme, or merely an unavoidable leak." Montagner and Courtois (1963) observed that hungry workers in hornets' nests do require food from the larvae, but that this phenomenon is not of primary importance for the maintenance of the colony. Montagner (1964) further notes that the males are incapable of feeding by themselves and subsist solely on food provided by the larvae. Ishay (1964) observed that the males tend and also feed the larvae, and are in turn fed by them. Morimoto (1960) has verified the findings of Brian and Brian (1952) by feeding radioactive P³² to *Polistes* larvae and examining their secretion at successive time intervals. No activity was noted during the first 30 min, but after 3 hr the radioactivity of the larval saliva reached a maximum. Adults examined after contact with treated larvae showed variable radioactivity, thus confirming the passage of saliva to adults. Maschwitz (1966) also reports that "the larval saliva is highly nutritious, containing about 9% sugars and considerable quantities of amino acids." Using radioactive tracers, this author discovered that only a few of the larvae serve as a source of the liquid and that only these provide saliva for the entire community, including other larvae which had not been "marked" for this function.

In colonies of *Vespa orientalis* grown under laboratory conditions, it is possible to observe the food exchange between the adults and larvae. Such food exchange is especially noticeable on rainy autumn days when the hornets are unable to forage for outside food. They are then observed to pay frequent visits to the larvae, tickling