populations of *P. cinerea* were larger during winter, whereas those of *P. pergandii* reached their relative peaks in the summer. This held true for both groves sampled, and for the entire period of the study. Such a situation is entirely different from all other interrelationships hitherto reported, whereby one species of scale insects completely displaces the other.

It seems safe to conclude at present that the populations of these 2 diaspidids have reached a certain degree of equilibrium. It is not, however, possible to infer whether this is only a temporary state of affairs, or if the 2 populations have already stabilized.

As the 2 diaspidids apparently infest all above-ground parts of the citrus trees to an equal degree, they may be considered to be the true homologues as to their feeding and settlement requirements. In this respect they differ from the 2 species of *Aonidiella* discussed. *A. aurantii* infests all above-ground parts of the citrus trees, but *A. citrina* infests only the leaves and fruits (Flanders 1956, DeBach and Sundby 1963).

During a concurrent investigation (Gerson 1964) it was found that both species of *Parlatoria* are parasitized by the same 2 hymenopterous species, and preyed upon by various predators. But no clear evidence was found to indicate differential parasite or predator action on these scale insects.

A partial explanation for the observed interrelationships between the 2 species of *Parlatoria* may be obtained from studying their geographical distribution. *P. pergandii* infests citrus trees almost wherever these are grown, whereas *P. cinerea* was collected, from the same plant-host, mostly in humid tropical regions (Morrison 1939). These differences in distribution suggest that the 2 species differ somewhat in their relative tolerance to desiccation. In Israel a dry and hot summer follows the cold, wet winter. Thus cyclic, seasonal changes in climatic conditions annually modify the habitat, determine which *Parlatoria* sp. will be dominant, and enable the coexistence of these species. Possibly similar relationships exist between other, closely-related species, helping to explain their coexistence in the same ecological niche.

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POPULATIONS OF *HEXAGENIA* MAYFLY NAIADS IN POOL 19, MISSISSIPPI RIVER, 1959–1963[1]

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Abstract. June populations of *Hexagenia* naiads in Pool 19 of the Mississippi River were estimated at 3.6, 18.7, 6.7, 23.6 and 11.9 billion in 1959 to 1963, suggesting an alternate year cycle of abundance. Although population density varied in different sections of the river, little pattern was evident. Water depths from 0.5 to 6 m and bottom deposits from soft mud to soft muds with shells or plant debris had little consistent relation to population density. Sand and gravel areas had few or no *Hexagenia.* Naiads increased in average size in June. In late July after major emergences, there were few naiads collected, but small naiads increased in August. Flood may have shifted part of the population in 1960. *Tendipes plumosus* larvae were more abundant in 1961, when *Hexagenia* populations were lower, than in 1960. Usually *H. limbata* was the more abundant species (among naiads over 16 mm) in early June and in August and *H. bilineata,* in late June and July. Sex ratios were usually near 50:50.

INTRODUCTION

The problems caused by large emergences of mayflies along the Mississippi River are not particularly ephemeral, although the adult insects are. Towboats have been forced to tie off along the river banks because of the attraction of mayflies to their powerful arc and mercury vapor searchlights. A towboat captain reported that his radar was "blacked out" for 3 hr before daybreak, July 12, 1959 by heavy mayfly concentrations between Galland and Fort Madison, Iowa. Highway bridges have been closed

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because the roadbeds were slippery from mayfly bodies. Lighted baseball parks, picnic areas, boat docking facilities, and other recreational areas are unusable during heavy emergences. Mayfly bodies pile up under street lights or at shop windows and, if not removed, may create odor and health problems. Many people are allergic to dried subimaginal cuticles and mayflies (Figley 1940, Parlato 1938).

Although the mayflies create a nuisance and hazard when abundant, they are food for fish, bats, birds, and possibly other animals. Hoopes (1960) found mayflies constituted over ½ of the summer food of channel catfish, freshwater drum, mooneyes, goldeyes, and white bass in the Mississippi River study area.

The Mississippi River from St. Paul, Minnesota, to St. Louis, Missouri, is a series of pools created by dams constructed by the U. S. Army Engineers (Carlander 1954). The quiet waters of the pools and the silty bottoms are very productive of large *Hexagenia* mayflies (Fremling 1960). Pool 19, from Burlington to Keokuk, Iowa, was selected for a study of the abundance and distribution of *Hexagenia* naiads.

Materials and Methods

A transect was established in each of 3 portions of Pool 19, selected after field observation and study of navigation charts (Fig. 1, Table 1). The upper 20 miles has many islands and sloughs adjacent to a rather narrow main channel, in which the current is sufficient to prevent much deposition of silt. The middle 22-mile section is about a mile wide and has little current except in the navigation channel and adjacent water. The lower 3.5 miles might properly be called Lake Keokuk and has more extensive areas of mud bottom. More description of the transects and sampling stations is given in a Master of Science thesis on file in the Iowa State Library (Carlson, C. A. Jr. 1960. Abundance of mayfly naiads (*Hexagenia* spp.) in Pool 19, Upper Mississippi River. 90 pp. typewritten).

Quantitative samples of naiad populations were taken with a 15.5 by 15.5 cm Ekman dredge. Four dredge hauls were taken at each station on each sampling date. All naiads collected in a screen washing pail (Fremling 1961)

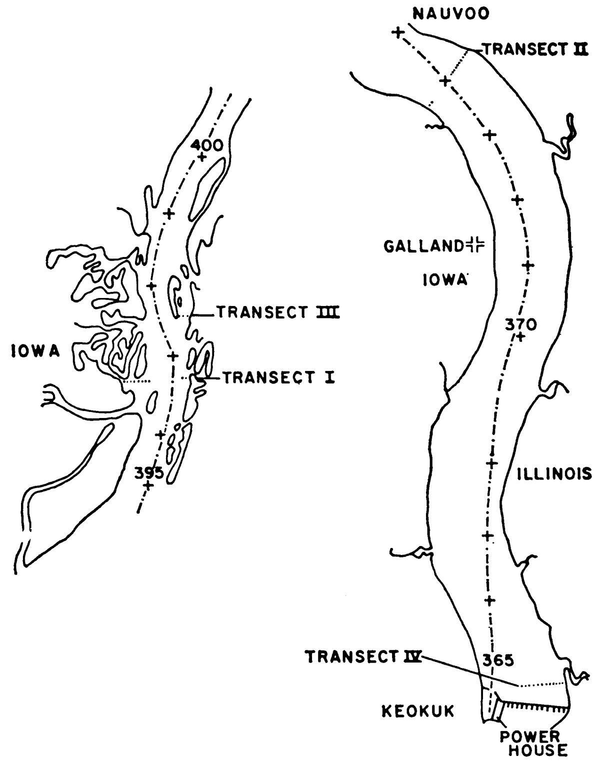

FIG. 1. Location of transects in Pool 19 of the Mississippi River. Miles numbers are indicated in the navigation channel.

TABLE 1. Description of Transects I, II, and IV, as of June 1959

	Estimated length in meters	Number of stations	Water depth in meters	Bottom type
Transect I Upper Pool[1]				
Section I	61	4	0.6–1.0	Soft mud or soft mud and plant debris
Section II	49	4	0.5–0.6	Same as above
Section III	15	1	3	Soft mud, debris and snails
Section IV	15	1	1.5	Soft mud
Unsampled[2]	15	0		
Unproductive	640	0		Hard sand and gravel
Transect II Middle Pool[1]				
Section I	64	3	.6–1.0	Soft mud and shells
Section II	244	8	1.0	Soft mud or soft mud and shells
Section III	61	1	3–6	Same as above
Section IV	30	2	2–3	Soft mud to soft mud and plant debris
Unsampled[2]	214	0		
Unproductive	823	0		Hard sand and gravel
Transect IV Lower Pool				
Sampled	690	16	1.2–3.7	Soft mud
Unsampled[2]	274	0		
Unproductive	640	0		Hard sand and gravel

[1] The sections are numbered as they extend from the Iowa Shore in Transect I and from the Illinois shore in Transect II. The channel is between Section III and IV in both Transects I and II.

[2] On the basis of limited sampling and observations, the unsampled area of Transect I was assumed to have bottom fauna similar to Section IV, that of Transect II similar to an average of Sections I, II and III, and that of Transect IV to the sampled area. These unsampled areas were in somewhat deeper water and were exposed to wind action which prevented adequate sampling.

were placed in 3-inch sections of glass tubing and preserved in 75% ethanol. Naiads were measured with a vernier caliper to the nearest mm from the tip of the frontal projection of the head to the end of the last abdominal segment, excluding caudal filaments (Hunt 1953).

For each collection date, numbers of naiads/sq m^2 in each section and in a strip 1 m wide at each transect across the river were estimated.

Data collected at the transects were considered similar to those that might have been collected at other parts of the upper, middle, or lower portions of the pool. The estimate for each strip was multiplied by the length of that portion of the pool.

Abundance of *Hexagenia* by Sections within Transects

Transects I and II were each divided into 4 sections on the basis of location and water depth, but Transect IV was uniform enough to be considered as a whole. Analyses of variance (as in Snedecor 1956, section 10.7) were employed to determine whether there were significant differences in the numbers of naiads in various sections of Transects I and II. To adjust for non-additivity and heterogeneity of variance introduced by the frequency of zeros, a sq root transformation of the data was employed. The number of mayflies collected in each dredge was increased by 0.5, and the sq root of the sum was used in the analysis.

Analysis of the data obtained at Transect II on June 17, 1959, yielded mean squares of 16.5533 for sections (3 degrees of freedom), .2018 for stations in the same section (11 degrees of freedom), and .1797 for dredges in the same station (45 degrees of freedom). An F value of 82.03 indicates highly significant section effect, but an F of 1.12 indicated that station effect was not significant at the 95% level.

In the upper transect, sections III and IV were combined for this analysis since, on June 30, collections from these sections were similar. (The June 30 collection is not included in the later analysis because storms prevented completion of other transects.) Analysis yielded mean sq values of 6.7050 for sections (2 degrees of freedom), .2628 for stations within sections (7 degrees of freedom), and .1450 for dredges in the same station (30 degrees of freedom). An F value of 25.51 was obtained from the test for section effect and 1.81 for station effect. Again we concluded that there was a significant difference between sections but not between stations of the same section.

These analyses indicate that at least prior to emergence in 1959 the separation of the transects into sections was valid. In most other collection periods there were equally significant differences between sections. Abundance of naiads showed different seasonal and annual changes in the various sections (Tables 2 and 3). In the June collections in Transect I, section I was the most productive in 1959 and 1961 but section II had the highest populations in 1960 and 1962. Section IV, which was lowest in 1959 and 1960, had quite a high population in 1961. In Transect II, section IV was highest each June but the other sections varied greatly from year to year. Section IV was the rather narrow band of suitable bottom on the Iowa side of the channel.

The July and August populations were usually low because of large emergences early in July. Section IV in Transect I and Sections III and IV in Transect II show relatively high populations in these months because of recruitment of small naiads.

Table 2. Average number of *Hexagenia* naiads per square meter in Sections of Transect I, 1959 to 1963

Date	Section I	Section II	Section III	Section IV
1959				
June 16	183	62	22	0
23	191	59	0	22
July 7	100	24	11	11
14	145	0	0	0
28	11	3	0	75
Aug. 11	5	0	0	151
18	8	0	0	205
25	8	3	0	323
1960				
June 24	73	519	86	11
July 27	11	46	0	377
Aug. 18	32	105	11	226
1961				
May 30	404	81	140	280
July 14	145	75	0	54
Sept. 1	11	46	11	32
1962				
June 27	186	474	0	70
July 23	19	13	0	0
Aug. 17	0	0	0	0
1963				
June 12	19	24	0	32
July 12	13	11	0	5
Aug. 13	0	19	0	43

Table 3. Average number of *Hexagenia* naiads per square meter in Sections of Transect II, 1959 to 1961

Date	Section I	Section II	Section III	Section IV
1959				
June 17	90	44	86	1292
24	65	58	129	1076
July 6	32	1	11	140
13	18	4	32	43
30	4	11	108	86
Aug. 10	0	8	280	32
17	0	19	54	0
24	0	9	22	312
1960				
June 10	865	486	527	947
July 22	517	188	129	140
Aug. 22	75	69	86	70
1961				
June 2	201	88	291	969
July 13	4	18	161	118
Aug. 30	40	8	97	694
1962				
June 26	606	772	775	920
July 24	72	191	11	81
Aug. 17	18	105	151	43
1963				
June 14	391	387	635	1,491
July 11	22	200	248	554
Aug. 14	0	11	11	43

Since large populations were found in each section there is no evidence that water depth, from 0.5 to 6 m, had any significant effect on abundance. Hard sand and gravel bottoms supported few or no *Hexagenia,* but the

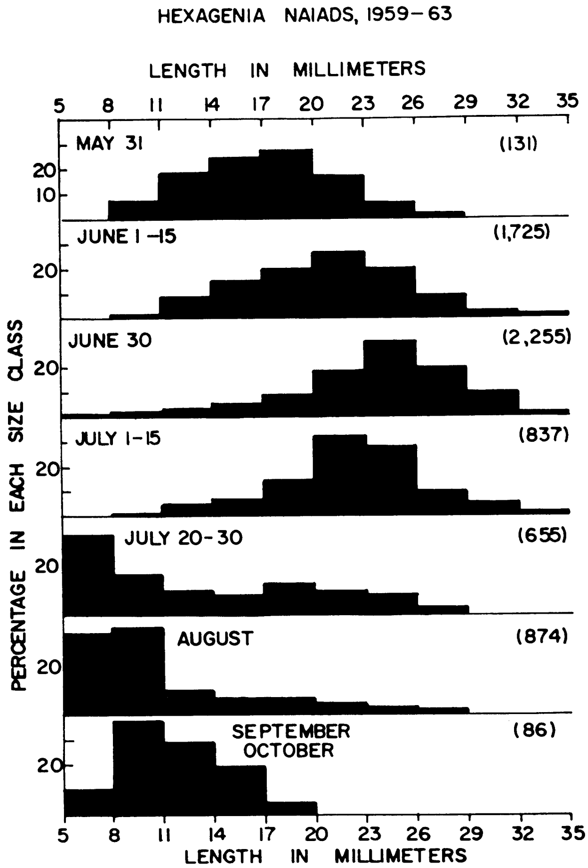

FIG. 2. Length frequencies of naiads at various periods in the summer. Data from various years, 1959 through 1963, and sections combined. The May 31 collection was only in 1961, in Transect IV; and the September and October samples, only in 1959 from near the dam at Keokuk. Number of specimens measured is in parentheses.

soil types in the more productive sections, ranging from soft muds to soft muds with shells or plant debris, seemed about equally favorable. These bottom deposits had 2.5 to 6.7% organic matter, as determined by the Iowa State University Soils Laboratory.

Size Distribution of Naiads

During June the average sizes of the naiads increased (Fig. 2). In late June and early July as the subimagoes emerge, the average size did not increase but the proportion of naiads under 20 mm in length decreased. In late July and August there were few large naiads and the young naiads reached a size to be retained by screens.

In June 1959, the deeper water stations near the river channel in Transects I and II had larger naiads than in the shallower areas (Fig. 3). By July 6 to 9 most of these had emerged and the larger naiads were mostly in the shallow water. In late July and early August few naiads were collected at any station. By mid-August, there was a marked increase in small naiads at the deep water stations. The 1962 and 1963 size distributions in these same sections showed similar trends to those noted in 1959 (Fig. 4). The 1960 and 1961 samples were not examined for these features.

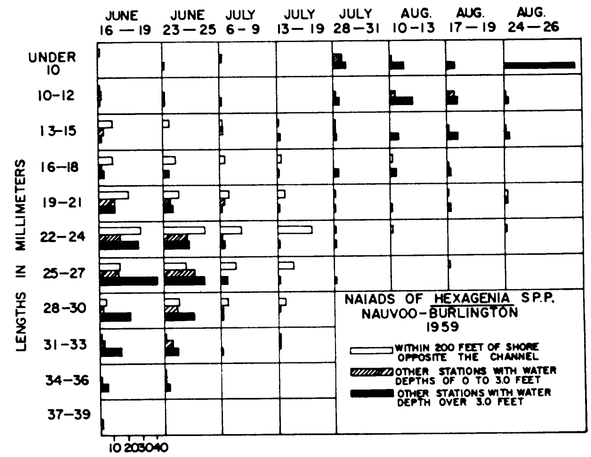

FIG. 3. Numbers of *Hexagenia* naiads, by size groups, in various sections of Transects I and II as the 1959 summer progressed.

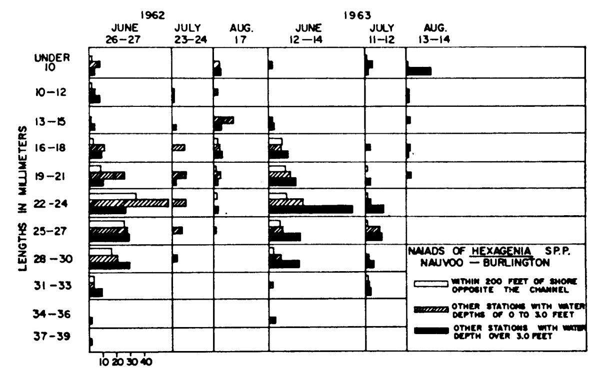

FIG. 4. Numbers of *Hexagenia* naiads, by size groups, in various sections of Transects I and II in 1962 and 1963.

Since it is unlikely that there is a seasonal difference in egg deposition at various depths, it is suggested that there is faster growth and growth to an overall larger size at the deep water stations. This may be due to small differences in bottom type (not evident in the soil analyses) which are dependent on the current. The current may also be involved in providing a more constant supply of nutrients to naiads at the deep stations.

Annual Abundance of Naiads

In 1959, over 3.5 billion naiads were present in the pool before the major emergences of July (Table 4). The estimated population dropped to near 700 million in mid-July after the major emergences. The slight increase in population noted in late July and August probably resulted from increased collection of small naiads that had reached sufficient size to be retained by the screen in the pail used in sampling. Although 3.5 billion in 1959 seemed a high population, later collections indicated that the population was relatively low in 1959. Several lockmasters and other persons along the river remarked that mayflies emerging in 1959 were less abundant than usual.

June populations were estimated at 18.7 billion in 1960 and 23.6 billion in 1962. The lower populations in 1961 and 1963, 6.7 and 11.9 billion, suggest a possible two-year cycle of abundance.

TABLE 4. Numbers of *Hexagenia* naiads per square meter of suitable bottom in various transects and estimated number of naiads in Pool 19, Mississippi River, 1959 to 1963

	Mean number per square meter			Estimated total in millions
	Upper Transect	Middle Transect	Lower Transect	
1959				
June 16–19	93	121	52	3,622
June 23–25	98	122	45	2,629
July 6–9	50	17	24	769
July 14–16	57	15	9	707
July 28–31	20	34	2	925
Aug. 10–13	32	69	1	1,817
Aug. 17–19	43	22	0	726
Aug. 24–28	67	24	1	916
1960				
June 9–24	168	604	647	18,746
July 15–27	92	249	414	8,628
Aug. 11–18	91	74	101	2,770
1961				
May 30–June 2	252	200	133	6,733
July 13–15	91	51	4	1,713
Aug. 29–Sept. 1	26	67	0	1,704
1962				
June 25–27	235	752	823	23.582
July 23–25	12	138	305	5,003
Aug. 17–19	0	95	277	3,767
1963				
June 12–14	21	477	75	11,890
July 10–12	10	194	44	4,920
Aug. 10–13	14	10	0	321

In 1959 and 1961, years of low population, the June population density of the upper pool was greater than that of the lower pool, whereas the reverse was true in 1960 and 1962, years of high population. In 1963, population density in both areas was low. Since Transect II represented most of the pool, the difference in total population was only moderately affected by population density in Transects I and III.

Although naiads were more abundant in 1960 than 1961 in the pool as a whole, populations in the upper pool were lower in 1960 than 1961. Severe flooding in the spring of 1960 may have destroyed much naiad habitat in the upper pool. Bottom sediment at several stations in Transect I were more sandy than in 1959. Naiads also may have been washed downstream by flood currents. Denham (1938) reports that *Hexagenia* were washed from their burrows at abrupt rises in stream levels.

Midge larvae *Tendipes plumosus,* were abundant in the lower pool in 1961 but few were collected in 1960. (Data are not available for other years.) *Tendipes plumosus* larvae are more tolerant to anaerobic conditions (Mundie 1957) and to pollution (Richardson 1928) than are *Hexagenia* naiads (Britt 1955). The decline of *Hexagenia* in 1961 may have resulted from temporary oxygen depletion which the *Tendipes* were better able to survive. Possibly the *Tendipes* were favored by the low abundance of *Hexagenia.* Midges and oligochaetes increased with decline of *Hexagenia* in Lake Erie (Britt 1963).

SPECIES COMPOSITION

Although *Hexagenia bilineata* and *H. limbata* were recognized on emergence from Pool 19, there was difficulty in identifying the naiads. The shape of the frontal processes used in keys by Burks (1953) and Hamilton (1959) did not prove diagnostic as a full range of intermediate shapes were found. Later in the study it was discovered that naiads of the two species over 16 mm in length usually could be separated on the basis of the tarsal spines (Gooch 1967).

Most of the naiads large enough to identify in the early June and in the August collections were *Hexagenia limbata,* but *Hexagenia bilineata* dominated in the late June and July collections (Table 5). *H. limbata* generally emerges earlier in the season than *H. bilineata* in the Mississippi River (Fremling 1960) and presumably the naiads reach 16 mm length earlier than those of *H. bilineata.*

TABLE 5. Percentage of identifiable *Hexagenia* naiads which were *H. bilineata.* (Numbers of *H. bilineata* and *H. limbata* identified in parentheses)

	Transect I	Transect II	Transect IV
June 8-11, 1959	(112) 12.5	(44) 34.1	(178) 24.2
June 16-19, 1959	(12) 41.5	(85) 60.0	(15) 53.3
June 23-25, 1959	(23) 56.5	(118) 80.5	(40) 90.0
June 30-July 9, 1959	(67) 73.1	(30) 96.7	(38) 97.4
August 25, 1959	(2) 0	—	—
June 9-24, 1960	(86) 50.0	(62) 27.4	(623) 3.9
July 15-27, 1960	(8) 37.5	(45) 60.0	(532) 70.9
August 11-18, 1960	—	(22) 9.1	(90) 0
May 30-June 2, 1961	—	(53) 17.0	(81) 0
July 13-15, 1961	(42) 83.3	(20) 45.0	—
June 25-27, 1962	(121) 94.2	(231) 93.0	(1126) 71.0
July 23-25, 1962	(5) 100.0	(60) 81.6	(149) 82.5
August 17-19, 1962	—	(20) 0	(22) 0
June 12-14, 1963	(16) 68.8	(218) 57.3	(100) 47.0
July 10-12, 1963	(7) 71.4	(106) 99.1	(62) 95.2
August 10-13, 1963	(3) 66.7	(4) 100.0	—

In 1959, the upper portion of the pool seemed to have a higher percentage of *H. limbata* than the other areas, but this difference in distribution was not evident in the other years. *H. limbata* becomes the more abundant species farther up the Mississippi River (Fremling 1960, 1964). The two species were frequently taken in the same dredge sample and nothing can be said about possible differences in the niches of the naiads at this time.

Annual differences in species composition are difficult to evaluate from these data because of the magnitude of the seasonal differences. Both species emerge in varying numbers each month from May to September.

SEX RATIO

Sex of naiads over 10 mm in length could be readily determined by the presence of genital appendages on the penultimate segment of the males. The sex ratios did not differ from 50:50, at the 95% level of confidence, except in three samples (Table 6). In 1959 male *H. bilineata* outnumbered females and in 1960 and 1962 female *H. limbata* outnumbered males. The reasons for these differences are not known.

DISCUSSION

The broad mud flats of Pool 19 provide much suitable habitat for *Hexagenia* naiads. The mayfly population is probably higher than it was before 1913 when the first

TABLE 6. Sex ratios of *Hexagenia* naiads over 10 mm

	Males to females	Percent males
Hexagenia bilineata		
1959	147:58	71.7*
1960	244:233	51.2
1961	23:24	44.2
1962	601:675	47.1
1963	153:118	56.0
Hexagenia limbata		
1959	149:134	52.3
1960	386:556	41.0*
1961	67:75	47.2
1962	172:247	41.1*
1963	61:68	47.2

*These are the only three which can be said with 95% confidence to differ from 50:50.

dam was completed at Keokuk. There had been natural impoundment of the river in this area but raising the water level greatly increased the silt bottom area needed by *Hexagenia* naiads. At low water stage the impoundment covers 150 km^2 compared with 90 km^2 prior to the dam construction (Carlander 1954). Ellis (1931) reported *Hexagenia* as scarce in Lake Keokuk (Pool 19) but his sampling, in July 1930, may have been after the major emergences.

The abundance of *Hexagenia* naiads suggests that this section of the river has not been greatly damaged (in a biological sense) by pollution. This does not mean that some species have not suffered, but *Hexagenia* naiads are considered relatively sensitive to low dissolved oxygen and to various pollutants. *Hexagenia* have been eliminated by unfavorable conditions in Lake Erie (Britt 1963), in the Illinois River (Mills, Starrett and Bellrose 1966), and in the Mississippi River below the Twin Cities and below St. Louis (Fremling 1964).

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LEOPARD SEAL PREDATION ON ADELIE PENGUINS

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Abstract. Systematic observations on a beach at the Cape Crozier, Antarctica Adelie Penguin (*Pygoscelis adeliae*) rookery provided data on the effects and form of Leopard Seal (*Hydruga leptonyx*) predation on adult and young penguins. Active predation, involving up to four seals, was observed during 56% of the time with average kill rates of 0.61 birds/hr.

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