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Environmental synchronization of mass *Hexagenia bilineata* (Ephemeroptera) emergences from the Mississippi River

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With 2 figures in the text

The burrowing mayfly (*Hexagenia bilineata* Say) was reported to be abundant along the Upper Mississippi River as early as 1863 by Walsh and 1890 by Garman. Their abundance, however, has apparently been increased by the construction of 27 navigation dams along the Upper Mississippi River between Minneapolis, Minnesota, and St. Louis, Missouri. Most of the dams were constructed during the 1930's. The silted impoundments afford excellent *H. bilineata* habitat and the insects often cause severe nuisance problems in river cities (Fremling 1968). The biology of *H. bilineata* has been reviewed by Needham, Traver & Hsu (1935) and by Fremling (1960).

Earlier workers (Needham 1920, Coker 1929) observed that mass emergences of *H. bilineata* often encompassed large expanses of the river. In an effort to discover the factors which coordinate the mass emergences, specimen vials and collecting instructions were distributed to ship captains, lock masters and other cooperators during the years 1957—1968. Over 1, 000 mass emergences have been reported during the 12-year study period. The data indicate (Figs. 1, 2) that *H. bilineata* apparently emerge en masse along most of the Upper Mississippi River at intervals of 6—11 days and that a single mass emergence often occurs coincidentally along a 1000-km expanse of river. The aforementioned pattern of emergence is not as obvious every year as it was in 1960 and 1963, but similar results have been reported for the years 1958 and 1966 (Fremling 1964, 1968).

Many factors operate together to coordinate the synchronous emergences. Emergence from a water environment can be expected to be better synchronized than from a terrestrial environment because temperature, light and substrate are generally more uniform in an aquatic habitat. The Upper Mississippi River provides an unusually uniform habitat. Although the river runs in a north-south direction, water temperatures (as determined from water intakes of power plants) are surprisingly similar over the entire study area. The average daily summer water temperature at St. Cloud, Minnesota, is only 2° C less than it is at St. Louis, Missouri, even though the two cities are 1295 river-km apart. The gradient of the river is very low and it drops only about 97 m from Pool 2 at Minneapolis to Pool 27 at St. Louis. Because of its north-south direction, large expanses of the river are influenced by weather systems which generally move from west to east. The silted navigation pools are about the same width because they occupy the vast flood plain of the glacial Mississippi River. From Minneapolis, Minnesota, to Dubuque, Iowa, the river lies at the bottom of a steep-sided canyon whose walls are as much as 166 m high. Throughout this river segment, phenological events in spring generally occur earlier than they would at the same latitude on the uplands.

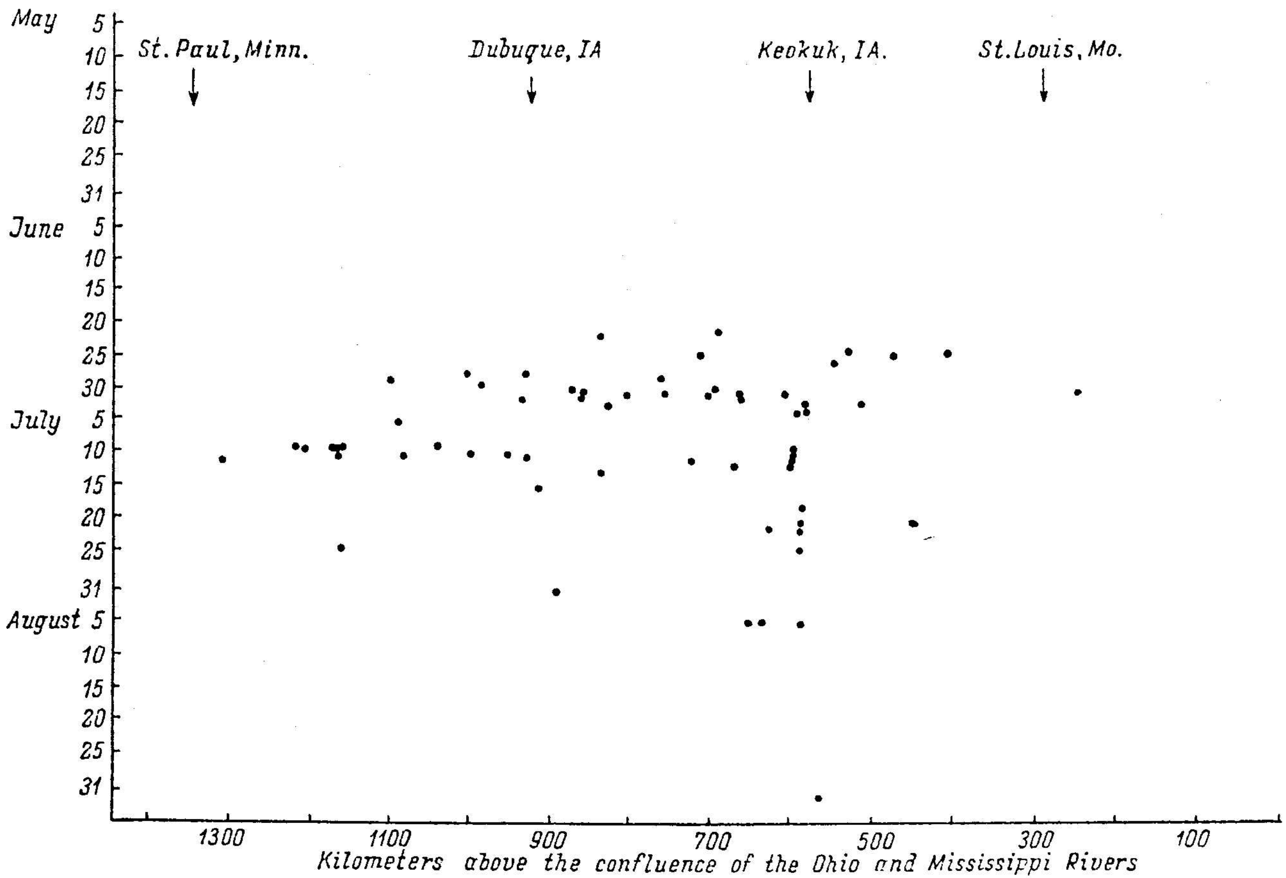

Fig. 1. Locations and dates of *Hexagenia bilineata* emergences on the Upper Mississippi River in 1960.

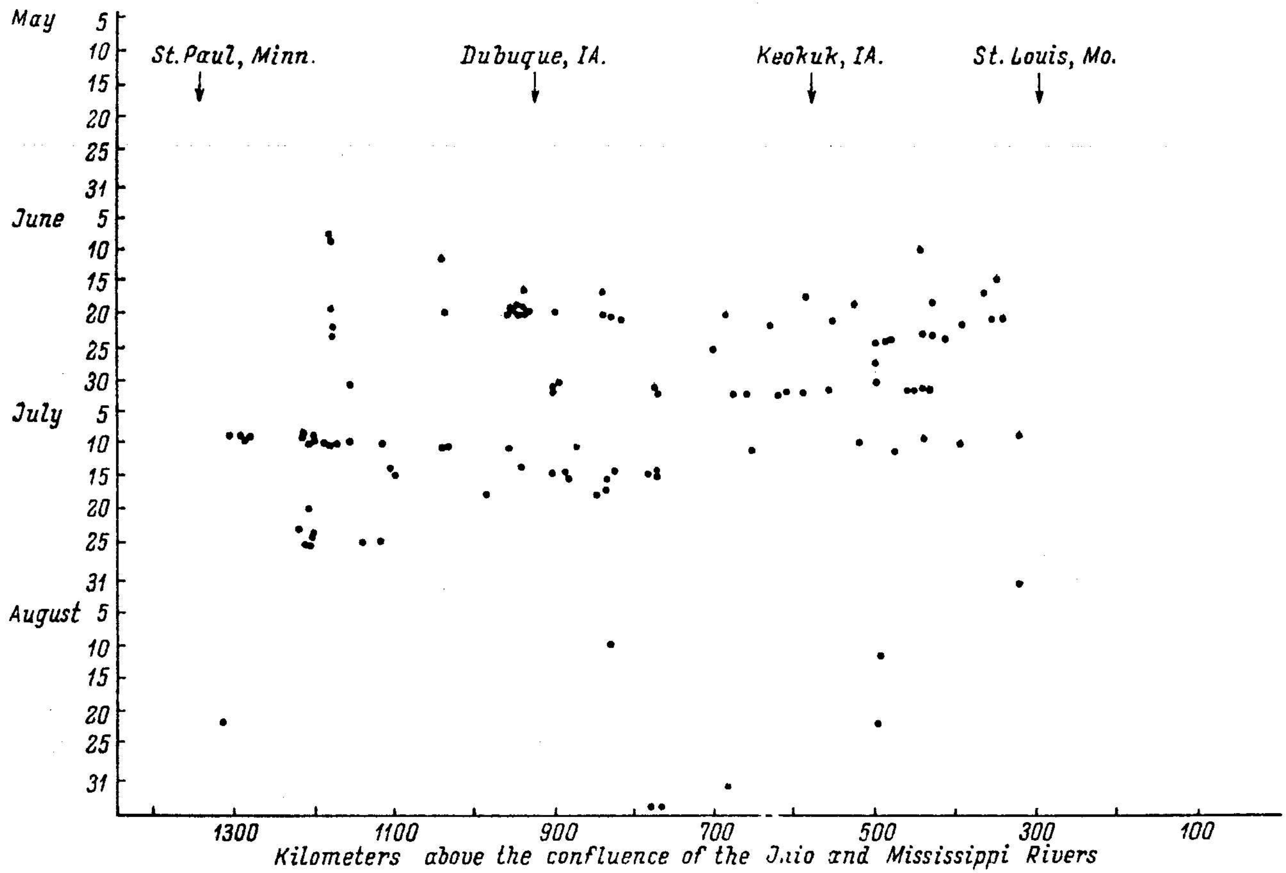

Fig. 2. Locations and dates of *Hexagenia bilineata* emergences on the Upper Mississippi River in 1963.

Innate characteristics of the insect enhance synchronous oviposition and emergence. The adult insect has no functional mouth parts and it exhausts its energy reserves at normal temperatures in about 24 hours. Thus, stragglers are seldom left to prolong the oviposition period. The adult is most active from dusk to dawn, therefore emergence and oviposition are restricted at midsummer to about 8-hr intervals.

The sculptured eggs of *Hexagenia* are adapted so that they drift into silted areas. Eggs laid at the water's surface disperse as they settle slowly (about 0.25 m/sec) to the river bottom. Some eggs undoubtedly drift for long distances downstream during their incubation period. Newly-hatched nymphs are positively phototropic and are probably further distributed downstream as plankters.

Intraspecific strife, low dissolved-oxygen levels and other factors cause older nymphs to drift downstream. Nymphal drift, which appears to be maximal during the first few weeks subsequent to the spring break-up, is facilitated by spring floods. An analysis of combined emergence records for all years indicates that the greatest concentrations of *H. bilineata* occur in the downstream pools (Fremling 1970). Downstream drift probably causes a partial denudation of the upper pools. Similar results have been obtained by Swanson (1967) on the Missouri River.

Even river traffic helps distribute mayflies along the river. Insects which are attracted to the brilliant search lights of towboats often blanket the surface of barges. A large tow can transport countless subimagoes downstream for over 200 km before they molt to imagoes, mate and lay their eggs.

H. bilineata nymphs are able to grow slowly at winter temperatures. They are unable, however, to complete the last nymphal instar at temperatures less than 19° C. Thus, there is an accumulation of last instar nymphs in early summer. The first emergence of the summer is thus coordinated by winter temperatures. The time between subsequent emergences may be the time required to complete the last nymphal instar.

Experiments with laboratory populations indicate that the first summer emergents are capable of producing adult offspring the same summer. In laboratory tanks, only 79 days were required to develop newly-hatched larvae to adults at temperatures which ranged from 24—27° C (Fremling 1967). It is likely that development could occur even faster in the river where space and food are not limited. The first emergents of the year are very large, but late summer emergents are often very small. Early June females range in size from 25—30 mm while late August females range in size from 18—24 mm (Jergens 1965). The smaller adults apparently mature quickly by decreasing the number of instars they would normally go through. Similar observations have been reported for *Baetis* mayflies in Austria by Pleskot (1961, 1961a). The late summer emergences along the Mississippi are sparse and are not as well synchronized as those of early summer.

Laboratory populations exhibit differential growth rates among nymphs which were stocked on the same date as eggs (Fremling 1968). Moreover, emergences occur sporadically from laboratory tanks over a prolonged period (up to 10 months). The differential growth rates and the prolonged emergence period are probably due to crowding. Downstream drift decreased the likelihood of crowding and subsequent differential growth rates in the river.

H. bilineata emergence is not directly influenced by air temperature. Flight activity is severely curtailed by cool weather, however, and mass emergences at such times often go unnoticed. In extremely cool weather, subimagoes may not moult to the imago stage for as long as 48 hr. On several occasions, emergences have been observed during wind storms, but the newly-emerged subimagoes were swept to shore by the wind and were destroyed by wave action before they could fly from the water's surface. Because nuisance conditions occur only on warm nights when winds are not strong, a given emergence can be reported along a vast expanse of river only when flight conditions have been good along the entire river segment. Thus, the arrays of observations in Figs. 1 and 2 more truly reflect periods of maximum flight activity than they do periods of maximum emergence (Corbet 1964). The arrays in Figs. 1 and 2 tell when emergences did occur, but the arrays do not reveal when all emergences occurred. Those emergences which occur during inclement weather often go unreported. Thus, the synchronous emergences are probably made to appear better coordinated than they actually are.

Finally, it is theorized that last instar nymphs suppress the development of younger nymphs by secreting ectocrines into the water. As each accumulation of last instar nymphs emerges from the river, it may enable the next group to mature and emerge. Because the river is flowing, ectocrines could be circulated more rapidly than they would in a lake.

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Discussion

Mildrew: Do the late summer emergents, which are smaller, lay fewer eggs?

Fremling: Yes.

Burbanck: Do the *Hexagenia* near St. Louis have a longer emergence time than in the northern reaches of the Mississippi?

Fremling: *H. bilineata* is very scarce below St. Louis because the last dam on the river is at St. Louis. I have few records of *H. bilineata* below St. Louis.

Edington: Can the presence of large populations of the mayfly be regarded as a consequence of the impoundment of the system?

Fremling: Yes. The carrying capacity of the river, for *H. bilineata*, has been increased by impounding the river.

Minshall: Do you have any evidence of mass movement of mayflies which would relate to the so called «recolonization cycle» hypothesis?

Fremling: Yes. The upstream oviposition flight of this species is easily observed from bridges which span the river. Most nuisance problems are caused by females which are attracted to brought lights during this upstream flight.