Biology of a Large Mayfly, *Hexagenia bilineata* (Say), Of the Upper Mississippi River

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CONTENTS

SUMMARY

Hexagenia bilineata (Say) and *Hexagenia limbata* (Serville) create nuisance problems by their sheer numbers in many cities along the Mississippi River. They also constitute a navigation hazard and may cause allergies.

H. bilineata is generally more abundant than *H. limbata* on the Upper Mississippi River, but *H. limbata* becomes increasingly abundant northward. The absence of intermediate-sized nymphs in late summer indicates that *H. bilineata* completes a generation in 1 year in the Keokuk area. *H. bilineata* nymphs live in burrows in the river bottom and are most abundant in impounded areas where there is little current and where the river bottom is silty. Keokuk is less bothered by *Hexagenia* spp. than are other river cities because it lies only partially along a silted, impounded area. Other cities which lie entirely along silted areas, such as Fort Madison, Iowa, receive greater quantities of adult *Hexagenia* spp. Detailed observations were made of *H. bilineata* mating flights and the emergence of the subimago from its nymphal exuviae. An analysis of 150 observations of *H. bilineata* emergences on the Upper Mississippi River indicated that waves of emergence occur at intervals of about 6-11 days, with the maximum emergence occurring in mid-July. A single wave of emergence usually occurred almost simultaneously throughout the river segment. During the maximum wave, 30 observations were made during a 3-night period over a 440-mile expanse of river.

H. bilineata nymphs, subimagoes and imagoes were heavily parasitized by metacercariae which were thought to be those of *Megalogonia ictaluri* and *Crepidostomum cooperi*.

Hexagenia nymphs, which occur predominantly in shallow, slow-water areas, may be vulnerable to wettable powder or granular insecticides. The nymphs are a prime food of fish, however, and such control measures may adversely affect fish populations. Modifications in lighting may alleviate the mayfly problem to some extent.

Biology of a Large Mayfly, *Hexagenia bilineata* (Say), of the Upper Mississippi River[1]

BY CALVIN R. FREMLING[2]

Invasions by vast numbers of mayflies (*Hexagenia* spp.) are familiar phenomena to people who live along the Mississippi River. Some of the river cities are virtually blanketed by mayflies on several nights each summer. Drifts of the insects form under street lights at such times, traffic is impeded, shoppers desert the streets, and, in extreme cases, snow plows are called out to reopen highway bridges which have become impassable. The insects accumulate in sufficient quantities to clog sewer gratings and to create an objectionable odor as drifts of them decay.

Subimagoes, as well as imagoes, are variously known in the Keokuk area as Mormonflies, mayflies, fishflies, riverbugs, willowbugs, sandbarflies, 24-hour bugs,

[1]Project 1373, Iowa Agricultural and Home Economics Experiment Station. Iowa Cooperative Fisheries Research Unit, sponsored by the Iowa State Conservation Commission and Iowa State University of Science and Technology, with the cooperation of the United States Fish and Wildlife Service. This project was also supported by the National Science Foundation grant G-3831. This paper reports a portion of the author's Ph.D. thesis, "Biology and possible control of economically important Trichoptera and Ephemeroptera of the Upper Mississippi River."

[2]Formerly graduate assistant, Department of Zoology and Entomology, Iowa State University of Science and Technology. Now assistant professor of biology, Winona State College, Winona, Minnesota. One of the most interesting and gratifying aspects of this study has been the unanimous cooperation and the sincere interest expressed by many people from many diversified walks of life. My major professor, Dr. Kenneth D. Carlander, initiated this investigation and provided guidance throughout the study and the preparation of this paper. David T. Hoopes assisted during two summers of field work. Mayor James O'Brien encouraged the research program at Keokuk and arranged for lodging, a boat and a motor which were provided by the City of Keokuk. The Jones Construction Company provided laboratory space for one summer. Lockmaster Donald Pullen and the personnel of Lock 19 provided laboratory space, allowed the use of their facilities, distributed collection materials to towboat captains and made daily observations of insect activities. Ray Buchan, power plant superintendent, allowed the use of the facilities and data of the Union Electric Company at Keokuk. My wife, Arlayne, served as laboratory assistant and typed the first drafts of this manu-

(footnote 2 continued)
script. Many observations and collections of insects were made by the captains and crews of towboats. Observations and collections also were made by lockmasters Frank Fiedler, Robert Cook and Thomas McKittrick at Locks 17, 18 and 20, respectively, and by F. J. Moore, Fort Madison bridge superintendent. Technical advice was received at Iowa State University from Drs. Jean Laffoon, Martin Ulmer, Edwin Hibbs and John Lilly. Thomas Thew of the Davenport Public Museum identified many mayflies. My fellow graduate students, James Schmulbach, Fred Meyer, Robert Johnson and Clarence Carlson, assisted at various times in the field.

Fig. 1. Subimagoes of *Hexagenia bilineata* weighting down a tree branch.

Fig. 2. *Hexagenia bilineata* imagoes at a picnic site near Keokuk, Iowa.

Canadian soldiers and Junebugs. Probably the most colorful, as well as descriptive, term is the one used by the crews of the river boats—"those big, black bastards."

The Des Moines Register News Service carried the following dispatch on July 14, 1958:

Dubuque, Iowa.—Fish flies controlled the Julian Dubuque bridge here for 40 minutes, then surrendered with heavy losses under an armored counter attack by highway commission scraper-trucks.

Traffic was stopped on both sides of the Mississippi River bridge by multitudes of fish flies, starting about 9 p.m. Sunday.

The battered bugs caused slipperiness on the bridge until highway commission trucks plowed a path through and sanded the surface.

The mayflies rest on terrestrial objects during the day, and under their weight tree limbs become pendulous and even break (fig. 1). Residents of summer homes along the river find their houses covered and their yards littered by the insects. A constant rustle is heard as the insects are disturbed and fly up from their resting places (fig. 2). The dead insects and their cast nymphal exuviae form foul-smelling drifts where they are washed up along the shore. Allergies caused by mayflies have been reported by Figley (1929 and 1940) and by Parlato (1938).

Crews of the towboats which transport freight on the Upper Mississippi River find mayflies to be a navigation hazard. As the insects emerge from the river at night, they are attracted by the powerful arc and mercury vapor searchlights which are used by the towboats. The boats, with their barges, may be a quarter of a mile long and depend entirely upon their searchlights to spot unlighted channel markers. Visibility is greatly reduced by the mass of insects in the searchlight beams. The crushed insects render the decks, ladders and equipment of the boats slippery and dangerous. The towboats must of necessity be completely hosed off with water after each encounter with a large swarm of mayflies.

The large mayflies which cause inconvenience on the Mississippi River belong to the genus *Hexagenia*, of which only two species, *Hexagenia bilineata* (Say) and *Hexagenia limbata* (Serville), were collected in 1957 and 1958 when the present study was conducted. Ship captains, lock personnel and bridge operators made many collections at various points along the river. These revealed that *H. bilineata* was by far the most abundant species of *Hexagenia*, but that *H. limbata* became increasingly abundant northward from Keokuk. The following discussion will be concerned primarily with *H. bilineata* because it is the major problem species, but *H. limbata* observations also will be included because it is fairly abundant. Hoopes (1959) revealed that *Hexagenia* spp. nymphs comprise over 50 percent of the food of channel catfish, freshwater drum, mooneyes, goldeyes and white bass and over 40 percent of the food of paddlefish and white crappies. The nymphs are also eaten by shovelnose sturgeon, bluegill sunfish, black crappies and black bullheads.

THE SUBIMAGO

Winged forms of *Hexagenia* spp. emerge from the water usually at night. The newly emerged form is known as a subimago or dun. This subadult form is peculiar to the Ephemeroptera. The subimago is a somber gray color with relatively short, coarse appendages. The cerci bear setae, and the wings are cloudy and translucent. After emergence from the water, the subimagoes fly to trees along the shore and remain almost motionless during the day, usually moving only when disturbed or to keep themselves shaded (fig. 3).

Eggs and sperm are mature when the subimago stage is reached, at which time stripped eggs may be fertilized in saline solution. About 25 percent of the body weight is lost, principally in the form of water, during the subimaginal stage. The subimaginal stage ends with a molt to the adult or imaginal stage.

On warm summer days, *H. bilineata* subimagoes usually begin molting about 2 p.m., 8 to 18 hours after emergence. Molting continues into the evening, with a peak being reached about 4 p.m. In cool weather, however, the insects remain longer as sub-

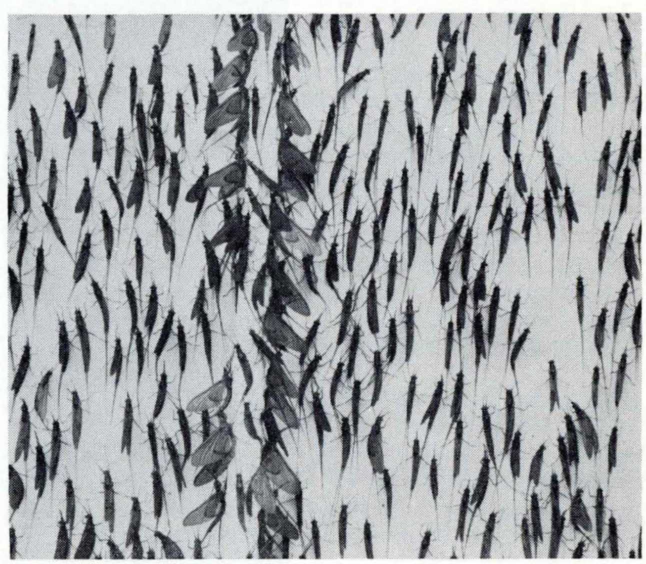


Fig. 3. Subimagoes of *Hexagenia bilineata* resting in the shade.

imagoes. One such instance occurred in June, 1958, when the air temperature was abnormally low. A large emergence of *H. bilineata* took place in the Keokuk vicinity at about 3 a.m. on June 21. Although a few subimagoes transformed during the evening on the day of emergence, the majority of them molted throughout the second day (June 22). The maximum air temperatures on June 21 and 22 were 71° and 68° F., respectively. The late-molting subimagoes lived an extra day because of the cool weather.

It is interesting to note that thousands of subimagoes are transported by towboats and their barges. A towboat with a full complement of 15 barges is approximately 2.5 acres in size, and when some of the open-top barges are empty, their surface area is much greater. During periods of heavy *H. bilineata* emergence, most of the towboats which pass through the Keokuk lock carry huge cargoes of subimagoes. The boats travel 24 hours a day and average about 10 miles per hour when downbound and approximately 8 miles per hour when upbound. Thus, during a cool weather emergence, many thousands of *H. bilineata* subimagoes may be transported over 350 miles downstream and over 250 miles upstream before they transform to imagoes and lay their eggs. Even with the usual time of 8 to 18 hours between emergence and molting, the mayflies may be carried over 100 miles up or downstream. Although the effects of this artificially increased range are unknown, its influence upon the gene pool of the species is interesting to contemplate.

The wings of *H. bilineata* subimagoes seem to be very easily damaged, since individuals which were picked up by their wings very often failed to molt successfully because the wings of the imago failed to pull free from the subimaginal cuticle. Such subimagoes lived as long as 36 hours in the laboratory before they died without molting successfully.

Hunt's (1953) description of the subimaginal molt of *H. limbata* fits that of *H. bilineata* very well. (See also photographs by Jahoda, 1950 and Hintz, 1952). In *H. bilineata*, a very reliable character was found which indicates when a subimago is about to molt. Normally the wings are held erect, their tips touching each other. Prior to a molt, however, the wings no longer touch, but become progressively farther apart. This "non-touching" criterion proved valuable in selecting individuals which could be depended upon to molt within a few minutes. As Hunt points out, mortality during the subimaginal molt is very low in nature, but is very high under laboratory conditions, presumably because of injury to the wings during capture.

THE IMAGO

The imago is noticeably more delicate than the subimago, but its powers of flight are greater. Its wings are gossamer and transparent, the eyes are larger, the legs are longer and more slender, and the cerci no longer bear setae. The somber body color of the *H. bilineata* subimago is replaced by delicate shades of brown and cream.

Occasionally, the subimaginal exuviae remain attached to the cerci of the imago. This seems to be no serious handicap, however, because such individuals were observed to fly and mate in a normal manner. As in *H. limbata* (Hunt, 1953), the males of *H. bilineata* are much smaller than the females.

The mating activity of *Hexagenia* spp. has been described by many authors (Needham, 1927; Neave, 1932; Needham, Traver and Hsu, 1935; Spieth, 1940; Lyman, 1944, 1955a; Cooke, 1952; Hunt, 1953). Since the mating activity of *H. bilineata* apparently differs in several respects from other *Hexagenia* species, it will be described in detail.

If imagoes, and sometimes subimagoes, are disturbed and forced to fly up from their resting places during the day, a few often mate while the mass of insects hovers before returning to rest again. The preponderance of mating activity, as in other members of the genus, occurs at dusk, however, when the male imagoes swarm in the lee of objects such as trees or buildings. Small swarms often occur at relatively low levels, sometimes at a height of about 6 feet, usually in the lee of relatively small objects. Immense swarms are found higher, in the lee of gross objects such as a bluff or the edge of a line of trees.

Male *H. bilineata* maintain fixed positions in the swarm, about 1 foot from each other, with their cerci spread as stabilizers. Observations of small swarms indicate that they seemed to orient themselves by means of visual reference points (the eaves of a building, the top rail of a fence, etc.). If a breeze was blowing, the hovering males faced into it, but on calm evenings they often formed a continuous swarm, completely encircling an object such as a small building. Unlike the males of *H. limbata* (Hunt, 1953; Lyman, 1955a), *H. bilineata* males did not engage in a repeated upward flying movement with a subsequent planing downward, but retained their fixed position in the swarm. Indeed, if a male at the edge of a swarm was touched so that it moved rapidly from its relative position it was immediately pursued by the surrounding males who attempted to copulate with it. Males of *Hexagenia occulta* have also been reported to maintain fixed positions in a swarm (Cooke, 1952).

Females which flew through a swarm were pursued by the males until copulation was effected. The male approaches the female from beneath and grasps her thorax with his long eversible forelegs. The abdomen of the male is turned upward and forward so that the genital forceps of the male clasp the female abdomen at the level of segment nine. Thus, the gonopores of male and female are brought into juxtaposition. The copulating pair leave the swarm to complete their brief copulation while still airborne. The male usually returns to the swarm to mate again. It is short-lived, however, and is dead or dying by the following mid-morning.

The following experiments indicate that males are stimulated to copulate by the sight of an object which moves through the swarm in a relatively fast, deliberate manner.

Living mayflies of both sexes were thrown, one at a time, into a swarm of males. As the thrown flies entered the swarm they were set upon indiscriminately by the males. Furthermore, males which deserted their positions to attack the incoming insect were themselves often pursued. When a mayfly was thrown into a small swarm, the whole swarm reacted—those most distant reacting least. When the thrown insect had succeeded in leaving the swarm, usually *in copula* if it were a female, the swarm quickly recovered, each member hovering in a fixed position as before.

A piece of brown paper towel which was folded into a cigarette-size bundle was tied by its middle to a 6-foot piece of nylon thread at the end of a long stick. When this crude decoy was swung rapidly through the swarm it was pursued by males who often succeeded in grasping it momentarily. When the paper was swung through the swarm in pendulum fashion the entire swarm swayed back and forth in unison with the oscillating decoy. If the observer ran through the swarm, with the stick held erect and the decoy trailing, the entire swarm followed the decoy for a distance of about 15 feet, and a few individuals succeeded in grasping it. Apparently, male *H. bilineata* do not recognize female mayflies, as such, but are stimulated by movement through the swarm. Spieth (1940) observed that male *Hexagenia* spp. attempted to mate with virtually any species of insect which passed through a mating swarm.

Female *H. bilineata* imagoes often extrude their egg packets before they die if they have not oviposited normally. When dead mayflies are removed from beneath a light in the morning, the dried and hardened egg packets often remain. Many people believe the white packets to be maggots which have been generated in the decaying mayflies.

Each female has two packets of eggs. Four *H. bilineata* females were found to carry a total of 8,576, 8,936, 4,252 and 6,664 eggs, respectively. The eggs of *H. bilineata,* which sift downward through the water after they have been laid, adhere to the substrate. The hatching time of the eggs is no doubt related to water temperature, as demonstrated by Hunt (1953) for *H. limbata.* Under laboratory conditions he found the incubation period to be 11-14 days at 75° to 95° F., 18-22 days at 67° to 81° F. and 20-26 days at 62° to 73° F. *H. limbata* eggs were killed when frozen.

THE NYMPH

The hatching of *H. limbata* eggs has been described by Hunt (1953) and by Lyman (1955b). Swimming and burrowing activities of *Hexagenia* nymphs have been described by Lyman (1943).

In the Mississippi River, nymphs were taken at depths ranging from 1 to 25 feet, principally in soft mud. In several instances, however, large numbers of nymphs were found in other bottom types. At the mouth of the Skunk River, for example, a large population of small nymphs (about 9 mm. long) occurred in a sand-silt bottom which contained about an equal volume of leaf fragments, small sticks, bark and pebbles up to ½ inch in diameter. After constructing a "U" shaped burrow in the river bottom, the nymph reposes in one arm of the "U," oriented so that it faces upward. A current of water for respiration is maintained in the tunnel by undulatory gill movements. The nymph feeds upon the mud and detritus in which it lives, appearing to gain its nourishment from the organic matter contained.

On July 9, 1958, there was an excellent opportunity to examine a nymphal *H. bilineata* population *in situ* at Keokuk. On this date, a guard gate at Lock 19 was raised from the river bed. The gate, which is actually a large, tank-like, pneumatic dam with a board deck, had been submerged at the river bottom for more than 3 months. Its deck was uniformly covered with about 3 inches of soft mud. Since the gate was floated upward very slowly from a depth of 18 feet, the nymphs were not disturbed. The mud layer atop the gate was heavily populated with *H. bilineata* nymphs (fig. 4), and its surface uniformly pocked with nymphal burrows (fig. 5). The mud from 10.5 square feet of surface contained 344 nymphs, virtually all of which were in their last stadium. Circulation in the nymphal burrows was evident, as small plumes of muddy water issued from them when they were covered with shallow puddles of clear water.

When the guard gate was raised from the river bed, a large chamber between it and a raised service gate was drained. This, in turn, exposed a subfloor of the service gate. The subfloor is always at least 6 feet beneath the surface of the water, and the mud upon its surface also contained a large nymphal population. Since the deck of the service gate shaded the watertight subfloor, the mud was slow in losing its water content and remained semisolid. Most of the nymphs deserted their burrows to crawl clumsily about upon

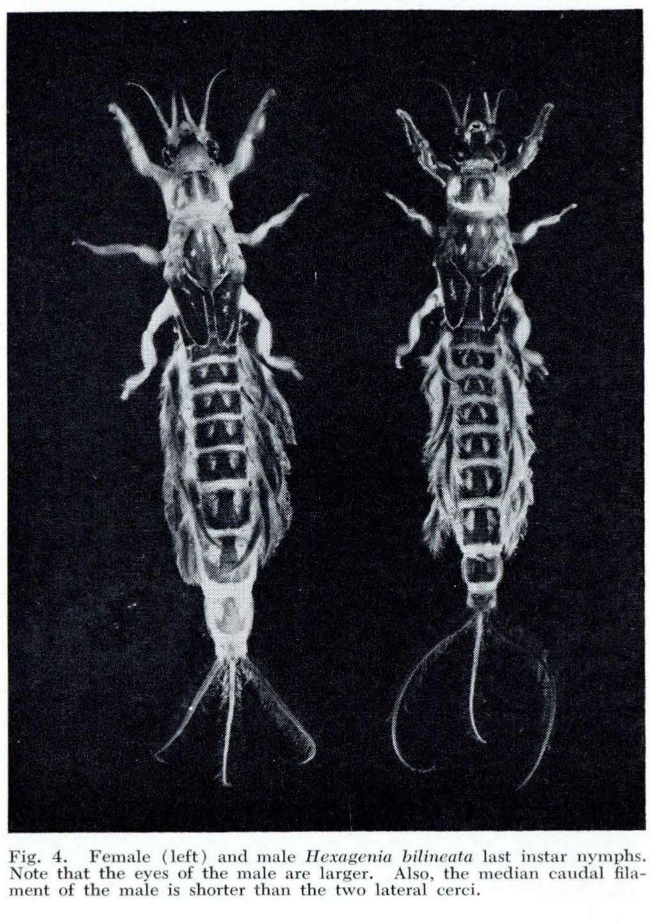


Fig. 4. Female (left) and male *Hexagenia bilineata* last instar nymphs. Note that the eyes of the male are larger. Also, the median caudal filament of the male is shorter than the two lateral cerci.

Fig. 5. Exposed portion of a guard gate raised from the bottom of the Mississippi River showing the nymphal burrows of *Hexagenia bilineata*.

its surface. As the mud gradually lost its water content, the nymphs became unable to move, but their gills remained moist because they were in contact with the wet mud in the furrows which they had made when crawling. Although the mud on the head and thorax of each nymph became powder dry, the drying seemed to have no adverse effect on them, since they swam vigorously when dropped into water.

Just prior to refilling the chamber, 12 days after it had been emptied, viable nymphs were still found in the most fluid mud on the service gate subfloor, even though the mud had become very foul smelling.

Since the mud atop the deck of the guard gate was well drained and not shaded, it contracted and cracked from exposure to the sun. Four days after the guard gate was raised, the mud had hardened into clods which had the consistency of stiff modeling clay. No nymphs, alive or dead, were found on the surface of the mud, primarily because of predation by red-winged blackbirds. When clods of mud were broken open, however, viable nymphs were found in well-defined burrows. A bushel of the clods was set aside in the shade and examined again a week later. No live *Hexagenia* nymphs were found at this time, although a few live chironomid larvae were observed.

When the guard gate was raised, a large number of nymphs were collected alive and placed in tubs of water for observation in the laboratory. As stated previously, almost all of them were last instar nymphs. The following criteria made it possible to identify last instar nymphs with certainty (fig. 4). (1) The wing pads of mature nymphs were black. (2) The two cerci (lateral) of mature *H. bilineata* nymphs were dark, while the caudal filament (median) was hyaline. The caudal filament is small in the subimago, hence the caudal filament of the nymph is hollow and hyaline in appearance. The black setae-covered cerci of the subimago cause the nymphal cerci to appear dark. (3) Careful observation revealed that the subimaginal legs could be seen inside the legs of the last instar nymphs. Development of the contained adult structures is virtually complete by the time the nymph terminates its last stadium.

Nymphal life is usually completed in about 1 or 2 years in various species of mayflies. The following observations are considered as evidence of a 1-year life cycle for *H. bilineata* at Keokuk. Extensive bottom sampling above the Keokuk dam on Aug. 28, 1957, revealed an absence of nymphs of all sizes. By July 9, 1958, however, a large population (about 30 per square foot) of mature nymphs was extant above the Keokuk dam—most of this population emerging as subimagoes on the night of July 14. Again no nymphs could be found above the dam on Aug. 20, 1958. Small nymphs were abundant above the dam again on Dec. 6, 1958, and on March 15, 1959. If a 2-year cycle were in effect at Keokuk, nymphs of different sizes should have been present during August in 1957 and 1958.

EMERGENCE

When ready to molt, the mature nymph swims to the surface, the nymphal skin splits, and the subimago pulls itself free from its nymphal exuviae. The process usually takes less than 1 minute. Mortality is high at this time largely as a result of predation by fish. Studies by Hoopes (1959) indicate that most game and pan fishes in the Mississippi River near Keokuk feed extensively upon nymphs of *Hexagenia bilineata* and *H. limbata*.

The morphology of the winged stages differs markedly from that of the nymph in several respects. Adult antennae are reduced in size, but adult compound eyes, on the other hand, are extremely large compared with those of the nymph. Adult vision is acute, particularly among the males. The jaws of the winged stages are vestigial, and the adults do not feed. The functional stomach of the nymph becomes an aerostatic organ in the adult, and it is generally believed that, in addition to increasing the buoyancy of the adult, this air-filled bladder aids in extruding the eggs and sperm. The familiar snapping noise which is heard when mayflies are stepped upon is caused by bursting of the air bladders.

The nymphs collected from the guard gate, July 9, 1958, started to emerge in the laboratory on July 13, the last emerging on July 16. The nymphs from the river emerged at the same time. Moving the nymphs from the river to the laboratory evidently had not disrupted their normal time of emergence.

Nymphs which were ready to emerge rose to the surface of the water in the tubs and sometimes swam around for a half-hour or so before they finally transformed. Those which remained at the surface for prolonged periods usually died or molted unsuccessfully. The nymphs which transformed most successfully did so within a few minutes after coming to the surface of the water. The wing pads of nymphs which swam at the surface of the water were noticeably silvery in appearance. The silver appearance was caused by a gaseous space which formed between the nymphal and subimaginal cuticles prior to molting. The grooves in the wing pads first became silvery while the nymph was swimming along the bottom, and the air space finally became sufficiently large to buoy the nymph to the surface. Britt (1950) observed that nymphs of *Ephoron album* were unable to regain the bottom after they had once surfaced. This was also true of *H. bilineata* nymphs.

Molting was initiated at the bottom of the tub in all observed instances. The nymphs seemingly attempted to remain at the bottom, but when they became too buoyant, they rose, still swimming, to the surface. By the time a nymph was ready to transform, its whole thorax was silvery; finally the abdomen also assumed a silver appearance.

Nymphs in the laboratory seemed to molt more slowly than those in the river. The trapped gasses between the nymphal and subimaginal integuments are subject to a pressure commensurate with the water pressure at which the nymph lives. As the nymph rises to the surface, the trapped gasses tend to expand as the water pressure decreases. This expansion probably aids in the separation of the integuments. If this is the case, it would follow that nymphs rising from the greatest depths would be facilitated most in transformation.

Once the nymphal cuticle between the wing pads was split, transformation was quite rapid. The thorax of the subimago was pushed up and forward and protruded progressively farther through the split. The abdomen contracted rhythmically, while the subimaginal abdomen and cerci were pulled free from, but were not yet pulled out of, those of the nymph.

Subimagoes which successfully emerged from their nymphal exuviae always kept their feet on their shed nymphal skins until they had completely freed their caudal filaments and their wings. Those which stepped prematurely from their exuviae into the water were unable to regain their foothold and pull their filaments and wings from the nymphal skin. This accident was observed in eight instances—all fatal. The wings were ready for flight as soon as they were pulled from the nymphal wing pads. The subimagoes which had difficulty in freeing their wings invariably became crippled and never attained the imago stage.

Subimagoes which freed themselves in a normal manner usually stood on their cast exuviae for 2 or 3 seconds before they flew away. Often they hopped only a foot or less and stood on the surface of the water for an additional 2 or 3 seconds before flying away. In all observed instances (about 20), the subimagoes, both male and female, expelled one to three large drops of an amber-colored, water-soluble fluid from their anus before they became airborne.

During the summer months of 1958, 150 observations were made of mass mayfly emergences by ship captains, lock personnel and by the bridge crew at Fort Madison. A letter of instructions and specimen vials were supplied to these cooperators (fig. 6). The time and place of the observations which were made during 1958 are plotted in fig. 7. In instances where imago mayflies were collected at night they were plotted as having emerged the previous night, since a lapse of at least 12 hours usually is required to pass from the subimago to the imago stage.

Although subimagoes were collected by river boat captains between 7 p.m. and 9 a.m. C.S.T., over half of the emergences were reported between 1 and 4 a.m.

Of the 150 reported emergences, two occurred in May, 36 in June, 90 in July, 17 in August and none in September. It is apparent that *H. bilineata* emergence reaches its seasonal peak about mid-July on the Upper Mississippi River. A rhythm of emergence obviously existed along the Upper Mississippi River in 1958 with waves occurring at intervals of about 6 to 11 days (fig. 7).

Needham (1920) summarized the data collected at Keokuk by Emerson Stringham in 1916. He indicated that emergences, most of which occurred in July, took place in waves which reached their height at about the 13th, 18th and 23rd of the month. Emergences took place simultaneously at Montrose and Fort Madison, smaller waves of emergence culminating on the 10th and 23rd of August.

Figure 7 indicates that *H. bilineata* emergences often encompass great expanses of river. One such emergence occurred in mid-July 1958. No observations of emerging mayflies were made anywhere on the Mississippi River on July 9, 10, 18, 19, 20 or 21. From July 11-17, however, 39 observations were made, 30 of which were made during a brief 3-night period. More remarkable still was the fact that the 30 observations were made uniformly over a 440-mile expanse of river. Emergences of this magnitude seem to be the rule, rather than the exception, during midsummer. There was no trend for a given brood to begin emerging a day or so earlier in the southern extremity of the Upper Mississippi River as might be expected. Indeed, a given emergence tended to occur during

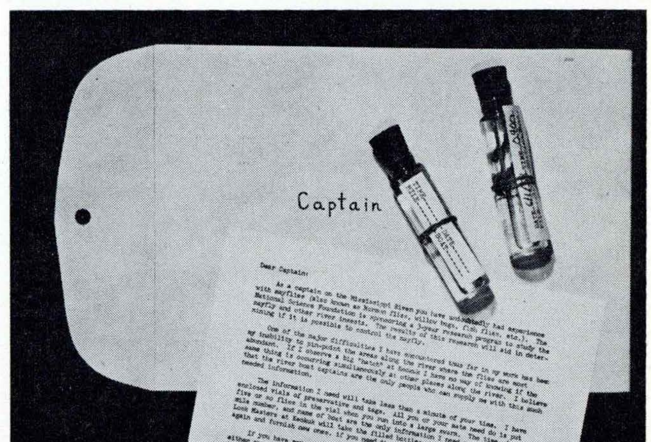
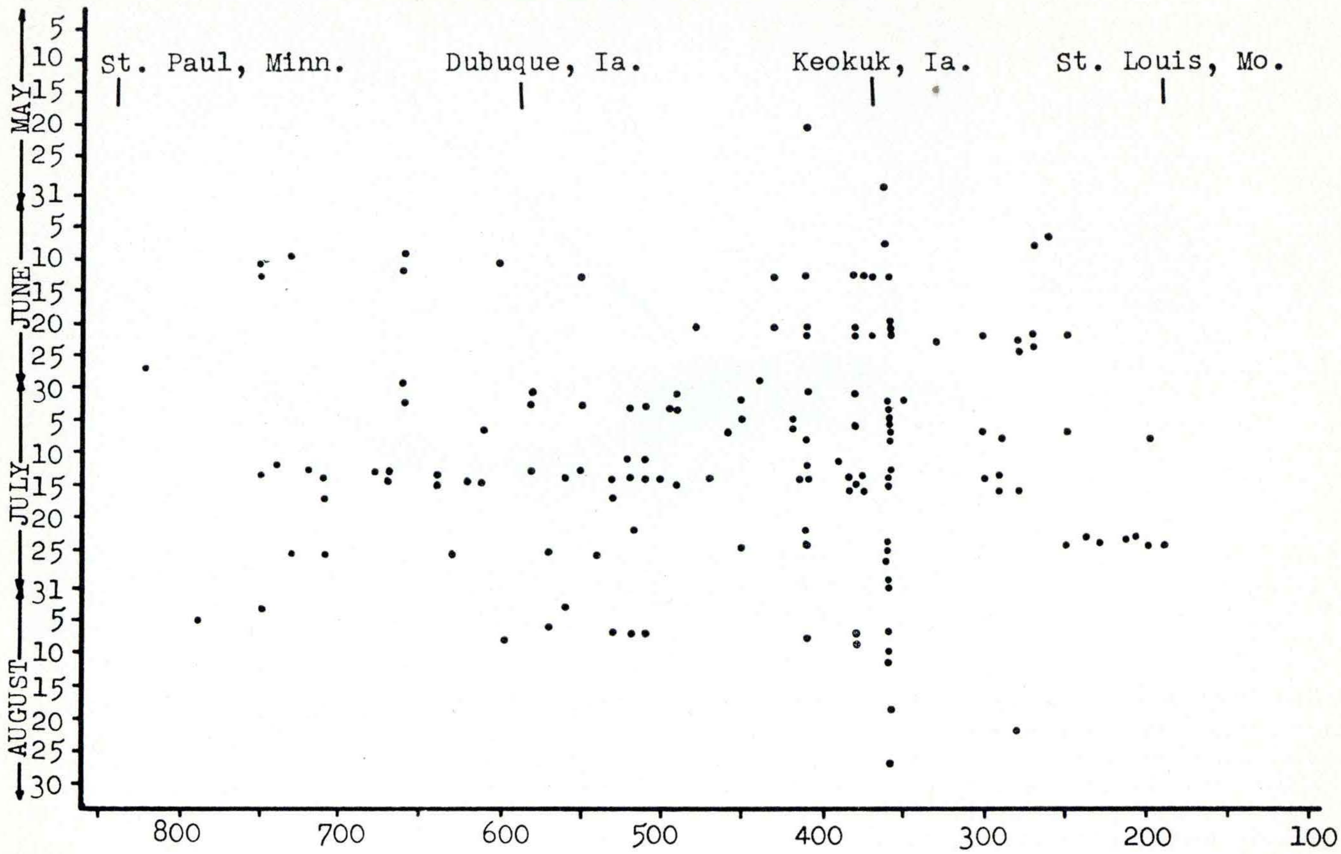


Fig. 6. Mayfly information sheet and collecting vials which were distributed to ship captains on the Mississippi River in 1957 and 1958.

REPORTED HEXAGENIA BILINEATA EMERGENCES IN 1958



MILES ABOVE THE CONFLUENCE OF THE OHIO AND MISSISSIPPI RIVERS

Fig. 7. Locations and dates of *Hexagenia bilineata* emergences which were reported on the Upper Mississippi River during 1958.

the same interval of time throughout the entire river segment (fig. 7). A similar phenomenon has been reported from Lake Winnipeg, where Neave (1932) observed that *H. limbata* did not emerge earlier in the southern end of that elongate body of water (a distance of 220 miles).

In the Keokuk area, a few specimens of *H. limbata* were collected as early as May 23 and as late as Aug. 18. Of 18 *H. limbata* collections made by cooperators, five were made during May, seven in June, two in July and four in August. Small numbers of *H. limbata* emerge conspicuously earlier in the year than *H. bilineata* in the Keokuk-Fort Madison area. Local fishermen and lockmen are able to distinguish between the light-colored *H. limbata* and the much darker *H. bilineata.* They commonly refer to *H. limbata* as "forerunners" because they portend large emergences of *H. bilineata.* All of the *H. limbata* emergences which were conspicuous enough to be noticed by the ship captains were recorded from Davenport, Iowa, northward. *H. limbata* were rarely observed at Keokuk, but they are quite common at Fort Madison 15 miles to the north. Apparently this species becomes increasingly abundant northward.

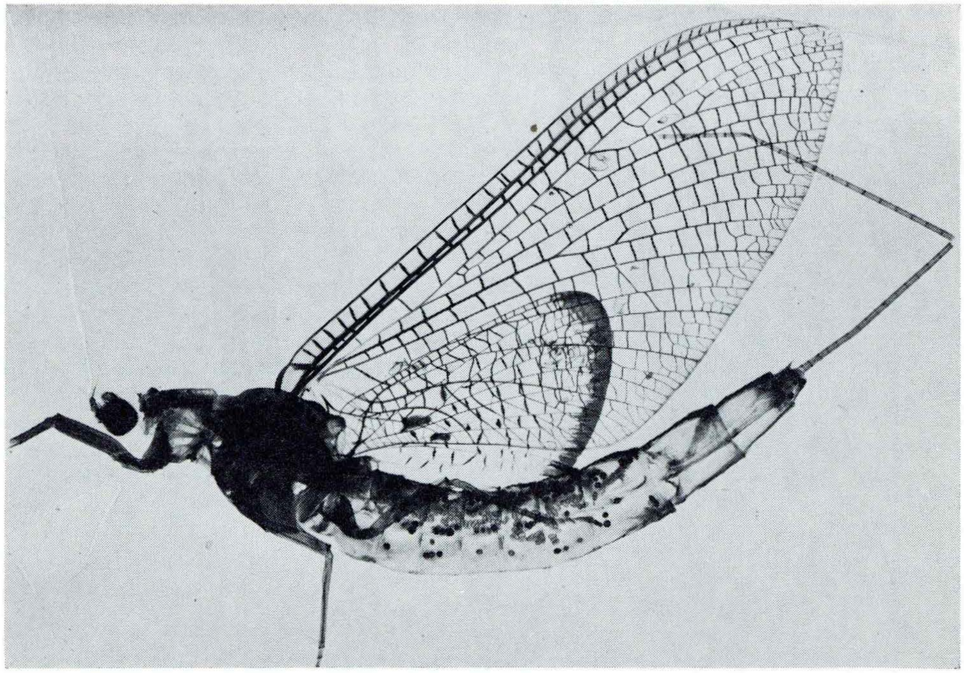
Particular attention was given to the *H. bilineata* emergences at Keokuk, Iowa, because field operations were centered there. Daily air tempratures were made available by the U.S. Army Corps of Engineers, and daily water temperatures and pool levels were provided by the Union Electric Power Company. No correlation was found between air temperature and emergence in the Keokuk area. Although it is generally thought that emergences occur after a succession of warm nights, no evidence was found in 1957 or 1958 to support this contention. In fact, one of the heaviest emergences which occurred at Keokuk during 1958 took place during a 3-day period (June 20-22) when the maximum air temperature was only 74° F. Needham (1920) also failed to find any correlation between emergence and air temperature at Keokuk during the summer of 1916. Similarly, no correlation was evident between emergence and water temperature, water level or phase of the moon.

PARASITES OF *HEXAGENIA BILINEATA*

Large numbers of trematode metacercariae have been observed in nymphs, subimagoes and imagoes of *Hexagenia bilineata.* Parasitized *H. bilineata* from the Keokuk area also were observed by Needham (1920).

Trematode cysts in *H. bilineata* occur principally in the tracheal gills of nymphs and in the abdominal musculature of nymphs, subimagoes and imagoes. In only one instance was a metacercaria observed else-

Fig. 8. Female *Hexagenia bilineata* imago which has been sectioned, eviscerated and cleaned to show the abdominal distribution of metacercariae. Mayfly eggs are also shown, but they are keg-shaped and transparent, while the metacercariae are round and black.



where in the body of the insect, where it was found encysted in a thoracic muscle of an imago. Metacercariae which are encysted within the nymphal gills are shed with the nymphal exuviae. Figure 8 shows the metacercariae present in half of the abdomen of a female imago. A few mayfly eggs also are visible in the photograph, but they are readily distinguished from the metacercariae by their barrel shape and transparency.

The number of metacercariae varied with the age of the insect. Small nymphs (13 mm. long) contained an average of three metacercariae per individual. Last instar nymphs were most heavily parasitized, often bearing as many as 185 metacercariae. Adults carried fewer metacercariae than did last instar nymphs, since losses of 10-20 of them occurred during the shedding of the nymphal exuviae. No metacercaria-free adults or large nymphs were observed during this study.

Metacercariae in viable or recently dead mayflies were fed experimentally to day-old chicks, ringed turtle doves and goldfish. No intestinal flukes were found in any of the experimental hosts as a result of the feeding experiments.

Dr. John E. Hall of the West Virginia University Medical Center has since identified the encysted metacercariae as those of a papillose allocreadiid (Trematoda :Allocreadiidae). These trematodes are known to utilize sphaeriid clams as first intermediate and fishes as definitive hosts. Although specific diagnosis could not be made from the metacercariae, Dr. Hall has suggested that both *Megalogonia ictaluri* (Surber, 1928) and *Crepidostomum cooperi* (Hopkins, 1931) may be involved. Hopkins (1934) found adult *C. cooperi* in perch, centrarchids and catfishes and found the metacercariae of *C. cooperi* in the abdominal musculature of *Hexagenia*. *M. ictaluri*, on the other hand, was found in the nymphal tracheal gills of *Hexagenia*. Adult *M. ictaluri* were found in the intestines of catfishes. Nothing is known of the effects of these parasites on the host fishes.

H. limbata adults which were collected near Keokuk were also hosts to metacercariae, but they seemed to carry considerably fewer of them than did *H. bilineata*.

POSSIBLE CONTROL

Nymphs of *Hexagenia* spp. in the Mississippi River are found only where currents are slow enough to permit the accumulation of silt. They have been abundant in the Mississippi River for many years. Walsh (1863, p. 199) stated:

> "In the middle of July, when on the shallow arm of the Mississippi, known as 'The Slough' at Rock Island, *bilineata* appears in prodigious swarms, so that the bushes absolutely bend down with their weight."

While working along the Mississippi River at Quincy, Illinois, Garman (1890, pp. 179-180) wrote:

> "The adults of certain species of this group [Ephemeroptera] are familiar to anyone who has visited our rivers in July. They blacken the willows at the water's edge and cause the limbs to droop, in such quantities do they collect upon them. In the evening, at times, they mount into the air, and may be seen in countless numbers moving for hours in one direction as if bent on migration."

Impoundments which have been formed along the Mississippi River have undoubtedly increased the habitat for *Hexagenia* mayfly nymphs and thus increased the intensity of emergence. General control of mayflies in such large areas probably is not feasible. Possibly water level regulation could provide effective control of the mayflies, but such water level regulation is not feasible because the level of the water in the navigable portion of the Mississippi River must always be kept high enough to maintain an 8-foot navigation channel. Furthermore, it has been demonstrated (Hoopes, 1959) that the mayflies provide an important source of food for fish. The elimination of the mayflies might cause more problems than it would solve.

Lieux and Mulrennan (1955) reported the elimination of *Hexagenia munda* mayflies from a 200-acre lake in Florida, treated April 13, 1954, with 0.24 pound of wettable powder BHC (gamma isomer) per acre. No living nymphs were found 23 days after treatment, although the pretreatment population had been estimated at over 125 million. No adult mayflies were observed at the lake in 1954. It was reported that the chemical treatment caused no apparent damage to fish or other aquatic wildlife.

Some of the river cities might secure local alleviation of their problem by killing nymphs in critical areas a short time before the first large emergence in June. Few *Hexagenia* mayflies fly more than 3 miles from their place of emergence, and the wind usually determines the direction of concentration. Wettable powder or granular insecticides may be effective if applied to the river shallows which are within a 3-mile distance from the city limits. One application would probably suffice for the entire season because the life cycle of *H. bilineata* is about 1 year. Treatment would be required yearly, however, because the area would be repopulated rapidly by drifting eggs and nymphs and by ovipositing females which could fly or be transported into the area. Because of the effects of such treatment on other aquatic organisms and of possible danger to man and animals in the use of treated water, no such application of chemical insecticides should be attempted without thorough study.

Since mayflies usually die within 24 hours after emergence, little would be gained by killing them with insecticide fogs or sprays. Furthermore, it is doubtful whether control of adult *Hexagenia* could affect the total population of the river to any appreciable degree. Mortality of eggs and young nymphs is very high, and any decrease in numbers in those stages would probably result only in reduced mortality among the survivors.

The most promising method of alleviating the mayfly problem in the cities along the river is through modifications of lighting. Shopkeepers and restaurant owners could lessen their mayfly nuisance problems by replacing their white lights in the summer with reds and yellows. Diversionary light sources along waterfront areas would help considerably. A row of bright street lamps might be effective in such an area if the riverside of each lamp was shielded with yellow or red transparent plastic during the summer. Such shielded lamps may not attract mayflies to them from the river but may, instead, attract city-bound flies back toward the river where they would congregate and die along the waterfront and thus create less of a nuisance.

LITERATURE CITED

Britt, Noah W.
1950. The life history and ecology of the white mayfly, *Ephoron album* Say, in Lake Erie. Unpublished Ph.D. thesis. Ohio State Univ. Library. Columbus, Ohio.

Burks, B. D.
1953. The mayflies, or Ephemeroptera, of Illinois. Bul. Ill. Nat. Hist. Surv. 25(1).

Cooke, Herman G.
1952. The occurrence of mass flight movements in *Hexagenia occulta* (Ephemeroptera). Ent. News 63(3):61-66.

Figley, Karl D.
1929. Asthma due to mayfly. Amer. Jour. Med. Sci. 178:338.
1940. Mayfly (Ephemerida) hypersensitivity. Jour. Allergy 11(4):376-387.

Fremling, Calvin R.
1959. Biology and possible control of economically important Trichoptera and Ephemeroptera of the Upper Mississippi River. Unpublished Ph.D. thesis. Iowa State Univ. Library. Ames, Iowa.

Garman, H.
1890. A preliminary report on the animals of the Mississippi bottoms near Quincy, Illinois, in August, 1888. Part I. Ill. Lab. Nat. Hist. Bul. 3(9):123-184.

Hamilton, E. W.
1959. Review of Ephemeridae (Ephemeroptera) in the Missouri River watershed with a key to the species. Iowa State Jour. Sci. 33(4): 443-474.

Hintz, Janice.
1952. A mayfly sheds its skin. Penn. Angler 21(3): 16-17.

Hoopes, David T.
1959. Utilization of mayflies and caddisflies by some Mississippi River fishes. Unpublished M.S. thesis. Iowa State Univ. Library. Ames, Iowa.

Hopkins, Sewell H.
1934. The papillose Allocreadiidae. Ill. Biol. Monogr. 13(2).

Hunt, Burton P.
1953. The life history and economic importance of a burrowing mayfly, *Hexagenia limbata,* in southern Mighigan lakes. Mich. Cons. Dept., Bul. Inst. Fish. Res. 4.

Jahoda, William J.
1950. Adult for a day. Nature Mag. 43:307-308.

Lieux, D. B. and J. A. Mulrennan.
1955. Mayfly control. Mosquito News 15(3):156.

Lyman, F. Earle.
1943. Swimming and burrowing activities of mayfly nymphs of the genus *Hexagenia.* Ann. Ent. Soc. Amer. 36:250-256.
1944. Notes on emergence, swarming, and mating of *Hexagenia* (Ephemeroptera). Ent. News 55(8):207-210.
1955a. Seasonal distribution and life cycles of Ephemeroptera. Ann. Ent. Soc. Amer. 48(5):380-391.
1955b. Occurrence and description of an embryonic egg burster in the genus *Hexagenia* (Ephemeroptera). Ent. News 66(10):253-255.

Neave, Ferris.
1932. A study of the mayflies (*Hexagenia*) of Lake Winnipeg. Contrib. Canad. Biol. Fish., N. S. 7:179-201.

Needham, James G.
1920. Burrowing mayflies of our larger lakes and streams. Bul. U.S. Bur. Fish. 36:267-292.
1927. The life history and habits of a mayfly from Utah. Canad. Ent. 59:133-136.
——————, Jay R. Traver and Yin-Chi Hsu.
1935. The biology of mayflies. Comstock Pub. Co., Ithaca, N. Y.

Paralto, Salvatore, J.
1938. The mayfly as an exciting cause of seasonal allergic coryza and asthma. Jour. Allergy 10(1):56-60.

Spieth, Herman T.
1940. Studies on the biology of Ephemeroptera. II. The nuptial flight. Jour. N. Y. Ent. Soc. 48:379-390.

Walsh, B. D.
1863. Notes and descriptions of about 20 new species of Pseudoneuroptera. Proc. Ent. Soc. Philadelphia 2:182-271.