BIOLOGY AND POSSIBLE CONTROL OF ECONOMICALLY IMPORTANT TRICHOPTERA AND EPHEMEROPTERA OF THE UPPER MISSISSIPPI RIVER

by

Calvin Rollins Fremling

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Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

Head of Major Department

Signature was redacted for privacy.

Dean of Graduate College

Iowa State University Of Science and Technology Ames, Iowa

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Several Iowa cities which lie along the Mississippi River have, at various times, expressed a desire to control the caddisflies and mayflies which plague the residents each summer. Comparatively little is known concerning the biology of the mayflies in the river, however, and the life cycles of the principal caddisfly species have never been worked out. It was deemed desirable, therefore, to initiate an investigation to (1) survey the caddisfly and mayfly populations before they are disturbed by control measures, (2) work out the life histories of the most abundant species of caddisflies, (3) determine the factors which cause extreme populations of the insects in some areas and not in others, (4) determine if control measures are desirable, and (5) determine which control methods would be most efficient if, indeed, measures are found to be practicable and desirable.

Keokuk is particularly well suited as a home base for a study of this type because it receives large populations of both caddis and mayflies. This city lies for the most part atop a bluff which overlooks Lock and Dam 19 on the Mississippi River (Fig. 1).

Lock and Dam 19, which is operated by the U. S. Army Corps of Engineers, is one of a series of constructions which makes the Mississippi River navigable from St. Louis, Missouri, to Minneapolis, Minnesota. These dams contain locks which allow navigation craft to be raised
Fig. 1. View of locks, power house and dam at Keokuk, Iowa, 1958. The river bluff at Keokuk is shown at left. Main street meets the river at the bottom of the picture. Photograph by Louis Facto. Drawing by Merle Banks.
or lowered from one impoundment to the next. The impoundments have become heavily silted and shallow except for the main channel where the current is faster and in which the water may be 40 feet deep. The tailwaters below the dams are areas of fast water and the river bottom in most of the tailwater areas is swept free of silt. Thus, two distinct habitats exist in this section of the Mississippi River; the lentic habitat which forms the bulk of the impoundments and the lotic habitat which includes the main channel of the river and the tailwaters below the dams.

Research was begun on this project during the fall of 1956 and it has received the support of a National Science Foundation grant since June 7, 1957. The City of Keokuk which was active in initiating this research, provided housing, a boat and a motor during two summers of field work. The U. S. Army Corps of Engineers provided laboratory space and allowed the use of their facilities at Lock and Dam 19 at Keokuk.

The area at Keokuk was most intensively studied but personal field work extended as far north as Dubuque, Iowa, and as far south as Louisiana, Missouri. Various cooperators collected specimens and made observations from St. Louis, Missouri, to Minneapolis, Minnesota.
TRICHOPTERA

The Caddisfly Problem

Although caddisflies are present in at least moderate numbers in all of the cities which lie along the Mississippi River, they are extremely abundant at Keokuk, Iowa. The caddisfly problem in this city is a manifold one and the caddisflies create serious nuisance and health problems.

Adult caddisflies swarm around the city lights during most of the summer. They blanket lighted store windows and mill around continually on the panes. When the doors of restaurants and stores are opened, large numbers of the insects enter to the discomfort of the patrons.

Masses of the insects dart into the faces of passersby, flutter under their eye glasses and fly down their open-necked clothing. The minute setae which are dislodged from the wings and bodies of the caddisflies cause swelling and soreness in the eyes of sensitive individuals. Many residents of Keokuk have become hypersensitive to the emanations from the insects and have developed typical hay fever symptoms. Some of the personnel of the Union Electric hydroelectric plant are especially bothered by this allergy because they work in close contact with the caddisflies from May until October.

Although many species of caddisflies occur along the Mississippi River (Ross, 1944), only Hydropsyche orris Ross, Cheumatopsyche
campyla Ross and Potamyia flava (Hagen) are abundant enough to contribute to the nuisance problem at Keokuk. All three species are members of the family Hydropsychidae.

_Hydropsyche orris_ forms large mating swarms along the river bluff at Keokuk and the swarms make outdoor living very unpleasant on summer evenings. It is inadvisable to paint houses along the bluff during the caddisfly season and outdoor lighting is impractical. Spiders are very abundant in the area and their webs become pendulous with captured caddisflies, making the riverside homes unsightly. The summer-long infestation by caddisflies probably reduces the value of real estate along the bluff at Keokuk.

Larval caddisflies create a minor problem at Keokuk. One of the problem species, _H. orris_, constructs rigid cases and catching nets on submerged objects in swift water. At the Union Electric hydroelectric plant the cases and nets form dense mats on cooling-siphon gratings and thus impede the flow of water to the generators. The cost of cleaning the siphon intakes amounts to about 8 man-days or about $200 per year.

Hydroelectric plants in other areas also appear to be troubled by caddisflies. Tillyard (1926, p. 392) reported,

_Hydropsyche colonica_ McL. is easily the commonest caddis fly in New Zealand, and sometimes becomes a perfect nuisance in hydro-electric works, being attracted to the light in countless thousands at night, and getting into the clothes, eyes and hair of the workmen.
Adult Trichoptera have created a nuisance problem along the upper reaches of the Niagara River for many years (Betten, 1934, p. 7).

Except in their important relation as fish food these usually unobtrusive insects are likely to arouse general interest only in certain localities where their enormous numbers make them a veritable pest. Thus at Buffalo, N. Y. it is well understood that it is useless to do any outside painting during the earlier summer months because freshly painted surfaces, at least if at all near the river, are literally covered with caddis flies. It is said also that it was largely on account of these insects that the Pan-American Exposition of 1901 was not located in the place which on other accounts was deemed the most desirable. On Squaw Island, opposite Buffalo, in the Niagara river, almost 500 specimens were taken in ten random strokes of an ordinary insect net through the grass. At Ogdensburg, N. Y., on the evening of my arrival I saw a very large picnic of several hundred persons utterly routed by caddis flies. The air of the well-lighted park was filled with these insects and the consumption of ice cream and cake unadulterated was impossible. The species occurring in such numbers at both of these places belong to the genus Hydropsyche, whose larvae live on rocks in swift water.

The caddisfly problem at Fort Erie, Ontario, has been the subject of many studies. Because of the obvious similarity between that problem and the one at Keokuk, the Fort Erie studies will be reviewed in detail. Hydropsyche bifida is the most abundant species in the Niagara River at Fort Erie and it comprised over 70 per cent of the adult specimens which were collected in 1950 (Munroe, 1951). Concerning the caddis problem at Fort Erie, Peterson (1952, p. 103) wrote,

Dense swarms of the insects formed over trees and other tall objects a few hours before sunset; these swarms slowly united to form a mass movement upstream in the direction of the lake, blanketing the area bordering the river to a distance of 1,000 yards from the water and extending upwards to an
estimated height of 300 feet. The density of this flight is indicated by the collection of an estimated 6,800 specimens with 10 sweeps of a net.

Peterson stated that the larval and adult collections made at Fort Erie indicated that the genera Hydropsyche and Cheumatopsyche comprise most of the pest species and that Hydropsyche specimens outnumber Cheumatopsyche specimens by over three to one. It is interesting to note that Cheumatopsyche and Hydropsyche also include the principal nuisance species at Keokuk.

The first case of allergy due to caddisflies was reported by Parlato in 1929. Setae and scales from the caddisfly are capable of being airborne and these structures constitute the allergy-causing emanations. Of 192 hay fever sufferers in the Buffalo, N. Y. area, 14 reacted positively to caddisfly antigens (Parlato, 1930). Five of the 14 hypersensitive individuals experienced allergic symptoms at all times of the year, presumably because of dead flies and their emanations in sweepings and dust. His studies indicated that caddisflies are not a rare cause of asthma and hay fever but are sufficiently common to create a menace to public health. He suggested (1932) that the extracts of caddisflies, butterflies and moths be mixed and used in routine skin testing. Parlato (1934) found that 5 percent of 850 allergic patients were hypersensitive to caddisfly emanations. It is interesting to note that in one hypersensitivity test a small amount of caddisfly extract is placed on the conjunctiva of the eye of the patient.
Many people at Keokuk suffer swollen, watery and reddened eyes when caddisfly "powder" is accidentally rubbed into their eyes. Parlato (1934) reports that he has successfully desensitized patients who were hypersensitive to caddisfly emanations. Of 623 allergic patients who lived in the vicinity of the Niagara River, 215 exhibited definite skin sensitivity to caddisflies and a positive correlation existed between nearness to the caddisfly area and strength of skin reaction (Osgood, 1957b).

Commenting on the caddis allergy problem at Fort Erie, Osgood (1957a, p. 117) stated,

On the Fort Erie side of the river the land does not rise far above the water level; dwellings and stores extend practically to the water's edge. In Buffalo the land rises considerably higher and the river front is occupied largely by harbor, canal, parks, and industrial plants; the dwellings stand farther back from the river's edge . . . . Cases of allergy to the caddis fly are more frequent in the Fort Erie population because of the more intense exposure.

Cases of caddisfly sensitivity are sufficiently common in Buffalo and Fort Erie that allergic patients are tested routinely with caddisfly extract along with the usual environmental inhalants (Osgood, 1957a). The clinical aspects of caddisfly allergy have been discussed by Osgood (1957b).

Parlato et al. (1934) found that immunologically the caddisflies give group reactions as the grasses do. Extracts, whether made from batches of separate species or from several varieties, gave similar positive tests.
Osgood (1934) found reagins of the caddisflies Macronema zebrata and Hydropsyche alterans in the blood of a hypersensitive patient. He found that allergens present in the two species were not identical.

Caddisfly allergies cause considerable manpower losses among the Union Electric Company employees at the Keokuk hydroelectric plant. This loss has reached a peak of about 50 man-hours ($150) in one week during the caddisfly season. It must be emphasized, however, that this cost is for a maximum week and that it is usually much lower. The labor cost of cleaning up the dead insects is also appreciable but it is hard to define. The direct seasonal cost has been estimated to be about $600 plus the cost of cleaning according to a personal communication dated April 22, 1959, from Mr. Ray Buchan, Plant Superintendent.

A case of water obstruction by caddis larvae has been reported from California (Simmons et al., 1942). In this instance the larvae of Hydropsyche occidentalis and Dolophilus gabriella formed such a dense mat of shelters and nets in a water tunnel in the Sierra Nevada foothills that they necessitated the shutting down and cleaning of the tunnel. The mat which was constructed by the larvae accumulated until the flow of water through the tunnel was reduced by 8 per cent. At this point it was felt that the expense of shut-down and cleaning was justified. When the tunnel was emptied, square foot samples were taken at intervals throughout the tunnel. The entrance of the tunnel had the greatest concentration
of larvae with 481 individuals per square foot. The number of larvae diminished steadily until only 21 were found per square foot at a distance of 2,500 feet from the tunnel entrance. In 1939 the job of removing the matting required the use of 15 men with scrapers, shovels and wire brushes. In 1941 high pressure streams of water were used with good results. Larvae have been reported to cause trouble in this tunnel since 1922.

Slack (1955) reported destruction of fish eggs by caddisfly larvae. *Phryganea varia* larvae were collected on MacDougal Bank in Loch Lomond at a concentration of about one larva for every 300 *Coregonus clupeoides* eggs. The *P. varia* larvae were found to have eaten the contents of 90 per cent of the *Coregonus* eggs in a 19-day period.

Caddisflies have created minor nuisance problems in some parts of Africa and Corbet and Tjønneland (1955) speculated that as industrialization increases around the shores of Lake Victoria factories will be liable to suffer inconvenience at their air conditioning inlets due to caddisflies.

**Generalized Caddisfly Life History**

The literature contains very little information concerning the biology of *Hydropsyche orris*, *Cheumatopsyche campylia* and *Potamyia flava*, the three most abundant caddisflies at Keokuk. A considerable amount of
life history information has been reported for other species, however, and these data have been summarized by Betten (1934) and Balduf (1939).

Caddisflies are inconspicuously colored insects which superficially resemble moths. North American Trichoptera do not have a coiled sucking oral tube, however, as most moths do and the wings of Trichoptera are usually covered with hairlike setae instead of scales.

The adults remain quite near their place of emergence and the power of flight is not well developed in many species. During the day the adults most commonly remain motionless in shady, sheltered locations.

The mouth parts of imaginal Trichoptera are not strongly developed and they probably eat no solid food. They take water, however, and the adult life of caddisflies has been more than doubled by providing them with sugar solution in addition to water. Little is known concerning the life span of the adults in nature but they are generally thought to live less than a month.

Two reports indicate that the females are inseminated shortly after they emerge from the water. Tillyard (1926) reported that the female Smicridea seldom escapes from the water without being inseminated owing to the swarm of males which descend upon her as she emerges. Denning (1937) raised adult Brachycentrus fulginosus from pupae and found them to copulate 1 hour after emergence.

The adults are mostly crepuscular and mating activity usually
reaches its peak at dusk and dawn. In several families the males engage in mating dances similar to those of Ephemeroptera. In copulation the male and female rest in a linear fashion with their caudal ends joined and their heads pointing in opposite directions.

The amount of time elapsing between copulation and oviposition varies but it is generally thought to be within 48 hours. From 300 to 800 eggs are laid in "cementlike" or "jellylike" masses in or near the water. Many species of Trichoptera enter the water to lay their eggs.

Denning (1937) observed an ovipositing female Agraylea multipunctata which remained continuously submerged for 1 hour and 8 minutes. The underwater oviposition of Hydropsyche angustipennis has been reported in detail by Badcock (1953). A female of this species was captured in the field by Badcock after it had laid 24 eggs under a stone. The fly laid 820 more eggs in the laboratory on the following day. It remained submerged for 37 minutes and air was seen to be carried on its hairy wings.

The eggs which have been cemented to some submerged object by the female fly hatch in from about 15 days to a month at summer water temperatures.

Trichoptera larvae possess a pair of large silk glands, the silk secretion of which is utilized in building portable cases and in constructing catching nets. Larval cases are of many types and some resemble snail shells, sticks and miniature log cabins. While the larval constructions
are of many diversified forms they are fundamentally alike in that all of them consist of a silken tube which is open at both ends. Hydropsychid larvae generally construct silken nets with which they filter small organisms from the water.

The caddisfly larvae which make portable cases are of the eruciform type. In general, the campodeiform larvae do not build portable cases but instead construct silken catching nets and strain their food from running water. Campodeiform larvae are generally lotic forms while the eruciform type larvae inhabit lentic environments. Hydropsychid caddis larvae are of the campodeiform type and they are restricted to running water habitats.

All caddisfly larvae are dependent upon moving water for respiration and the case-bearing species which live in still water force water through their cases by means of undulatory body movements.

There are about six or seven larval instars between the egg and pupa. The duration of the instars is dependent upon such factors as food abundance and water temperature.

Most caddisfly larvae are omnivorous. Hydropsychidae, Limnephilidae and many Hydroptilidae eat mostly diatoms and other plants, however. Psychomyiid larvae are thought to be generally carnivorous.

Some species complete their larval development in as little as 25 days out others take much longer depending upon water temperature. The
last instar larvae or prepupae construct cocoons of various types in which they pupate. The pupae are of the exarate type and the appendages are movable. The pupae possess very highly developed mandibles which are thought by some to aid the pupa in escaping from its cocoon. The pupa leaves its cocoon by strong undulatory body movements and swims or crawls to the surface of the water. Emergence usually takes place at night. The pupal integument is shed slowly if the insect has crawled out of the water and rapidly if the insect molts on the surface of the water. The species which emerge in swift water emerge almost instantly.

The number of generations per year has been determined mostly by the number of flight periods per year. An uninterrupted, season-long flight has been interpreted as indicating one generation per year. Two flights of shorter duration and which are separated distinctly by an interval of time have been interpreted as signifying two generations per year.

Methods and Materials

Caddisfly adults, larvae and pupae which were collected during this study were preserved in 75% ethyl alcohol and were identified according to Ross (1944). Pennak (1953) was used as a supplementary reference source. All locations on the Mississippi River have been plotted according to U. S. Army Corps of Engineers navigation charts (1957).
Adult caddisflies were collected with insect nets, light traps, by hand picking from lighted windows and by means of emergence traps. A light trap for use under water was developed during this study (Fig. 2). The source of light for this trap was a 6-volt sealed-beam headlight. The metal housing which normally mounted the light in the automobile was left intact and it served as a foundation for the attachment of a metal harness to the light. The harness, which was made of strap iron, held an inverted gallon jar beneath the light so that the beam from the light shone through the bottom of the jar and out its mouth. The apparatus was weighted with a sash weight, which was suspended by nylon lines from the jar rim. The trap was capable of being lowered into the water to any desired depth by the electric cord which connected the light to a 6-volt storage battery. Caddisflies which were attracted to the light source entered the jar, came to rest in the trapped air space and thus captured were raised to the surface. The light was not turned on until it had attained the depth where sampling was desired.

Emergence traps were constructed of 2 inch x 2 inch wooden boards which were placed together to form a square whose inside area was 1 square foot. A dome made of plastic window screen was tacked to the aforementioned frame. The traps which had captured caddisflies were carefully lifted into a boat and the insects were collected in vials of alcohol. The caddisflies seldom escaped because they hesitated to fly
Fig. 2. Navigation buoy and its anchor chain being raised from the river.

Larval Hydropsyche orris mat on a navigation buoy.

Underwater light trap which was used to capture ovipositing caddisflies.

Blacklight caddisfly trap used at Keokuk. Recommended for use in possible control measures.
during the daylight hours and they usually remained motionless on the screen while the trap was lifted from the water.

Two pieces of apparatus were constructed to study the underwater oviposition habits of adult caddisflies. A system of wooden floats was rigged whereby one float remained at the surface and was anchored to the river bottom by a sash weight. Another float was similarly anchored but was adjusted so that it floated at varying depths beneath the surface of the water. The two anchors were connected to each other by a 15-foot nylon line. Both floats were made of 12-inch pieces of 6 inch x 6 inch wooden plank and the apparatus was set in such a manner that the two anchors and their buoys were 15 feet apart. The anchors and their interconnecting cord sank a short distance into the silt of the river bottom and it was assumed that female caddisflies, therefore, could not walk from the visible float to the submerged float via the interconnecting line. If caddisflies were to oviposit on the submerged float they would be forced to find it while swimming underwater or by walking on the bottom of the river and ascending the anchor cord.

A second piece of equipment was constructed to determine the depth at which maximum caddisfly oviposition occurred. A wooden dowel 2 inches in diameter and 12 feet long was weighted with lead at one end so that it floated vertically with its unweighted end protruding 1 foot out of the water. The pole was anchored by a short length of cord to a sash
weight. After a specified period of time in the water the pole was lifted and the number of egg masses was tallied for each succeeding foot of depth.

It was found desirable to take nightly quantitative samples of adult caddisflies at Keokuk. The operation of a light trap in the downtown area each night seemed impractical as well as time-consuming, however, and an alternative method of sampling was devised. A restaurant was found which remained open until past 10 p.m., 7 days a week. This establishment, which was only 2 blocks from the river, had blue argon-mercury vapor lights in its window. At 10 p.m. each night a sample was taken of the insects which had collected on the lighted window. A collecting pan (Fig. 3) was filled one-half full with 75% alcohol and the pan was pushed up the window from the bottom to a height of about 8 feet. Most of the insects congregated about the middle of the window where the light was brightest, thus the 6-inch-wide swath began at the bottom of the window and ended where there were very few insects. Two sweeps with the pan were made each night, one on the left and one on the right side of the window. Both collections were made in the same pan, one immediately following the other, and the insects, alcohol and an identifying label were transferred from the pan to a one-pint bottle for temporary storage. The whole procedure took less than 2 minutes.

At intervals throughout the summer, when a number of pint bottles of insects had accumulated, the insects were transferred to more suitable
Lotie aquarium used to rear and observe hydropsychid larvae.

Collecting pan, funnel, sections of glass tubing and curtain material used to collect, concentrate and store large numbers of small insects. Photograph by Louis Facto.

Experimental light trap which tested three types of lights as caddisfly attractants.

A compartment of the experimental light trap. A blacklight lamp is suspended over a pan of detergent water. Note that the front of the trap is hinged.
containers. The insects and alcohol in the pint bottle were swirled around and poured quickly through a funnel into a 3-inch section of one-half inch glass tubing (Fig. 3). The lower end of each tube was covered with Nylon curtain material which was held in place by a rubber band. The alcohol passed readily through the curtain material but the insects remained in the tube. The label was then placed in the tube and a piece of netting was fastened over the open end of the tube with another rubber band. The sealed tubes were stored in a large jar of alcohol. Since both ends of the tube were covered with mesh, alcohol was free to circulate through the tubes. This system allowed the preservative to be changed in all of the vials simultaneously. The greatest advantage to this system, however, was elimination of the tedious job of stuffing hundreds of small insects into vials with forceps. The insects also received less damage from handling by this method, since they were never picked up with forceps. This method was also used for caddisfly larvae and for mayfly adults and nymphs.

The window samples were analyzed in the laboratory and the Ephemeroptera and Trichoptera were sorted out. Trichoptera were separated further and the specimens of Hydropsyche orris, Cheumatopsyche campyla and Potamyia flava were sexed and counted. If the sample contained less than 150 of a particular species, all of the individuals of that species were sexed. If the sample was estimated to contain well
over 150 individuals, however, 100 of that species were examined and the resulting sex ratio was applied to the whole species sample. Trichoptera, other than the three aforementioned species, were not identified but were preserved for future study.

Window samples were first taken on June 25, 1957 and they were continued until September 10 of that year when field work was discontinued for the summer. Workers were hired in 1958 to take window samples during the spring and fall when the investigator could not be in the field. Caddisflies were thus taken at the window as early as May 6 and as late as October 6 during the 1958 season.

In 1953 Philipson described a method by which he successfully reared *Hydropsyche instabilis*, *Wormaldia subnigra* and *Polycentropis flavomaculatus* larvae to adults. He used motor-driven stirrers which turned at 65 r.p.m. and circulated the water in 2-pound glass jam jars which served as aquaria.

An observation aquarium consisting of a standard 28 x 7 x 10 inch classroom aquarium and an electric stirrer was constructed (Fig. 3) so that oviposition could be observed and so that caddisflies could be reared through a complete generation from eggs through adults. Standing on edge in the aquarium was a 2-inch thick, concrete partition which was as high as the aquarium but 6 inches less than the aquarium in length. At one end of the aquarium a one-quarter horse power electric motor
turned a propeller at about 1728 r.p.m. and thus caused a current to flow around the cement slab. The electric motor used in this experiment was sufficiently powerful to run for months without burning out. A flat, 2 1/2 inch, aluminum disc with incisions around its periphery served as the propeller. A screen box fitted with a net sleeve covered the aquarium. Adult caddisflies, which were introduced into the screen cage via the net sleeve, laid their eggs on the cement slab, on the aquarium floor or on the glass. As the female flies descended beneath the surface of the water to lay their eggs, their movements were traced by an observer on the aquarium glass with a wax pencil. The time of each observation was also written on the aquarium glass with the wax pencil. Submerged insects could not be identified as to species because their features were obscured by the silvery air space which was carried on their wings. It was found necessary, therefore, to put only one species into the lotic aquarium at a time. The larvae, which hatched from eggs in the aquarium, constructed their nets on the concrete partition, along the floor or in the corners of the aquarium. About 2 gallons of water were siphoned from the rearing aquarium each day and they were replaced with an equal volume of concentrated, plankton-rich water from the river or with river water which had been fertilized with commercial fertilizer and allowed to develop an algal bloom in the sunlight. The adult caddisflies which died and fragmented in the apparatus were most
likely also consumed in part by the larvae. The water temperature in the aquarium ranged from 70° to 85° F. during the experiment. A vibrator air pump bubbled air constantly into the water of the aquarium. This apparatus will henceforth be referred to as the lotic aquarium.

Large numbers of caddisflies of a particular species were obtained for use in oviposition experiments in the following manner. A mass of insects was netted from around a light at night and the insects were lightly anesthetized with ethyl ether. The individuals of the desired species of caddisfly were quickly isolated from the rest of the insects under a stereoscopic microscope. When the selected caddisflies had recovered from the effects of the anesthetic they were utilized in various oviposition experiments.

Several other techniques were used in an effort to induce the caddisflies to oviposit in the laboratory. Oviposition vials patterned after those of Weerekoon (1956) were tried. These glass tubes were loosely stoppered at both ends and contained a wet strip of blotter. Paper bags were also used as oviposition containers. Caddisflies were placed in paper bags, the bags were sealed with paper clips and floated in pans of water. The caddisflies were then able to rest on the dry paper or to lay eggs on the wet portion of the bag. Both methods proved successful on only a few occasions.

A technique employing polyethylene bags proved to be quite useful.
The caddisflies which had recovered from their anesthesia were placed in small, thin-gauge polyethylene bags. A wad of paper toweling, which was inserted in the mouth of the bag, was held in position with a rubber band. The polyethylene bag was floated in water and the paper toweling quickly became saturated. A high relative humidity was maintained in the bag and since polyethylene is permeable to oxygen and carbon dioxide the oxygen supply in the bag was undoubtedly ample. When egg masses were found on the bag, a patch of the polyethylene was cut out with scissors and the patch was floated egg side down in a Petri dish of water. Since the polyethylene is transparent the egg masses could be readily observed with a microscope as development occurred. If desired, the polyethylene patch can be used as a crude cover slip when it is mounted egg side down in the water on a microscope slide.

The most successful method of obtaining large numbers of egg masses was the following. An aquarium was filled half full of water and an untreated board was floated on the water. The top of the aquarium was covered with netting and the caddisflies were introduced through a sleeve. They oviposited on all sides of the water-soaked board. If desired, a chip of wood containing an egg mass could then be easily removed with a knife and transferred to a Petri dish of water for incubation of the eggs.

Mating swarms of caddisflies were observed from the ground with
binoculars or with the naked eye. At times the swarms formed around a structure which could be climbed and observations were then made within the swarm itself. The sex ratio of the insects within a swarm was determined by examining a sample of the insects which were collected by sweeping an insect net through the swarm.

Caddisfly larvae were collected in several ways. Hydropsychid larvae were usually found attached to large rocks and other cumbersome, submerged objects. Consequently, dredging with either the Petersen or the Ekman dredge was futile. Samples were frequently collected from rocks by wading below the dam at Keokuk, but in most of the area below the dam the water was too swift and too deep to wade. Samples were collected in water up to 7 feet deep by swimming in the following manner. A boat was anchored over the sampling location and by using a long anchor lead the boat was prevented from dragging its anchor in the swift current. The swimmer wore canvas sneakers as protection against being cut on the trash which littered the river bottom. A line was secured to the sampler's wrist and the line was played out by a man in the boat as the sampler dived to the bottom and picked up several rocks. In addition to being a safety precaution the line allowed the swimmer to be pulled back to the boat after each dive. This method proved very satisfactory as it enabled the swimmer to sample without becoming fatigued by swimming against the current while carrying samples.
Hydropsychid larvae were kept alive and transported in the following manner. A large rectangular enameled pan was filled half full with river water and a paper towel was floated on the surface of the water. Caddis-fly larvae were distributed on top of the towel and another towel was placed atop the larvae. The towels quickly became saturated and successive layers of caddisfly larvae and towels were added. When all of the larvae had been layered, the water was drained from the pan except for about one-fourth inch in the bottom. In addition to providing a large surface for oxygen diffusion the paper towels effectively separated the larvae and prevented them from killing each other. Larvae have been kept alive for 30 hours in this way and they would have undoubtedly remained viable much longer.

A measurement of the water velocity was made at each sampling location with a Gurley current meter. Three readings were taken at each station and they were averaged to obtain an estimate of the water velocity. The lead weight of the meter was suspended beneath the water vanes and the apparatus was lowered until the weight just touched the bottom. The water vanes, which measured the water velocity, were then about 5 inches above the river bottom. It is recognized that this technique does not measure the water velocity on the surfaces of the rocks where the larvae live, instead it measures the current to which an area of river is subjected. In this study it was deemed more desirable to work with water velocities
and their relation to larval populations than to the effect of water velocity upon individual larvae. Consequently, the aforementioned technique was used in lieu of a more refined one.

The United States Coast Guard maintains a large series of navigation buoys which mark the navigable channel of the Mississippi River. These buoys are periodically lifted from the water, cleaned, repainted and replaced (Fig. 2). An excellent opportunity for sampling caddisfly larvae presented itself when these buoys were raised. A log book is maintained by the captain of the buoy tender and a complete record is kept of the time each buoy is cleaned or replaced. The exact position of each buoy is then plotted on a map and each buoy is assigned a mile number, thus the location of each sampling station was plotted exactly.

A series of samples was taken during the ice-free part of each year from buoys which had been in the water for at least 6 months and which had obviously not been recently scoured clean by ice floes. A barnacle-scraping iron was utilized to scrape several swathes through the larval mass on the upstream side of the buoy and the whole sample, including larvae, nets, rust and paint was run through several changes of alcohol and preserved. In the writer's absence, one of the crew of the U.S.C.G. C. Lantana collected samples. A subsample was later taken from the original sample in the laboratory and all of the larvae and pupae were hand picked from the debris, measured and counted.
In addition, estimates were made of the comparative abundance of larvae on the buoy chains throughout the river segment. The chains of the buoys are always in the water, are not cleaned, and are beyond the reach of scouring action of the spring ice floes. The relative volume of the larvae and their cases was described as "light", "medium" or "heavy" if the links of the chain were clean, partially closed or completely closed by the larvae and their structures. Each chain was so designated as it was raised from the water and a qualitative larval sample was quickly taken.

The maximum head capsule width of the caddisfly larvae was measured with an ocular micrometer.

All photography unless otherwise stated was done by the author with a Tower 23, single lens reflex, 35 mm. camera. A bellowscope was used for extreme close-ups.

**Hydropsyche orris Ross**

**Adults**

During the day, the adults of this species remain in shady, sheltered locations. Shrubbery, the undersides of bridges and the leeward walls of buildings are favored resting places. If their resting places become exposed to the sun or they are disturbed they fly rapidly and erratically to another nearby location. They are quite docile, however, and they may
be caught easily by hand when they are at rest. The newly emerged adults are distinctly marked with gray and white but as they become older these markings are worn off and the caddisflies become a uniform slate-grey color. After two days in captivity the distinctive markings are almost always rubbed off, even when the adults are kept in a large cage. Variations in color pattern make field identifications difficult without considerable practice. H. orris and C. campyla are the most difficult species to distinguish from one another in the field because their markings are very similar. Adults of H. orris are larger, however, than adults of Cheumatopsyche campyla and Potamyia flava which are the other most common species.

At dusk throughout the summer, and to a lesser extent during the pre-dawn hours, the mating activity of H. orris reaches peaks. At dusk the caddisflies swarm above and in the lee of the trees along the Mississippi River bluff at Keokuk, Iowa (Fig. 1). From the river the swarms appear as dense plumes of black smoke which undulate slowly in the breeze. This species also swarms on the lee side of objects such as buildings, towers, dragline booms and light poles which are near the river. The swarms occur in the same locations nightly and they persist until after darkness has fallen. While the swarms are familiar phenomena at Keokuk, many river residents two miles from the Keokuk dam have never observed the mating swarms. Swarms were never personally observed more than a
mile up or downstream from the dam. The swarms are composed almost entirely of males and net captures from these swarms yield only an occasional female (e.g., 179 males and one female, 55 males and 0 females, 120 males and 1 female).

Corbet and Tjønneland (1955) suggest that in most of the African species of caddisflies which they studied, flight is inhibited by light intensities which are above those of crepuscular intensity. They suggest further that flight may take place at all intensities below the threshold for inhibition but that it is stimulated strongly by light of a crepuscular intensity and that up to the threshold for inhibition there may be a positive correlation between the level of activity and light intensity.

_H. orris_ was observed to mate, without swarming, during the daylight hours and such mating was especially prevalent on dull, overcast days. Light of a low intensity definitely seems to stimulate the mating behavior pattern in _H. orris_. On clear days, mating swarms occur during the very early and very late daylight hours, but on dark overcast days meager mating swarms were observed during most of the daylight hours. An extreme example of daytime swarming was observed on the afternoon of June 22, 1958 when it was very dark and cool in advance of a heavy rain. At 4:30 p.m. C.S.T. dense swarms formed at many places on Lock and Dam 19 and the caddisflies became so numerous that most of the tourists left. No swarms of caddisflies were observed above the bluff at this time,
however. On a clear day, at this time of year, swarming would not usually occur until about 7:30 p.m.

Adult *H. orris* which were retained in a large glass container in the laboratory exhibited a marked light intensity preference. During the day the caddisflies moved little in their container and remained dispersed randomly about its surface. At dusk, or when the sky became extremely overcast, the caddisflies milled around excitedly but were always most concentrated on the side of the cage toward the windows. When the cage was turned 180 degrees, they quickly shifted their positions and once again congregated on the window side. When a 100-watt incandescent lamp was held 5 feet away from the cage, on the side opposite the window, the caddisflies immediately left the window side and dispersed, but did not become attracted to the incandescent lamp. When the lamp was turned off they once again returned to the window side of the cage.

Corbet and Tjønneland (1955) suggest that Trichoptera may have a lunar periodicity of activity at Jinja, Uganda. In the Trichoptera which they investigated at Lake Victoria, the all-night flight activity was significantly greater during a night when the age of the moon was 17.5 days. No attempt was made at Keokuk, however, to determine if the Hydropsychidae caddisflies exhibited a lunar periodicity of activity.

Mating swarms have been observed during extremes in weather at Keokuk. On the evening of May 31, 1958, large swarms were seen over
the trees along the river bluff at Keokuk. The swarms were very active in spite of a very strong, gusty wind and a driving rain. The swarms were repeatedly forced down to the level of the street by the wind and rain, but they rose again between gusts to the level of the tree tops. Mating pairs fluttered down continually during the storm and when darkness fell the swarming was still in progress, even though the rain and wind were severe.

The males within the swarms maintain a rapid up and down, zig-zag flight pattern. The mass behaves as a unit and responds quickly to gusts of wind. A strong gust of wind may blow the tail of the swarm out and away from the head of the swarm but the dispersed individuals recover quickly and the swarm contracts to become a dense mass again.

The female caddisflies exhibit a deliberate, straight-line flight pattern and those females which fly through a swarm or very near to one are attacked by the males. The male seizes the abdomen of the female with his legs and clings to her. He ceases to fly and his dead weight causes the female fly to flutter slowly to the ground or to the object around which the swarm occurred. The male appears to be partially in copula with the female during her descent from the swarm. When they land, the wings of the female rest upon those of the male. The male turns around after the landing and assumes the characteristic caddisfly mating position with the male and female facing in opposite directions.
The male then spreads his wings and lays them over those of the female. If the caddisflies are disturbed, or if they land on the water, the female drags the male behind her as she runs on the ground or skims along the surface of the water.

The objects around which swarming takes place are usually large enough to provide some shelter from the wind. On windless nights, however, mating swarms may form all around an object instead of just in the lee of the object as they do under breezy conditions. The caddisflies, instead of using the objects as windbreaks, often seem to be using them as visual landmarks as proposed by Weerekoon (1956). Such an object may be a tree limb, a light pole, a wall, a flag pole, or the eaves of a building.

A type of caddisfly mating activity similar to that of *H. orris* has been reported by Betten (1934, p. 85).

At about 7 o'clock in the evening of July 30th while walking along the Niagara River some distance above the falls, I observed that there were numerous swarms of *Chimarrha* mostly out of reach and extending as high as the tree tops. The pairs came down and settled on vegetation and were apparently not fully copulated while in the air.

A definite descendence of caddisflies is seen to take place from the Keokuk bluff, where the swarming is taking place, toward the river. Samples of these caddisflies were collected with an insect net as the caddisflies flew toward the river. About as many males as females were collected. The significance of this descendence is not understood at the
present time.

The female caddisfly seems to have scent attractant glands along the sides of her abdomen. When a female is approached by males, while they are on a surface such as a window or in a laboratory container, the males run excitedly around the female and nuzzle her along the sides of her abdomen before mating. Scent glands exist as eversible structures arising from behind the head in the genus *Hydroptila* (Mosely, 1919, 1924; Eltringham, 1919).

Most females mated more than once under laboratory conditions. Mating pairs which were collected as they descended from a swarm often remained in continuous copulation for 12 hours or more. If the pairs were separated, mating usually took place again, often several times.

Silfvenius (1906) reported the duration of copulation of *Hydropsyche angustipennis* to be from 8 a.m. to 10 p.m. in several pairs. He also reported that copulation is commonly repeated in *H. angustipennis*.

**Oviposition**

During the twilight hours, when the caddisflies were swarming, the surface of the water above the dam was a mass of ripples and it appeared that a light rain was falling. On occasion, some of the marks were made by rising methane gas bubbles but close inspection revealed that most of the tiny swirls on the surface were caused by caddisflies emerging from
beneath the surface of the water. In addition to the small single swirls which were caused by caddisflies entering or leaving the water, there were swirls caused by caddisflies which repeatedly skipped over the water. These skipping caddisflies were observed to touch the surface as many as 37 times in succession. After the last skip, the caddisflies were often observed to climb straight upward and slightly toward the Keokuk shore until they were lost from view.

In an effort to determine the significance of the skipping, a boat was anchored in an area of high caddisfly activity and an insect net was used to catch only the caddisflies which had been observed to skip repeatedly. The captured caddisflies, on the evening of June 27, 1958, included six females of *H. orris*, one male of *H. orris* and one female of *C. campyla*. Three of the *H. orris* females contained only well-developed eggs, two contained well-developed eggs plus some small egg primordia in the proximal ends of their ovarioles. The remaining female *H. orris* was void of eggs except for a small number of minute ones. The female *C. campyla* contained well-developed eggs only. The significance of the skipping activity remains obscure.

Weerekoon (1956) has observed that the ovipositing female *Mystacides azurea* dives from a height of about a meter to the surface of the water where she rests for about a second before flying again. She repeats this procedure a number of times before a spherical mass of
eggs is washed into the water from the tip of the abdomen. Although Weerekoon suggested that the succession of dives seems necessary for the extrusion of the egg mass, he was unable to determine what function it serves.

On July 11, 1957, two emergence traps were set out at each of three stations above the dam at Keokuk. These traps were operated on most nights until September 4, 1957. The catches of the traps are summarized for the three most abundant species of caddisflies in Table 1.

The results of this experiment show that the preponderance of the caddisflies which leave the water on a given night are females. Most of the females which were captured have obviously not emerged from pupae in the traps. If they had done so, the sex ratio would be closer to one. The captured females contained mature eggs or were void of eggs and they were assumed to be returning to the surface after they had descended into the water to lay their eggs. Great care must be taken, consequently, in using emergence trap catches as a measure of caddisfly populations. A count of males alone would probably give a truer account than a tally of both males and females. No evidence was found to indicate that the male enters the water again after its initial emergence.

Morphological modifications for swimming have been described in the caddisflies of the Amphipsyche group (McLachlan, 1878). Badcock (1953), however, found no such adaptations in H. angustipennis. Betten
Table 1. Weekly total of caddisflies captured in emergence traps above the Keokuk dam, August 12, 1957 to September 9, 1957

<table>
<thead>
<tr>
<th>First day of week</th>
<th>H. orris</th>
<th>P. flava</th>
<th>C. campyla</th>
<th>Unidentified caddisflies</th>
<th>Total trap nights</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
<td>Male</td>
<td>Female</td>
<td>Male</td>
</tr>
<tr>
<td>Aug. 12</td>
<td>1</td>
<td>32</td>
<td>1</td>
<td>55</td>
<td>2</td>
</tr>
<tr>
<td>Aug. 19</td>
<td>2</td>
<td>34</td>
<td>0</td>
<td>76</td>
<td>6</td>
</tr>
<tr>
<td>Aug. 26</td>
<td>1</td>
<td>28</td>
<td>0</td>
<td>39</td>
<td>1</td>
</tr>
<tr>
<td>Sept. 2</td>
<td>0</td>
<td>36</td>
<td>0</td>
<td>39</td>
<td>0</td>
</tr>
<tr>
<td>Totals</td>
<td>4</td>
<td>130</td>
<td>1</td>
<td>209</td>
<td>9</td>
</tr>
</tbody>
</table>
(1931) states that in the females of many species of Hydropsychidae and of Rhyacophilidae the tibiae and tarsi of the middle legs are very much dilated and flattened. The midtarsi and midtibiae of female _H. orris_, _C. campyla_ and _P. flava_ are flattened whereas the corresponding structures of the male are not.

A light trap (described previously) was utilized to determine which caddisfly species enter the water to lay their eggs, and to also determine how deep they swim. To avoid possible contamination of the trap by aerial insects, the light was lowered into the water before it was turned on. Before the apparatus was taken from the water, an insect net was pulled snugly across the opening of the jar to determine if any of the captured flies had emerged from pupae while in the trap. If they had done so, their floating pupal skins would have been caught by the net. No flies were found to have emerged from pupae in the trap. Also, no males of any species were collected in the underwater light trap. The captured females either contained eggs which were full sized and loose in the ovarioles or they were void of macroscopic primordia. _H. orris_, _P. flava_, and _C. campyla_ were taken at considerable depths where they are presumed to be laying eggs (Table 2).

On July 30 another experiment was initiated in an effort to determine (1) if the caddisflies must walk down some partly exposed object into the water or if they are capable of finding small, completely submerged
Table 2. Catches made of female caddisflies in an underwater light trap at Keokuk, Iowa

<table>
<thead>
<tr>
<th>Date</th>
<th>Time</th>
<th>Operation time in minutes</th>
<th>Depth ft.</th>
<th>H. orris</th>
<th>C. campyla</th>
<th>P. flava</th>
<th>Unidentified</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aug. 18, 1957</td>
<td>7:35 PM</td>
<td>10</td>
<td>3</td>
<td>3</td>
<td>41</td>
<td>28</td>
<td>5</td>
</tr>
<tr>
<td>Aug. 19, 1957</td>
<td>7:40 PM</td>
<td>5</td>
<td>3</td>
<td>9</td>
<td>2</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>June 27, 1958</td>
<td>8:00 PM</td>
<td>30</td>
<td>2</td>
<td>5</td>
<td>32</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Aug. 4, 1958</td>
<td>7:35 PM</td>
<td>10</td>
<td>6</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Aug. 16, 1958</td>
<td>7:35 PM</td>
<td>7</td>
<td>3</td>
<td>0</td>
<td>220</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Aug. 16, 1958</td>
<td>7:45 PM</td>
<td>7</td>
<td>12</td>
<td>1</td>
<td>8</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>Aug. 16, 1958</td>
<td>7:55 PM</td>
<td>7</td>
<td>20</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Aug. 18, 1958</td>
<td>7:35 PM</td>
<td>7</td>
<td>3</td>
<td>0</td>
<td>29</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Aug. 18, 1958</td>
<td>7:45 PM</td>
<td>7</td>
<td>12</td>
<td>1</td>
<td>3</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Aug. 18, 1958</td>
<td>7:55 PM</td>
<td>7</td>
<td>20</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
</tbody>
</table>
objects upon which to lay their eggs, and (2) the depths at which the caddisflies lay their eggs. A tandem float arrangement previously described was set out in 24 feet of still water, 100 feet upstream from the dry dock, at the Keokuk dam. The submerged float was adjusted to remain 4 feet beneath the surface of the water. When the floats were examined 6 days later more caddisfly egg masses were found per area on the submerged float than on the surface float.

This experiment was repeated four more times, with the lower float being as deep as 24 feet beneath the surface. In all instances numerous egg masses were found on the lower float. No attempt was made to determine to which species the egg masses belonged.

It is evident from the foregoing experiments that several species of hydropsychid caddisflies descend to considerable depths to lay their eggs. They need not descend via a solid object into the water. To the contrary, they seem quite able to locate and lay eggs upon objects which lie as deep as 24 feet and which are not visible from the surface. The females may not find the submerged objects too readily as evidenced by the fact that most of the females in the emergence traps still contained mature eggs.

On August 23, 1958 a simple experiment was initiated to determine at which depth caddisfly eggs were most often laid. A wooden dowel (previously described) was placed in the water on this date. The dowel was removed from the water after 6 days and the number of egg masses was tallied for each succeeding foot of depth (Table 3). No attempt was made to determine
Table 3. Relationship between water depth and caddisfly oviposition on a 12-foot weighted wooden dowel, August 23-29, 1958

<table>
<thead>
<tr>
<th>Depth interval (feet)</th>
<th>0-1</th>
<th>1-2</th>
<th>2-3</th>
<th>3-4</th>
<th>4-5</th>
<th>5-6</th>
<th>6-7</th>
<th>7-8</th>
<th>8-9</th>
<th>9-10</th>
<th>10-11</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg masses</td>
<td>0</td>
<td>18</td>
<td>33</td>
<td>68</td>
<td>56</td>
<td>30</td>
<td>28</td>
<td>21</td>
<td>18</td>
<td>14</td>
<td>24</td>
</tr>
</tbody>
</table>

to which species the egg masses belonged. Oviposition was most concentrated at a depth of about 3 to 5 feet.

Although several attempts were made to determine the length of time between mating and oviposition for *H. orris*, the time was not fixed with certainty. Large numbers of mating pairs were placed in large containers and were provided with cotton swabs saturated with water and with sugar water. Pans of water were placed in the cages in the hope that the caddisflies would lay eggs in them. No eggs were laid by *H. orris* females in these experiments even though the females copulated repeatedly as late as the fifth day and remained alive for as long as 10 days. Sillvenius (1906) found that *Hydropsyche angustipennis* oviposited during the night following insemination. One female *H. colonica* which was kept alive by Glasgow (1936) for 6 days died without laying its eggs. Glasgow suggests that female *H. colonica* live for some time prior to oviposition as the ovaries are much smaller in a newly emerged specimen than they are later. Male
H. colonica lived longer than females, the longest life for a male being 11 days.

Female H. orris lived as long as 10 days and males as long as 13 days in the previously described mating pair experiment. Males and females usually began dying on the second day of the experiment and the death rate continued quite uniformly for both sexes throughout a 10-day period. Caddisflies which were not supplied with water generally died within 3 days. H. orris which were provided with sugar solution in addition to water lived an average of about 2 days longer than those which received water only.

From experiments to be described later it appeared that H. orris females die soon after oviposition. If this is the case the life of the H. orris females may have been prolonged in the preceding experiments because they did not lay their eggs.

Unfortunately adults known to have been newly emerged were never available for longevity experiments. It was assumed, however, that the copulating males and females which descended from mating swarms were quite recently emerged. It seems probable that the life span of H. orris adults is at most 15 days. Most likely it is considerably less than this in nature. Other authors have also felt that hydropsychid caddisflies are comparatively short lived. In fact, Corbet and Tjønneland (1955) considered it likely that the adult Trichoptera which they studied at Lake
Victoria lived only about two days.

Twelve *H. orris* females which were collected by means of the underwater light trap were introduced into the screen cage of the lotic aquarium. One-half hour later two of the females were found dying on the water surface. When dissected they were found to be void of macroscopic eggs. The other females were not to be found on the following morning and were presumed to have died and been destroyed by the propeller. It seems probable that *H. orris* females die soon after they have laid their eggs. The small undeveloped eggs which are often found in the proximal ends of the ovarioles probably never develop. *H. orris* females have been observed in the laboratory to die after only a portion of their eggs were laid. The eggs which remained in the ovarioles were difficult to dissect out and were assumed, therefore, to be not fully developed. Glasgow (1936) found that none of the female *Hydropsyche colonica* which he collected were void of eggs and he suggested, therefore, that the females die soon after they have laid their eggs. Badcock (1953) observed a female *H. angustipennis* to live for a day and a half following oviposition.

The form of the female trichopteran reproductive organs has been illustrated by Cholodkovsky (1913). He found the ovaries to be composed of many metamerically arranged meroistic egg tubes.

*H. orris* females were found to have small egg products in the proximal ends of their vitellaria at all times. When female *H. orris*, which
were found dying in longevity experiments, were dissected, their eggs tumbled loosely from the ovarioles. Females which were collected in the underwater light trap also contained eggs which were held loosely in the ovarioles. Females which were collected as they descended from mating swarms, on the other hand, contained eggs which were very difficult to remove from the ovaries even though the eggs were fully as large as those of the females in the preceding two instances. Apparently a short time, at most a day or two, elapses between mating and oviposition. During this time the eggs complete their development. Four female H. orris, which died in captivity after they had mated, contained 465, 371, 331 and 423 mature eggs, respectively.

Larvae

A female H. orris which had mated on June 22, 1958 was seen to be dying on June 26 and its eggs were dissected into a Petri dish of river water. Larvae began to hatch in 8 days and continued to do so until the eleventh day. It is unlikely that the eggs were fertilized intra-ovarially or that they were accidentally fertilized during dissection. Probably the eggs developed parthenogenetically. This group of eggs was the only batch of H. orris eggs to be hatched successfully although several other attempts were made. Glasgow (1936) reported that the eggs of Hydropsyche colonica take at least 16 days to hatch.
The newly hatched *H. orris* larvae are virtually colorless, except for their prominent eye spots, and they are easily recognizable as caddisfly larvae. Eye spots were prominent for several days before the larvae hatched. In addition to crawling over the substrate, the first instar larvae also wriggle much like mosquito larvae. Such capable swimmers could obviously exist as planktonic organisms during their first stadium.

Most first instar Trichoptera larvae are capable of swimming and first instar hydropsychid larvae have been observed to do so in a laboratory aquarium (Siltala, 1907). The first instar larva of *Hydropsyche colonica* swims actively, is positively phototrophic and does not exhibit marked thigmotropism. After the first instar the larva does not swim, is phototropically indifferent and is strongly thigmotropic, preferring an inverted position (Glasgow, 1936). Weerekoon (1956) has reported that the first instar larvae of *Phryganea* sp. are planktonic and that larval Trichoptera most likely repopulate McGougall Bank in Loch Lomond as plankters.

The tandem float apparatus which was used in oviposition experiments also yielded information concerning the wanderings of caddisfly larvae. The float apparatus was set out and recovered four times and each time hydropsychid or psychomyiid larvae were found on the submerged float. The larvae included 2 large *H. orris* larvae (10 mm. long), 14 *Psychomyiidae* sp. larvae (7-10 mm. long) and 1 *Potamyia flava* larva (8 mm. long). A single first or second instar larva was collected from the buoys
but it could not be identified except as the family Hydropsychidae. It is probable that more larvae of this size existed on the buoys but were not found because of their extremely small size. Numerous Cladocera, Hydra, chironomid larvae and Amphipoda were also found on the buoys.

The large hydropsychid and psychomyiid larvae could have reached the floats (1) by actively swimming, (2) by crawling over the bottom and up the anchor lines, or (3) by drifting with the current, either alone or as a rider on water-carried debris. The larvae, except for the first instar, have never been seen to swim in the laboratory and it seems unlikely that they would be able to do so in the river. The floats were anchored in a fine silt bottom and it is improbable that the larvae crawled over the bottom to the anchor lines. It seems very possible that current-carried trash could have transported the larvae to the floats. At no time, however, was debris found to be lodged on the floats or the float lines. Glasgow (1936) found that if the larva of Hydropsyche colonica is dislodged from its shelter it attaches its silk thread to some object as it is swept past. In this way the larva anchors itself until it has regained a foothold. H. orris and P. flava larvae, when placed in the lotic aquarium, have been observed to spin threads and to use them as anchor lines. The threads were spun, however, after the larva had become attached to an object and larvae were never seen to spin a thread while they were being swept along by the current. The larvae are quick to grasp an object with
their legs as they are swept past and they cling tenaciously with the claws on their anal prolegs. If the larva spins a strand of silk and is then dislodged by the current, it seems to have considerable difficulty in returning to its foothold unless it is swept back by the current. Dying larvae often have been observed to swing in the current on the end of their silken line until they died and decomposed.

It is possible that caddisfly larvae drift downstream using silken threads to catch the water currents much as small spiders "balloon" for long distances via air currents. No evidence of this was observed in the laboratory, however.

Larval *H. orris* occur in greatest abundance in areas of the river where the current is fast and where there are solid, silt-free objects for them to build their cases and nets upon. *H. orris* larvae were never observed to inhabit wooden structures as *C. campyla* and *P. flava* often do.

Detailed descriptions of *Hydropsyche* larval constructions and nets have been prepared by Clarke (1884), Fielde (1887) and Noyes (1914). Wesenberg-Lund (1911) compiled all of the records of larval net construction and, in addition, presented complete descriptions of the nets of *Hydropsyche pellucida* and *Hydropsyche angustipennis*. Additional descriptions and drawings of the houses and nets of *Hydropsyche* sp. were provided by Wesenberg-Lund in 1913. In 1925 Alm described the larval tube-house and catching net of *H. angustipennis* in great detail. His
descriptions suit the larval tube and net of *Hydropsyche orris* remarkably well and
discussion of net construction is especially detailed. This portion of
Alm's work appears to have been neglected in the English literature. It
was deemed desirable, therefore, to present the following direct trans­
lation of the most pertinent portions of his paper.

The actual catch net is very sturdy, spun from thick threads
which cross one another regularly in quadrangular fashion (Fig.
12a). These threads, which are about .016 mm in diameter, are,
as Lucas and Wesenberg-Lund have already proved, double threads.
Observing a part of the net under the microscope, one sees that
the threads going in one direction are spun first, and that after
the threads crossing these have been drawn across, they are
glued together at the points of intersection (Fig. 12b). I have
studied many nets to gain some clarity about the construction of
them.

The quadrangular meshes, which are 0.33 to 0.66 mm in size,
are not equal everywhere, but the smallest and also the most even
ones are situated in the lower and central parts of the net. From
here the meshes radiate, so to speak, in two directions to become
largest and most irregular in the upper and peripheral parts of the
net. By examinations with a magnifying glass I have become con­
vinced that the threads of the net must be spun in one direction
first. These threads are quite straight and upon them the cross­
wise threads are fastened. I think that the larva, when spinning the
net, first begins to build the forecourt and therewith the frame at
the sides of the mouth of the tube. After almost having completed
this, it spins cross threads from the mouth between the sides of the
frame. Some of these threads are often quite thick, apparently
originated from several spinning threads. Those threads crossing
the former are probably spun later. (pp. 264-265)

Quite unique is the great cleanness of the catch net of *Hydro­
psyche*. Almost never does one find a dirty net, which means that
the larva must have a means to clean and polish it. I believe that
the forelegs perform this task. On the tarsi of this pair of legs
are situated thick, stiff bristles or setae spaced at regular inter­
vals, and these must be very well suited to carry out the cleaning
of the net. (p. 266)
When I put a specimen into a small bowl, it mostly crawled around restlessly. Occasionally it stretched out threads in all directions, especially in the corners. I was later able, after disposing of the water, to examine the threads and their method of attachment under the microscope. The threads, as I have already pointed out, are very thick and always double. They are usually straight; here and there, however, fastened partly to the substrate and partly to each other. These points offer special interest. When the thread is fastened to the substrate or other threads, it seems to be flattened, often, in finer threads, completely dissolved. Almost always the double thread is dissolved in both its branches, and furthermore, it seems to flow out in a sticky secretion (Table X, Fig. 23). I emphasize this especially, for no special secretion is apparently discharged, but one gathers the impression that the thread immediately upon discharge is sticky, still flexible and pliable and that afterwards, when it is drawn out, it stiffens in the water.

The larva, when spinning, seems first to press the labium against the substrate. When it then turns back, the fastened thread runs out of the labium. It is then fastened to a new point, by strongly pressing the labium. It is, therefore, very clear that the thread, flexible and sticky at the discharge, is simply glued to the substrate. The thread is also very elastic, which one may easily observe when the larva is pulling it along.

The same applies also for the threads in the net areas. These are also apparently simply glued to one another. I can, therefore, not agree with Wesenberg-Lund when he says that wherever threads cross each other, the corners are strengthened by a special secretion. This I have been unable to see, and the figure drawn by Wesenberg-Lund does not agree with mine. As is to be seen from this, the thread which is drawn over the first one is flattened at the intersecting point and thereby glued to it. A special grainy secretion, as Wesenberg-Lund shows, I am unable to discover (See Fig. 12). (p. 268)

In contrast to the previously mentioned Polycentropidae larvae whose spinning glands probably function interchangeably and, in this connection, were not in steady uninterrupted operation, conditions are just reversed in case of Hydropsychidae. In all Hydropsyche larvae examined by me the spinning glands
on both sides of their whole length were always filled which justifies the assumption that they have no rest period, but are in constant secretion. With this the appearance of the spun thread is in agreement, for it is built up from the secretion of both spinning glands glued together.

In regards to the secretion; it is yellow, oily, recognizable as a thick thread inside the spinning gland (Table X, Fig. 21-22). In cross section it has the appearance of layers which points to an uninterrupted discharge of secretion. (p. 271)

The larval dwellings and catching nets of *H. orris* are illustrated in Fig. 4.

More recently, Philipson (1953) has discussed the case construction and other biology of the larva of *Hydropsyche instabilis*.

The larva of the *H. orris* builds a silken case which it attaches to a firm, rough surface such as rock, cement or rusted iron. The larval case is not a tube, but rather a half tube which rests upon, and is firmly attached to, a substrate by the silken strands which make up the case. If small sand particles, shell fragments or other materials are available, they are incorporated as a reinforcing veneer on the case. Even bryozoan statoblasts have often been observed to be used as a building material. In the laboratory, larvae have constructed perfect cases and nets with no sand at all. In this situation the larvae chose crevices and concavities in which to build their abodes. They circumvented the need for riprap reinforcement by extending a series of silken reinforcing strands to the edges of the concavity in which they lived. Lloyd (1921) states that
Fig. 4.

H. *orris* larval dwellings and catching nets.  

H. *orris* catching net. Note where the net has been patched. Photograph by Louis Facto.  

H. *orris* catching net. Note the double nature of the strands and the flattening of the strands at the points of intersection. Photograph by Louis Facto.
caddisfly larvae secrete glue-like silk through openings in the labium. This silk is produced in large, modified salivary glands similar to those of lepidopterous larvae. Silk is emitted as a liquid which has the remarkable character of adhering to set, silted objects and of hardening immediately after expulsion from the body of the larva. He adds that the silk is not usually spun in fine strands, as is that of the Lepidoptera. Being more glue-like, it may be spread in a homogeneous sheet over the objects to be cemented.

In the Mississippi River, which carries a large volume of soil particles, the larval cases are always sand- or silt-encrusted. Thus reinforced, the cases may even be constructed on convex surfaces.

The screenlike net of *H. orris* is a modified portion of the wall of the larval dwelling (Fig. 4). At first the net is windowlike and it extends from the mouth of the tube backward for about one-third of the tube length. As the tube is made larger, however, the net window seems to increase at a disproportionately rapid rate. The net finally becomes so exaggerated in size that it no longer resembles a window. Instead, it extends forward and upward and appears to be stretched between two armlike supports. The supports are, in reality, segments of the rim of the tube mouth. Water enters the mouth of the larval tube, which may be extremely large, and passes out through the huge screen window. The larva clings to the roof of its case (usually, then, with its back to the
substrate) and gleans food from the screen as it is filtered from the water.

Clarke (1884) presents a description of the net-supporting framework of *Hydropsyche* sp. The framework which she describes could well be that of *H. orris*. She wrote (p. 68), "The supporting framework is always formed of vegetable bits, and is sometimes a simple arch, sometimes a complete ring, and sometimes a short cylinder."

In the lotic aquarium, the larvae had no vegetable matter with which to construct the supporting framework of their nets. They adjusted to the situation by constructing their nets between the sides of the crevices in which they resided. From the foregoing discussion it is obvious that the larvae are very versatile and that no single description can fit all of the *H. orris* cases and nets. *Hydropsyche* nets were photographed as early as 1902 by Simpson.

Abel (1955) stated that the larval cases of *Limnophilus flavicornis*, in addition to protecting the larva, also has the function of shielding the larva from light. She found that naked larvae were very sensitive to blue light (360-500 m/μ) which corresponded closely to the complementary color of the animal. Milne (1938) also found that the caddisfly larval case is not just a protective device. She maintains that it provides for more efficient circulation of water, as evidenced by the fact that naked insects made much more rapid respiratory movements than encased
insects.

Large concentrations of _H. orris_ larvae were found on the buoys which mark the navigable channel of the Mississippi River (Fig. 2). The buoys and their anchor chains are made of iron which is usually pitted and rusty and they provide excellent sites for attachment by the larvae. The buoys rise and fall with fluctuations in water level and because they lie in the main channel of the river they always receive a rapid flow of water. A relatively stable environment is thus afforded the larvae which attach on the buoys during the summer months. Those larvae which overwinter on the buoys are often scoured off by floating ice during the spring breakup, however.

During the summers of 1957 and 1958 over 100 navigation buoys and their anchor chains were examined in the area from Louisiana, Missouri, to Burlington, Iowa. _H. orris_ was found to be the principal trichopteran larva on the buoys and chains throughout the entire river segment. Furthermore, an analysis of the larval populations on the anchor chains indicated that, on any given date, all of the chains were about equally populated with _H. orris_ larvae. It would follow then that this entire main channel segment of the Mississippi River is potentially good _H. orris_ habitat and that the principal limiting factor for large populations is a lack of silt-free objects for them to attach upon.

The larvae on the buoy chains extended down the chains to the mudline
The larval cases and the pupal cocoons which were at the bottom of the chains were usually composed of larger sand grains than those at the tops of the chains, probably because the larger, heavier sand grains remain near the bottom of the river. Pupae, in their cocoons, were found at all depths. The heaviest concentrations of larvae were always found on the upstream side of the buoys.

Nine quantitative samples of larvae were collected from navigation buoys during the interval from June, 1957, to March, 1959. A subsample was taken from each collection and all of the larvae in the subsample were measured. A frequency distribution of the measurements is presented in Fig. 5. It is evident from these data that *H. orris* has a minimum of five instars during its larval life. One or two other instars must exist between the egg and the smallest larvae shown in the figure.

Wesenberg-Lund (1911), Ussing (1909) and Noyes (1914) have reported that *Hydropsyche* larvae constructed no catching nets during periods when the water temperature was near freezing. Wesenberg-Lund and Ussing believed that the larvae were virtually dormant during the coldest winter months. Noyes, on the other hand, believed them to be quite active and found an abundance of food material in their digestive tracts in February. Murphy (1919) stated that the larvae of *Brachycentrus nigrosoma* feed very little in the winter and that they eat
Fig. 5. Size distribution of Hydropsyche orris larvae collected from navigation buoys between Hannibal, Mo., and New Boston, Ill., July 23, 1957 to March 5, 1958.
SIZE DISTRIBUTION OF HYDROPSYCHE ORRIS LARVAE COLLECTED FROM
23 JULY 1957 TO 5 MARCH 1959

WIDTH OF HYDROPSYCHE ORRIS LARVAL HEAD CAPSULE IN MM.

NUMBER OF LARVAE
diatoms principally at that time. Alm (1925) never observed Hydropsyche nets during the winter in northern Europe and he reported that Hydropsyche larvae are very sluggish in the winter and lie wound up in spirals in dome-shaped houses made of silk, sand grains and fine earth particles.

When commercial fishermen in Pool 19 set their nets during late spring, summer or early fall, the nets become covered with hydropsychid larvae in about a week. If the fishermen's nets are set in early fall and they are not lifted until winter, the nets are still covered with caddisfly larvae. If the fishermen's nets are set during the winter, however, they remain free of larvae and larval constructions all winter long. The activity of Hydropsychidae larvae must, therefore, be lessened considerably during the winter. Their ability to populate newly submerged objects during the winter is very obviously curtailed.

Larval activity is probably not reduced to a state of hibernation during the winter but activity is very markedly lessened. Hanna (1957) found that four species of caddisfly larvae grew very little during the winter months and he considered food supply and temperature to be the limiting factors.

H. orris larvae were collected from a navigation buoy on March 5, 1959 when the river still contained ice floes. Some of the H. orris larval nets were erect and intact but others had apparently been torn away and
not reconstructed. All of the nets were covered with fine, flocculant organic matter. During the summer months, however, the nets are kept clean of residue at all times. Since the larvae are sluggish in the winter it is doubtful if they build or repair nets at that time. The nets which were erect on March 5 were probably nets which had escaped damage since the previous fall.

Nets which were undamaged and clean, and which were obviously being used, were observed on April 12, 1959. The nets were smaller than those of midsummer even though they were constructed by last instar larvae.

Pupae

Prior to pupation, in laboratory aquaria, the larva of Hydropsyche instabilis generally leaves its old larval shelter and constructs its pupal shelter in a new location (Philipson, 1953a).

Two H. orris larvae constructed their tubes and nets just 4 inches from the propeller in the lotic aquarium and daily observations were made of their activities. The larvae did not leave their tubes to pupate. Instead, each larva extended its tube into the vestibule behind its catching net. When the anterior end of one pupal case was almost closed, the larval net was still intact. A day later, only shreds of the net remained and the pupal case was complete. The second larval net was gone by the time the larva had begun to seal itself in its cocoon. Evidently, the larva cuts the net loose or weakens it sufficiently so that the current can carry
it away. The two previously mentioned H. orris larvae were very tolerant of one another and they joined the exteriors of their larval dwellings even though they were the only two larvae in the immediate area.

Hickin (1949) stated that after the case of Hydropsyche is plugged by the larva, the larva becomes stiff as the head and abdomen lose their usual flexibility. The intersegmental grooves of the abdomen become very indistinct and the legs come to occupy positions characteristic of this phase only. Sibley (1926) stated that a caddisfly larva often remains in a case as a prepupa for a space equal to, or longer than, the duration of the pupal period.

No observations were made of the emergence of the adult H. orris from its pupal exuviae. It is known, however, that they complete this molt on the water's surface and that the emergence takes place mostly at dusk or at night. Cast pupal skins of H. orris often appeared in large numbers on the surface of the water at dusk. During their mass rearing of Limnephilus indivisus, Mickel and Milliron (1939) found that nearly all of the adults emerged at night.

Generations per year

The H. orris adults, which were collected in the 1957 and 1958 window samples, were sexed and counted. The sex ratio of males to females was 1.49 in 1957 and 1.48 in 1958. The disproportionate number of males probably occurs because the females return to the river to lay
their eggs before it is completely dark. The males, however, are most likely attracted from their swarming areas to the downtown lights which are only a few blocks away.

The nightly catches of *H. orris* are plotted in Fig. 6. Window sampling was not begun until the latter part of June in 1957. Residents along the river bluff reported, however, that the *H. orris* swarms were very bad during the latter part of May and during the first half of June. The residents added that the caddisfly swarms are always largest and most bothersome during late spring and early fall. There is evidence in the 1957 window samples of increased emergence in late August and early September. In 1958 only an early summer peak is evident from the sampling. It is felt, however, that a second emergence peak occurred during late summer even though it is not well shown in Fig. 6. Field observations definitely indicated a second peak of emergence during the late summer of 1958.

A size-frequency distribution is presented in Fig. 7 for each quantitative larval sample which was collected from navigation buoys. The size distributions substantiate the supposition that there are two principal emergences of *H. orris* per year. In bivoltine species such as *H. orris*, eggs which are laid in early summer hatch and become adults during the same summer. Larvae which hatch from eggs laid in late summer will, on the other hand, take at least 8 months to become adults since the flies
Fig. 6. Nightly catches of *H. orris* and *P. flava* from a lighted cafe window in downtown Keokuk during the summers of 1957 and 1958. A broken base line indicates nights when collections were not made.
<table>
<thead>
<tr>
<th>Year</th>
<th>Species</th>
<th>Details</th>
</tr>
</thead>
<tbody>
<tr>
<td>1957</td>
<td>Potamyia flava</td>
<td>48, 73, 58, 78, 68</td>
</tr>
<tr>
<td>1958</td>
<td>Potamyia flava</td>
<td>48, 73, 58, 78, 68</td>
</tr>
<tr>
<td>1957</td>
<td>Hydropsyche orris</td>
<td></td>
</tr>
<tr>
<td>1958</td>
<td>Hydropsyche orris</td>
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</tbody>
</table>
Fig. 7. Length-frequency distribution of *H. orris* larvae collected from navigation buoys at various times during 1957 and 1958, between Hannibal, Mo., and New Boston, Ill.
WIDTH OF *Hydropsyche orris* LARVAL HEAD CAPSULE IN MM.
do not emerge during the winter months.

The size-frequency distributions also indicate that mature *H. orris* larvae tend to pass the winter as last instar larvae or prepupae instead of pupae. Indeed, it seems that the less mature larvae continue to grow in late fall and early spring and "catch up" to the quiescent last instar larvae. Larvae of varying ages are thus able to pupate as a group in May and to emerge en masse in late spring.

*Potamyia flava* (Hagen)

Adults

*Potamyia flava* is more abundant than *H. orris*, but less abundant than *C. campyla* in downtown Keokuk. Instead of having a black and white color pattern as *H. orris* and *C. campyla* do, *P. flava* is uniformly straw-colored and macroscopically its eyes appear to be unusually black and beady. The antennal segments do not bear diagonal black streaks as do the antennal segments of *H. orris* and *C. campyla* and the antennae of *P. flava* superficially resemble thin canes of bamboo. *P. flava*, like *H. orris* and *C. campyla*, seeks sheltered locations during the daylight hours and is thus inconspicuous.

Mating swarms of *P. flava* were not observed, but they, like *H. orris* and *C. campyla*, have been seen to mate on lighted windows. Several males often run excitedly around a female as they nuzzle her along the
sides of her abdomen. Often as many as 5 males may thus surround a single female. When one of the males succeeds in mating with the female, he lays his wings over hers just as the males do in *H. orris* and *C. campyla*.

**Oviposition**

Female *P. flava* were taken consistently in underwater light trap catches and they were collected at a depth of 20 feet in two instances (Table 2). The oviposition process of this species was also studied in the laboratory. About 100 *P. flava* females were collected from around a light, anesthetized, isolated from the other captured insects and then placed in a covered aquarium which was half full of aerated but not circulating water. By 10 a.m. the following morning some of the insects had laid egg masses on a floating board which was almost water-logged. About half of the flies were dead and had sunk to the bottom of the aquarium. The remainder of the caddisflies floated motionless on the surface. When the floating board was jarred, however, two of the floating caddisflies walked to its lower surface and remained there for about an hour without laying eggs. All of them were dead by evening, many of them having laid eggs. In several instances female *P. flava* have been seen to walk beneath the surface of the water and to rest motionless on some submerged object, only to be found dead an hour later. Upon examination they were found to be full of mature eggs. The
significance of this is not understood.

**Larvae**

On the night of August 8, 1958, 20 female *P. flava* were collected at a light, anesthetized, sorted and placed in a polyethylene bag which had a wet paper towel secured in its neck. Six egg masses were found on the polyethylene bag the following morning. The egg masses, on polyethylene patches which were cut from the bag, were floated egg-side down in a Petri dish of water. The eggs exhibited pronounced eye spots on August 17 and larvae were visible in the eggs on August 19. The larvae in the eggs were very active on August 22 and the first eggs hatched on August 24. Eggs which remained viable continued to hatch until August 30. Eggs which were laid loosely on the periphery of the egg mass hatched first and those in the center of the mass hatched last or died. In the warm water of the Petri dish, the difference in hatching time may have been due to less oxygen being available to the eggs which were most crowded.

Larvae of *P. flava* often construct loose, flowing nets like those of *C. campyla* on rocks and the two species are often found together. The greatest concentrations of *P. flava* larvae, however, are found in sand, silt-free areas of the river where the current is considerable. The larvae apparently prefer to construct their nets and dwellings on a firm, rough object such as a stone which lies partially buried in a sand bottom. *P. flava* larvae are often very abundant on the large concrete
blocks which anchor navigation buoys. Larvae are usually most abundant along the line where the surface of the block intersects the sand bottom. They incorporate a large amount of fine sand into their constructions and although the tubes, nets and cocoons are sand-encrusted, they remain pliable. The tubes and nets collapse when their substrate is lifted from the water. Consequently, detailed observations of them were not made.

The *P. flava* larval habitat has not been sampled well, since the water is usually too deep and fast and the bottom too rocky for swimming or dredging. The larval habitat has been indirectly sampled by Hoopes (1959), however. In examining the stomach contents of the shovelnose sturgeon, *Scaphirhynchus platorynchus*, he found that *P. flava* larvae form 68 per cent of the volume of the food of this sturgeon and that the stomachs, when filled with *P. flava* larvae, contained a considerable amount of sand, but no silt. These observations substantiate the supposition that *P. flava* larvae occur most frequently in sandy areas.

Leonard and Leonard (1949) reported that *P. flava* has been collected in Michigan during the third quarter of May, the last three-fourths of July, all of August and during the first three-fourths of September. Edwards (1956) recorded *P. flava* collections as early as the first week in May and as late as the last week in August at Reelfoot Lake, Tennessee. *P. flava* has been collected at Keokuk as early as May 16 and as late as September 25.
Generations per year

An analysis of the window samples (Fig. 6) reveals that \textit{P. flava}, like \textit{H. orris}, has two peaks of emergence each summer and that \textit{P. flava} is another bivoltine species.

\textbf{Cheumatopsyche campyla Ross}

\textbf{Adults}

\textit{Cheumatopsyche campyla} is usually the most abundant caddisfly in downtown Keokuk (Figs. 8 and 9). Superficially, the adult \textit{C. campyla} resembles adult \textit{Hydropsyche orris}. They may be readily separated from the latter by size, however, as they are smaller than \textit{H. orris}. A positive identification can be made by an examination of the genitalia according to Ross (1944). Both \textit{C. campyla} and \textit{H. orris} bear a diagonal black stripe on each antennal segment and this character quickly separates them from the other common species in the Keokuk area.

In many respects the adult behavior of \textit{C. campyla} is like that of \textit{H. orris} and the two species are found resting in the same niches during the day. Although \textit{C. campyla} adults have been observed to mate on lighted store windows at night and in shady locations during the day, mating swarms have not been observed.

Corbet and Tjønneland (1955) collected light-trap samples of Trichoptera throughout the night at 10-minute intervals at Lake Victoria, Uganda.
Fig. 8. Number of *Cheumatopsyche campyla* and the total number of caddisflies collected nightly at a lighted cafe window in Keokuk, Iowa, during 1957. A broken base line indicates nights when collections were not made.
1957

- Total caddis flies
- Cheumatopsyche campyla

Graph showing the total caddis flies and Cheumatopsyche campyla for the months of April to October 1957.
Fig. 9. Number of Cheumatopsyche campyla and the total number of caddisflies collected nightly at a lighted cafe window in Keokuk, Iowa, during 1958. A broken base line indicates nights when collections were not made.
1958

- Total caddis flies
  | Cheumatopsyche campyla
Among 12 species of Trichoptera they found eight species, including *Cheumatopsyche* sp., to exhibit bimodal flight activity. The dusk flight was of greater magnitude than the dawn flight in *Cheumatopsyche* sp. and in five other species. *Cheumatopsyche* sp., like most of the species, showed a marked preponderance of males. The aforementioned authors observed *Cheumatopsyche* sp. copulation frequently at dusk, but never at dawn, and oviposition was restricted mainly to the dusk flight.

**Oviposition**

*C. campyla* laid eggs in the laboratory much more readily than *H. orris* and observations were made of oviposition. A large number of caddisflies were collected with an aerial net from around an incandescent light on the night of August 16, 1958. These caddisflies were anesthetized and the *C. campyla* were quickly isolated from the other insects. When the caddisflies had regained consciousness about 100 of them were placed in the lotic aquarium for oviposition. Two minutes after they had been placed in the aquarium, one of the caddisflies walked down the side of the glass, laid one large and one small raft of eggs on the glass and floated to the surface. The total time from entering the water to leaving it was 1 minute and 45 seconds. The individual was lost among the others in the aquarium and it could not be ascertained how much longer it lived. On the following morning, however, all of the specimens of *C. campyla*, both males and females, were dead. Egg masses were found on all
surfaces of the floating, waterlogged board but most of them occurred on its wet upper surface.

In four oviposition experiments which involved several hundred female \textit{C. campyla}, none lived longer than 24 hours in the laboratory after they had laid their eggs. \textit{Cheumatopsyche} sp. males and females which Corbet and Tjônneland (1955) confined in the laboratory failed to live longer than 68 hours. They thought that low relative humidity in their holding containers may have made them die prematurely, however.

\textit{C. campyla} females remained submerged for prolonged periods of time. In one instance, a group of females was placed in the lotic aquarium late in the evening. On the following morning at 8:30, one female was seen resting on the concrete partition just under the surface. Its position was marked with wax pencil on the glass and its movements were followed with the pencil mark. Except for its silvery appearance the insect appeared as if it were at rest on a terrestrial cement wall. Its antennae moved gently with the current much as they move in the wind when the insect is on land. By 9:45 a.m., the caddisfly had moved 5 inches lower and was still facing downward. It angled 3 inches upward, faced the surface and was motionless at 11:20 a.m. When the caddisfly was to be checked again at 11:30 it was gone and could not be found because it had mingled with others on the surface of the water. The female laid no eggs even though it had remained submerged for about 3 hours.
C. campyla females were consistently taken in greater numbers than either P. flava or H. orris when the submerged light trap was used at moderate depths (Table 2).

More male C. campyla than females have been collected consistently at the lighted store windows in downtown Keokuk. Light traps which were operated on the Keokuk dam, however, collected 15,690 females and only 48 male C. campyla from July 21 to August 8, 1958.

The preponderance of females at the dam is most likely due to two factors. (1) Since the females must return to the river to lay their eggs, they may be expected to be more abundant there than the males which remain ashore. (2) Gravid females probably fly upstream to lay their eggs just above the tailwaters and thus congregate around the dam.

Upstream flights of gravid female caddisflies have been reported previously. Harris (1952) cited female Hydropsyche as flying upstream to fast water to lay their eggs. The problem caddisflies at Fort Erie, Ontario, swarm above the trees in the evening and later move upstream en masse toward the outlet of Lake Erie (Petersen, 1952). Roos (1957), in his experiments on the River Ammeran in Sweden, found that females of Cheumatopsyche lepida were collected in greater numbers flying upstream than down. He found this to be true for other lotic Trichoptera also. Although males were collected more often flying upstream than down also, the proportion was much less than that of the females which
flew upstream. Female *C. lepida* and *Rhyacophila nubila* with immature eggs were indifferent to direction of flight. Roos believes that impregnation stimulates or even releases oogenesis and that after oviposition a new portion of oocytes may start developing but probably not until the female has mated again. The instinct of upstream movement develops during oogenesis and is distinct when the time for oviposition comes. Females which showed an intermediate stage of egg development were poorly represented in the trap collections and this is an indication that there is a period of relatively low flight activity between copulation and oviposition. Roos stated further that there is a marked decrease in the number of upstream-flying females as soon as the uppermost rapid of a river section is passed and unruffled water is reached. He added that the upstream oviposition flight is a simple solution to the problem of recolonization. The colonization cycle was discussed in detail by Muller (1954).

**Larvae**

*C. campyla* larvae construct loose funnel-shaped nets which have no rigid supports as do those of *H. orris*. Consequently, the larva often constructs its net in a concavity in which its net can be supported. When one rock lies loosely atop another, the space between them is usually utilized as a net-building site. In the lotic aquarium, the larvae selected the angles along the floor of the aquarium. They also constructed nets
between the cement partition and the glass where the two were about three-fourths inches apart. The net is composed of irregularly woven strands and is not a regularly spaced screen as was the case in *H. orris*. It is comparatively flimsy and is adapted to slower water velocities than the *H. orris* net. The net becomes green as algae accumulate in its meshes. The larva resides in a crescent-shaped, tubular extension of the silken funnel trap. The tube, in all observed instances, was actually only half a tube as the substrate formed the floor of it. Although pulverized fingernail clam shells and other small objects are sometimes incorporated into the larval constructions, the net and tube are supported principally by the current and they fall into a shapeless, slippery, green mass when the current stops or when they are lifted from the water. *C. campyla* nets are very efficient filters, for when the water in the lotic aquarium was made extremely turbid, it was filtered clear in about 2 hours.

In the aquarium, larvae were observed to rest ventral side down as well as ventral side up and the larval tube was often constructed vertically. The larvae seemed to be continually active and they seemed constantly to be gleaning food from their nets. They frequently turned temporarily end for end in their tubes and occasionally the larvae crawled onto the outside of their abodes, but no matter how far they stretched, the larvae always kept their anal claws hooked into some part of their larval constructions.
C. campyla larvae were observed to have either brown or green abdomens. In fact, the larval population upon a single rock was often composed of both brown and green individuals. The significance of this is not understood but it is plausible that the green individuals are larvae which are feeding actively. The brown individuals may have stopped feeding as they prepared to molt.

Pupae

The cocoons of C. campyla at Keokuk are pliable, elliptical structures which usually incorporate small amounts of sand, fragments of fingernail clam shells and toilet tissue in their construction. The pupae of C. campyla often have red compound eyes when dissected alive from their cocoons. The color fades rapidly, however, and has never been observed in preserved specimens.

The lotic aquarium yielded confirmatory information concerning the length of time necessary for C. campyla to complete one generation. The first adult C. campyla were placed in the aquarium to lay their eggs on July 7, 1958 and when the aquarium was drained and inspected on August 27 it contained 63 mature C. campyla larvae, 3 mature C. campyla pupae and 2 large Psychomyiidae larvae. The pupae appeared to be completely developed and the aquatic life of C. campyla, from egg to adult, was estimated to be about 51 days under laboratory conditions.
After the aquarium had been drained it was scrubbed with alcohol to kill any undetected larvae or pupae and it was restocked on August 27 with a large number of H. orris, P. flava and C. campyla larvae which had been collected from the rubble below the Keokuk dam. The aquarium was drained again on September 2 and while it was being drained a C. campyla pupa emerged from its cocoon. The entire pupal instar had been completed then in 6 days, under laboratory conditions, at temperatures ranging between 75° and 85° F. Four more mature pupae were found still in their cocoons. It is possible that the draining of the aquarium may have hastened the emergence of the pupa from its cocoon because in C. campyla, as well as in other species, pupae often emerged from their cocoons when their substrate was exposed to the air. Philipson (1953) reported that in Hydropsyche instabilis, 18 days elapsed between the time pupal case construction commenced and the emergence of the adult in the laboratory. Hanna (1957) found the length of the pupal period of Limnephilus marmoratus, Molanna angustata, Limnephilus politus and Anabolia nervosa to be 18, 23, about 21 and about 21 days, respectively, at room temperature.

Two C. campyla cocoons which were obtained in the previous experiment contained prepupae. The black eyespots (lateral ocelli) of these C. campyla larvae were absent from the white patches in which they are usually centered. Close observation revealed, however, that the eyespots
were faintly visible through the integument slightly posterior to the white eye patches. Dissection showed that each eyespot was now located on the posterior edge of one of the compound eyes of the pupa which was forming inside the larval integument. In more mature pupae the black eyespots were no longer visible because they seemingly had atrophied or had been grown over by the enlarging compound eyes. The significance of this phenomenon has not been investigated but disappearance of the eyespots has been found to be a very good criterion with which to identify C. campyla larvae which are ready to pupate. Also, the disappearance of the pigment spot behind the compound eye of the pupa indicates when the pupa is mature and is ready to emerge from its cocoon.

**Generations per year**

Leonard and Leonard (1949) reported that C. campyla were collected in Michigan during the first three-fourths of May, during the last week of June, all of July, the first three-fourths of August and during the first quarter of October.

Marshall (1939) in her work at Put-in-Bay, Ohio, found C. campyla to be the most abundant caddisfly in her light collections. She found the C. campyla seasonal frequency of abundance to be definitely bimodal with peaks in early June and the latter part of August and was of the opinion that there were probably two generations per year. Specimens of C. campyla were reported by Marshall from May 25 to October 12.
Figs. 8 and 9 present a summary of the numbers of *C. campyla* which were collected in the previously described window samples at Keokuk. Adult *C. campyla* were collected as early as May 6 and as late as October 6 during this study.

It is unfortunate that sampling was not begun earlier in 1957 because it is difficult to surmise if there were one or two emergence peaks during that summer. Furthermore, the apparent high in 1957 occurred during midsummer and in 1958 the low occurred at this time. The 1958 data, however, indicate that a peak of emergence occurred during the early summer and that another occurred during the latter part of the summer. The rearing experiments which were conducted in the laboratory proved conclusively that *C. campyla* could complete a generation in less than two months. Both lines of evidence strongly indicate that *C. campyla*, like *H. orris* and *P. flava*, is a bivoltine species in the Keokuk area.

Ecological Distribution of Caddisfly Larvae

The hydropsychid and psychomyiid larvae in the Keokuk area are, for the most part, sessile animals and they depend upon water currents to bring their food to them. Of prime importance to these larvae are (1) a silt-free, solid substrate upon which to construct their catching nets and dwellings, and (2) a constant current of water which will carry food into their catching nets.
The underwater structures of Lock and Dam 19 at Keokuk and the submerged rubble area below the dam provide a very large area which is suitable for habitation by the larvae.

Water velocity is a critical factor to the net-spinning larvae and it consequently limits, to a large extent, the distribution of the various species. To better understand the relationship between water velocity and species composition, a series of larval collections was made in the tailwaters of the Keokuk dam.

On August 7, 1958, collections were made from rocks at eight stations. The rocks were obtained by wading or by swimming and all of the larvae were hand-picked from them and preserved. Water velocities were measured at each location with a Gurley current meter as previously described. The sampling units were by no means identical and at best the larval samples provide only an approximation of the relative numbers of each species in fast and slow water.

It is evident from Table 4 that H. orris is less abundant in the areas of slower water velocity. The slower current areas (which constitute most of the tailwaters) are inhabited predominantly by C. campyla and in some areas by P. flava and species of Psychomyiidae.

A large portion of the tailwaters was never sampled at all. This area included the tail race below the hydroelectric plant where the bulk of the water from the turbines is conducted. The tail race is excavated 25 feet
Table 4. Composition of the larval caddisfly population at various water velocities and depths on August 7, 1958. The number of each species is expressed as a percentage of the total specimens in the sample.

<table>
<thead>
<tr>
<th>Water velocity ft/sec</th>
<th>Station</th>
<th>Water depth ft.</th>
<th>H. orris</th>
<th>C. campyla</th>
<th>P. flava</th>
<th>Psycho-myliidae</th>
<th>Total larvae</th>
</tr>
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<tr>
<td>.4</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>90</td>
<td>0</td>
<td>7</td>
<td>31</td>
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<td>5</td>
<td>3</td>
<td>60</td>
<td>30</td>
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<td>98</td>
</tr>
<tr>
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<td>7</td>
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<td>93</td>
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<td>28</td>
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<td>5</td>
<td>29</td>
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<td>1</td>
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<td>91</td>
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<td>2</td>
<td>6</td>
<td>86</td>
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<td>94</td>
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<tr>
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<td>67</td>
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<td>3</td>
<td>97</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>95</td>
</tr>
</tbody>
</table>
into the limestone bed of the Mississippi River--from the upper end of the power house to the railroad bridge (Mississippi River Power Company, 1913). This area is dangerous, as the water is very swift and it is difficult to even anchor a boat in it. The depth of the water in tailwaters was in excess of 40 feet in many places and dredging or diving for samples was impractical. This fast water area almost certainly has a very high H. orris population, however.

The flat limestone slabs which compose most of the rubble in the tailwaters are piled quite loosely and their total surface area is much greater than that of the river bottom. If water is able to circulate beneath a rock, larvae are usually found on the underside of the rock as well as on its upper surface. A single rock in fast water often supports a line of H. orris nets on its leading edge and scattered H. orris nets atop prominences and in niches which are exposed to the force of the current. C. campyla, P. flava and Psychomyiidae sp. were found in the inter-spaces between the H. orris nets and on the surfaces where the current was lessened. P. flava larvae seemed to prefer the line at which rocks met the bottom, provided that the bottom was a sandy one. The psychomyiid larvae which were collected in the tailwaters were represented principally by Cynnellus marginalis and when examined grossly their nets were virtually indistinguishable from those of C. campyla. The cocoons of the psychomyiid larvae are not as rigid as those of C. campyla,
however, and while *C. campyla* utilized a considerable amount of sand in the shell of its cocoon, the psychomyiid larvae incorporated vegetable matter and large pieces of fingernail clam shells.

An inverse relationship exists between the catching-net size and the water velocity in which the larva lives. If it is assumed that the larvae consume approximately the same volume of similar food, it is obvious that the larvae must filter somewhat equal volumes of water. The larva of *H. orris* inhabits faster water than the other species and consequently requires less net area to filter the same amount of water. The loose, voluminous nets of *P. flava*, *C. campyla* and the psychomyiid species are adapted for slower water and since the water moves through the nets at a slower rate the area of their nets must be greater. Also, the force exerted by the faster currents effectively curtails the construction of voluminous nets and the net of *H. orris* is of necessity a compact, rigid structure.

Indeed, *H. orris* never constructed a catching net in the laboratory unless the water in the aquarium was rapidly circulated. Philipson (1954) found that *Hydropsyche instabilis* would spin only a crude shelter in still water but made shelters and nets readily when the water in the aquarium was stirred to 30 cm. per sec. *Wormaldia subnigra* would not make a net at this speed but made a net when the water velocity reached 60 cm. per sec. Philipson found that both *H. instabilis* and *W. subnigra* were capable of resisting dislodgement at water velocities of 200 cm. per sec.
Several excellent opportunities were afforded to observe larval populations intact on submerged structures at Lock and Dam 19, and these instances will be reported in detail because they clearly illustrate the effect of water velocity upon larval distribution.

On August 11, 1957, the Union Electric Power Company shut down one of its turbines at the Keokuk hydroelectric plant for repair. The scroll chamber which normally conducts water to the turbine was dammed off and partially drained. The floor of this hall-like, concrete chamber is about 40 feet beneath the surface of the water and on this date less than 15 feet of water remained in the chamber. Although it was drained in the morning the humidity was so high in the chamber that the larvae remained in their shelters on the walls instead of descending to the water on individual silken threads as they usually do. The exposed cement walls of the scroll chamber were inspected from a raft which had been lowered into the chamber. About 100 H. orris larvae were found on each square foot of the walls and roof of the chamber. Additional larvae were found on every structure in the tunnel except for the polished steel blades of the turbine. No other species of larvae were found. The scroll chambers remain virtually in total darkness at all times when the turbines are functioning and the velocity of the water along the midline of the chambers is 5 feet per second (Union Electric Company engineers).

Large iron grills guard the entrances to the scroll chambers and
when they were raised for repair it was found that they accommodated very large *H. orris* larval populations. The larval cases and nets virtually blanketed the grills at times and the larvae extended downward in undiminished numbers to the bottom of the water inlet which is 40 feet below the surface of the river. *C. campyla* were also found on the grill but only in a ratio of three *C. campyla* to 100 *H. orris*.

Observations of many navigation buoy chains indicated that larvae were as abundant at the river bottom as near the surface. Two samples were taken from such a chain on October 30, 1958 to determine if the size distribution and species composition of larvae was the same at the bottom (24 feet) as at the top of the chain. It is evident from these data (Fig. 10) that the size distribution of the *H. orris* larvae on the chain was very similar at top and bottom. Proportionately more *P. flava* and *C. campyla* larvae were found at 24 feet than near the surface, but too few of either species were collected to allow any generalizations to be made. It seems plausible, however, that *P. flava* and *C. campyla* could be most abundant near the bottom since the current is most likely moderated there.

The water which is impounded directly behind the Illinois half of the dam at Keokuk has virtually no current because the main channel courses the Iowa side of the river and is directed through the power installation. One of the vertical-lift steel gates on the dam was examined when it was raised from the water on June 24, 1958. Sponges covered much of the
Fig. 10. Size distributions of three species of hydropsychid caddisfly larvae near the top and bottom of a 24 foot buoy chain, New Boston, Ill., October 30, 1958.
SIZE DISTRIBUTION OF LARVAE ON A BUOY CHAIN

PERCENT OF TOTAL LARVAE

WIDTH OF LARVAL HEAD CAPSULE IN MM.
face of the gate and a few lentic caddisfly species (Leptoceridae) were found. No net-spinning caddisfly larvae were found on the face of the gate where water movement was negligible. Along the edges of the gate, on the other hand, water leaks had developed and these leakage areas were well defined by the presence of many net-spinning caddisfly larvae. The ratio of *C. campyla* to *H. orris* was 58 to two in the leakage areas and psychomyiid larvae were represented by four *Cyrnellus marginalis*. This species composition indicated that the leaks had created small niches in which the current was sufficient for *C. campyla* but less than optimum for *H. orris*.

An excellent opportunity to observe the effect of water velocity upon caddisfly larval distribution presented itself on August 27, 1958. A vertical concrete pit which is about 6 feet wide, 12 feet long and 20 feet deep extends downward from the surface level of Lock 19 into the main water-conducting tunnels. Large metal trap doors normally seal off the bottom of the chamber and it is kept full of stagnant water. If the aforementioned floor plates, due to a malfunction, do not close completely, however, an 8-inch pipe automatically conducts water into the chamber so that it remains full at all times. Such was the case during the summer of 1958. In order to repair the steel floor plates, the pit was completely drained by shutting off the 8-inch pipe.

When the exposed walls of the pit were examined it was immediately
evident that the faulty floor plates had allowed considerable water circulation to take place. The walls of the chamber bore a large population of the net-spinning psychomyiid *Cyrinellus marginalis*. Pupae of this species were particularly abundant and a cumulative count of both larvae and pupae was made. The concentration of both was estimated to be about 100 per square foot of surface.

The 8-inch pipe, which functions when floor plates are ajar, jets a current of water across the chamber, through the water, about 3 feet from the floor. On the wall opposite the pipe outlet a well-defined circular area was seen, which in contrast to the rest of the chamber was bare of sponges and bryozoans. Further examination revealed that *C. marginalis* larvae were replaced by *H. orris* larvae in the circular, fast water area. As a practical consideration it seems that leaks could be detected and water velocity patterns could be plotted accurately and inexpensively in many situations similar to this one by an examination of the larval caddisfly populations.

It is interesting to note that the aforementioned pit is covered at all times and is virtually inaccessible to ovipositing female caddisflies from the outside. Adults which were reared in the chamber could live and mate in the air space at the top, however, and then further populate the chamber by laying eggs in it. Thus the species which initially populated the pit by means of current-carried larvae could quickly become
the dominant species. In the Keokuk area C. campyla and the psychomyiid caddisflies seem to prefer the same habitat and yet C. campyla is dominant in almost every instance. In the chamber, however, no C. campyla were found. C. marginalis probably was the pioneer species in the chamber when the lock was made operational for the first time in 1956. This hypothesis seems plausible because C. marginalis is almost always the first larva to appear on newly immersed objects such as emergence traps, trotline buoys and the underwater floats.

It is doubtful if the dissolved oxygen concentration of the river water is a limiting factor for caddisfly larvae. Philipson (1954) found that Hydropsyche instabilis larvae remained active in flowing water at oxygen concentrations (3.5 ml. per liter) which would have been lethal to the larvae in still water. Philipson's observations seemed to be confirmed when the air supply failed in the previously described lotic aquarium. H. orris and C. campyla larvae remained active in the circulating water even though the water temperature reached 90°F. No tests were made of the dissolved oxygen at the time, however.

Trichoptera Control

Adulticides

Only one caddisfly control program has been reported in the literature and it is being carried on at the present time in the city of Fort Erie,
Ontario. Measures were undertaken in 1949 in that city to study the biology of the pest species of caddisflies and to ultimately find methods for controlling them. Progress reports concerning the caddisfly program at Fort Erie have been made by the Fort Erie Times-Review (June 28, 1951 and June 10, 1954) and by the Buffalo (New York) Courier-Express (August 13, 1950). These newspaper accounts, and personal communications with Mr. H. E. Thompson of the Fort Erie Lions Club and Dr. D. G. Peterson, Canadian Department of Agriculture, form the basis for the following account.

The caddisfly study and the subsequent control measures at Fort Erie were undertaken as a long-term service project by the Fort Erie Lions Club. The biological investigations of 1949, 1950 and 1951 were done principally by volunteer workers who cooperated with the University of Toronto. As a result of the knowledge gained in the biological survey it was decided to direct control measures at breaking the life cycles of the most troublesome species.

The adult caddisflies, after emergence, congregate for a day or two in trees and shrubbery along the river bank prior to swarming up the river to lay their eggs at the outlet of Lake Erie. It seemed hopeless to attack the caddisflies after they had commenced to swarm up the river. Instead, the foliage along the river front was sprayed with a DDT contact poison. The 5% DDT was applied with a large tree sprayer and 3 miles
of the river front were sprayed every two weeks. It was hoped that the number of egg-laying females could gradually be reduced over a period of years so that the larvae in the river would be correspondingly reduced to a point where their natural enemies could keep them in check. In two years the number of caddisflies was reported to have been reduced considerably so that they were no longer a hindrance to painting and allergy sufferers obtained considerable relief.

In 1954 the Fort Erie Lions Club purchased a model 100 John Bean Rotomist sprayer and presented it to the town of Fort Erie. Wettable DDT (50%) was used at first, but because of excessive nozzle wear a change was made to 25% DDT in oil base. No complaints concerning oil damage to shade trees have been received during the spraying program.

Spraying is begun on the first of June and it is continued until the middle of September. The spray is a 2% DDT oil-water emulsion (5 Imperial gallons of 25% oil base DDT in 80 Imperial gallons of water). An effort is made to apply 2 tanks of the spray (100 U.S. gallons each) on each working day. In 1957 about 7000 Imperial gallons of spray were applied in 43 out of 90 calendar days. In 1957 the results were not as good as had been expected and it was thought that the concentration of the spray should be doubled.

The authorities at Buffalo, New York, on the American side of the river, have not initiated control measures and the Canadians believe that this has slowed control to a large degree.
The *H. orris* and *C. campyla* adults, which emerge below the Keokuk dam, rest in the shrubbery along the shore during the day as do the Fort Erie species and they would probably be vulnerable to contact poisons such as those used at Fort Erie. The portion of the *C. campyla* and *P. flava* which emerge and rest downstream from Keokuk and then migrate up the river to oviposit would be little affected by such a spray, however.

*H. orris* adult males are also vulnerable when they are swarming over the trees along the river bluff at Keokuk. The swarms of males are very obvious at dusk and the meteorological conditions at this time are usually conducive to the use of space sprays. Since the swarms occur in the same locations, night after night, a spraying schedule could be planned accordingly. An oil solution of DDT and lethanes would probably deal effectively with the swarming male caddisflies just as it deals with house flies. A Rotomist type sprayer could easily apply the insecticide at the height desired. The drift from the spray directed at the swarms would undoubtedly kill many females which approach the swarms from the trees and from the river. It is doubtful if a fogger would have sufficient range to reach the swarms unless it were employed from a boom.

Unfortunately, the early summer peak of *H. orris* emergence coincides with the songbird nesting season and an insecticide application at that time would most likely meet public opposition. The late summer
peak, on the other hand, occurs at a time when songbirds are least vulnerable to insecticides.

A large apiary is situated directly across the river from Keokuk and the apiary officials became concerned when airplane spraying of insecticides was suggested by some Keokuk residents. The apiarists felt that the prevailing winds would carry an insecticide drift from such a large scale operation into their bee yards. The apiarists had reason for concern as they value their breeding stock of bees alone at $25,000. Talks with officials at the Dadant apiary revealed, however, that they had no objection to sprays which were applied from the ground instead of from the air.

It is doubtful if DDT, applied properly from the ground, would injure the apiary bees to any appreciable degree. Palmer-Jones et al. (1954), as a result of their work and their review of the work of others, were of the opinion that DDT, even when applied to pastures in bloom, does not affect apiaries severely. Furthermore, DDT was reported as strongly repellent to bees and its repellent quality was greatest when its toxicity was highest.

Space sprays may also prove of value in lessening the caddisfly infestation in the downtown area. Each of the street lamps serves as a light attractant as does each lighted store window and a DDT fog would probably be effective if applied about one hour after the street lights are turned on in the evening.
Light traps

The most abundant caddisflies in the shopping district of Keokuk are the males of *C. campyla*. The males do not restrict themselves to the river as do the ovipositing females, hence the flight of many is directed toward the city lights. The main street of Keokuk, which is well lighted, runs directly to the river and it probably provides an avenue for a constant influx of males from the river to the shopping district. Since the caddisflies are initially attracted by light it seemed logical to consider light as an aid in control measures.

Lepidoptera, which are similar in many respects to Trichoptera, have been shown to be especially attracted to black-light lamps (radiation peak 3500-3650 Angstroms) (Glick, 1954; Pfrimmer, 1955; Glick and Hollingsworth, 1955). Trichoptera are reported to be especially susceptible to wave lengths of 3200 to 3800 Angstroms (Frost, 1953, 1954; Pfrimmer, 1955; Frost, 1955). Trichoptera are also attracted to blue neon (mercury vapor) lights (Burks et al., 1938). Edwards (1956) found the next most attractive light to be green, while red and yellow were the least attractive.

Most of the data which concerns the responses of the caddisfly to light have been collected in light trap experiments which were not designed specifically for caddisflies. It was deemed necessary, therefore, to establish with more precision the ranges of the short wave lengths of
light which are most attractive to the caddisflies of the Keokuk area. An experimental light trap (Fig. 3) was devised to test the relative attractiveness of 3 types of lights. These were a cool-white fluorescent lamp (F4T5/CW), a blacklight fluorescent lamp (F4T4/BL) and a germicidal lamp (G4T4/1). These lamps, each of which was rated at 4 watts, peaked at 5650 Angstroms, 3500 Angstroms and 2537 Angstroms, respectively. The lamps were supplied through the courtesy of Sylvania Electric Products, Incorporated.

To eliminate the effect of light position upon the catches, the three lights were arranged in all possible permutations (6) and each permutation was randomly scheduled for a different night. The complete experiment was run twice for a total of 12 trap nights.

The exterior of the trap was painted yellow and the inside of each of the three lighted compartments was painted aluminum. Each light was suspended horizontally over a pan of detergent water and as the insects were attracted into the light chamber they foundered in the detergent water. The bare bulbs were not readily visible to the insects because they were placed low inside the compartments. The lights were fitted with long electric cords so that they could be interchanged easily from chamber to chamber. The ballasts and starters for the lamps were secured permanently to the bottom of the trap. The lights were turned on simultaneously and were left on for exactly 5 minutes each evening. The experiment was
initiated on July 21, 1958 and the lights were arbitrarily turned on at 8 p.m. on the first evening. Each evening, thereafter, the starting time was made 2 minutes earlier to make the interval from sunset to starting time fairly constant.

The _H. orris, C. campyla_ and _P. flava_ were separated from the other trapped species and they were sexed and counted. The nightly catches for each light are presented by species and sex in Appendix Table 6 and are summarized in Table 5.

On the evening of July 30 a cold rain fell and a strong wind blew straight at the face of the light trap. The catch of insects was insignificant on this night (only 10 caddisflies were captured) and the sample is considered to be aberrant. It will be excluded, therefore, from the following discussion.

It is immediately obvious that the black light (3500 Angstroms) is by far the best attractant for caddisflies, collecting in all instances more individuals than the germicidal and cool-white lights combined.

Females of all three species were collected in much larger numbers than males at all three lights. It is doubtful that females are attracted more to light than males, however, since in the downtown area the ratios of males to females over two seasons for _H. orris, C. campyla_ and _P. flava_ were 1.4, 2.6, and .59, respectively.

The preponderance of females at the dam is probably due to two
Table 5. Caddisflies captured at the Keokuk dam in 12 nightly periods with three types of light, 1958

<table>
<thead>
<tr>
<th>Light</th>
<th>Wave length in Angstroms</th>
<th>C. campyla</th>
<th>H. orris</th>
<th>P. flava</th>
<th>Unidentified species</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Male</td>
<td>Female</td>
<td>Male</td>
<td>Female</td>
<td>Male</td>
</tr>
<tr>
<td>Black</td>
<td>3500</td>
<td>40</td>
<td>11,818</td>
<td>103</td>
<td>512</td>
<td>67</td>
</tr>
<tr>
<td>Germicidal</td>
<td>2537</td>
<td>4</td>
<td>2,453</td>
<td>30</td>
<td>89</td>
<td>16</td>
</tr>
<tr>
<td>Cool white</td>
<td>5650</td>
<td>4</td>
<td>1,419</td>
<td>16</td>
<td>30</td>
<td>7</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>48</td>
<td>15,690</td>
<td>149</td>
<td>631</td>
<td>90</td>
</tr>
</tbody>
</table>
factors. (1) Females return to the river to lay their eggs and thus spend more time in that area than do the males which seem to desert the river for the shore immediately after emergence. (2) As was previously mentioned, females probably migrate upstream to lay their eggs and thus congregate at the dam. This seems to be especially true of _P. flava_ females.

_P. flava_ females were consistently more abundant than males both at the dam and in the downtown area. The relative scarcity of males may indicate that the _P. flava_ females have migrated upstream a considerable distance from their place of emergence, leaving most of the males behind. This assumption seems to be a logical one since _P. flava_ larvae were less common in the tailwaters than either _H. orris_ or _C. campyla_. _P. flava_ larvae have been found to be quite abundant in the sandy parts of the main channel of the river, both up and downstream from Keokuk.

_C. campyla_ larvae are known to be abundant in the tailwaters of the Keokuk dam and the large number of males which were taken in the downtown window samples indicates that a large part of the pest population of _C. campyla_ originates just below the dam. While some female _C. campyla_ most likely migrate upstream, the migrants probably do not constitute the largest portion of the _C. campyla_ population in the downtown area or at the dam.

The sex ratio of _H. orris_ is closer to 1 than is the sex ratio of either
C. campyla or P. flava. This is true both at the dam and in downtown Keokuk. H. orris females probably migrate little and most of the males and females at Keokuk have probably emerged from the tailwaters. This supposition is substantiated by the fact that H. orris larvae were found to be very abundant in the faster water of the tailwaters. Furthermore, male H. orris often swarm at the dam and these males probably increase the ratio of males at the oviposition site of the species.

It seems likely that if an extensive series of blacklight insect traps were placed along the water front and at the foot of main street they would intercept many of the resident caddisflies and upstream migrant species which are attracted to the downtown lights. Such light traps should (1) require little care, (2) be able to withstand heavy rain and wind, and (3) be efficient and inexpensive. Several such traps were designed for use at Keokuk. The most effective traps utilized blacklights as attractants and one such trap is illustrated in Fig. 2.

A 20-watt blacklight was mounted opposite a quarter section of a 50-gallon drum which was bolted to the rim of an intact 50-gallon drum. A standard fixture for the fluorescent lamp was sealed against the weather with rubber tape. The drum was filled two-thirds full of water and 5 gallons of fuel oil were floated upon the water. A section of rubber garden hose, which extended upward from the bottom of the drum, acted as a standpipe and it maintained a constant liquid level in the barrel. Insects
which were attracted to the light fell into the oil and sank to the water level since their specific gravity was greater than that of the oil. The insects decomposed in the water at the bottom of the barrel. The oil layer prevented water evaporation and each time it rained a portion of the water in the barrel was forced out the standpipe. The trap was flushed automatically by rain in this manner. If the trap was to be emptied the standpipe had only to be lowered. By enclosing the light units in polyethylene bags the complete traps may be stored outside to save space during the winter months.

The materials necessary for construction of such a trap cost less than $10.00. Counts were made of the insects which were killed by this type of trap in three instances and the nightly kill was estimated volumetrically to vary from 625,000 to 800,000 caddisflies per trap. These estimates were crudely made by counting the number of caddisflies in a small paper cup (3936), counting the number of paper cups per one pound coffee can (10) and then tallying the total number of cansful captured per evening.

The ultraviolet light was a poor attractant for mayflies. This was an advantage in a caddisfly trap since a heavy emergence of Hexagenia mayflies would quickly fill any trap which was attractive to them. The traps are not unsightly as they are painted with aluminum paint and their action is impressive to the public. This psychological advantage should
not be overlooked because the public can see immediately that something is being done.

Two of the sites at which light traps could be effectively placed are the following: (1) the city water works garage which is located at the foot of Main Street. It has a sewer inlet atop its roof and the 8 or 10 traps which would be placed here could be easily turned on and off by the water works employees. These traps would probably intercept many of the insects which fly up Main Street. (2) Near the Mississippi River bridge toll house which is located at the Keokuk end of the bridge. Several traps here could be supervised and turned on and off by the toll collectors, who are city employees.

Since the waterfront area itself is not equipped with city-owned electrical outlets, private parties may of necessity be called upon for assistance. The operators of boat liveries at the downstream end of Keokuk's waterfront have offered to allow traps to be operated on their 110-volt circuits. Industrial firms along the river would probably be happy to operate traps on their premises as a public service.

Traps placed along the Keokuk locks would undoubtedly collect many caddisflies. The U. S. Army Corps of Engineers would most likely allow traps to be placed upon the Lock and the lock maintenance staff would probably tend them.

It would be more difficult to utilize this type of trap on the dam itself
and the powerplant because only 25-cycle electrical current is supplied to these areas and it is not satisfactory for the standard 60-cycle black-lights.

Two disadvantages exist for the suggested light traps. The water in the bottom of the barrels becomes foul-smelling due to the decomposing insects. This is noticed only when the traps are emptied, however, because the floating oil layer prevents the odor from escaping while the traps are in use. The traps should be placed at a sewer inlet or in a position so that the effluent can run directly into the river. The traps will undoubtedly be subject to vandalism; consequently they should be operated in areas where they can be supervised.

Shopkeepers and restaurant owners could simply and inexpensively reduce their caddisfly problems by altering their outside lighting. Blue and green "neon" tubes are very good caddisfly attractants and they should be replaced by red or yellow tubes which are much less attractive to the caddisflies.

Larvicides

The most direct approach to caddisfly control at Keokuk would obviously be the use of larvicides against the resident larval populations in the tailwaters of the dam. Such a plan immediately calls to mind the following problems: (1) finding an insecticide which will kill caddisfly larvae but not fish, (2) eliminating the larvae might deprive fish of their
food supply, (3) the "biological balance" may be upset, and (4) miscellaneous problems such as application, dilution, and pollution.

Susceptibility of hydropsychid larvae and fish to DDT. Several studies indicate that caddisfly larvae are extremely susceptible to DDT and that they may be killed without decimating fish populations. Hoffmann and Merkel (1948) have reported on the treatment of several Pennsylvania streams during 1945, 1946 and 1947 with a DDT oil solution by airplane at a rate of 1 pound of DDT per acre (an average of .23 pounds of DDT per acre reached the surface of the stream). Oil solutions and water suspensions were both lethal to caddisfly larvae, but oil solutions of DDT were more toxic to invertebrates in general than were water suspensions. All streams had more invertebrates per square foot a year after treatment than they had prior to treatment. Unimportant losses of small fish were reported after both sprayings. Annelids and molluscs showed little or no effect.

During May, 1947, 413,500 acres of northern Idaho forest were sprayed with an oil solution of DDT at 1 pound of DDT per acre. Trichoptera larvae were severely affected in all streams. Rainbow, eastern brook and cut-throat trout were apparently not affected by the insecticide. Speckled dace and redside shiners also appeared to be unaffected. Cottoids, mountain suckers and black bullheads suffered heavy losses, however, in certain limited areas (Adams et al., 1949).
Black-fly larvae, caddisfly larvae (Hydropsyche sp. and Halesus sp.) and rainbow trout were placed together in troughs of running water by Gjullin et al. (1949). The insects and fish were exposed to insecticides for 15 minutes and were then placed in screen cages in a stream. Observations were made during the treatment and after 24 hours. The caddisfly larvae were more susceptible than either the trout or the black flies to an acetone solution of DDT at 20 p.p.m. In field conditions, however, black fly larvae were controlled (detached) at concentrations in which caddisfly larvae remained alive (e.g., 0.3 p.p.m. acetone solution of DDT for 15 minutes).

An oil solution of DDT was sprayed upon 52,000 acres of watershed in Pennsylvania at the rate of 1 pound of DDT per acre during May and June, 1948. Hydropsyche, like most other Trichoptera, was exceedingly susceptible to DDT as evidenced by the fact that where a prespray population of 70 larvae per square foot existed, only occasional individuals were found for 16 months subsequent to spraying. Not until September, 1949, had the caddisfly larval population returned to normal. Most other orders of insects recovered more quickly than Trichoptera and in many cases normal numbers were found 3 months after spraying (Hoffmann and Drooz, 1953). Relatively few fish were killed in either the lakes or streams in this watershed (Hoffman and Surber, 1949).

A 0.9 mile section of Back Creek, West Virginia, was sprayed with
wettable DDT at 1 pound of DDT per acre. Caddisfly larvae, principally *Chimarra* sp., *Cheumatopsyche* sp. and *Hydropsyche* sp. were very susceptible and those in the lower stations were almost exterminated. It was thought that the catching-nets of these species may have concentrated the insecticide and thus increased their susceptibility to it. Although several species of minnows, stonerollers and smallmouth bass were abundant in the stream, only 61 native fish were found dead. Of 452 large-mouth bass, bluegills, golden shiners and goldfish which were placed in live boxes only five fish died of DDT toxicity. Only one small brown bullhead of 9,000 which were placed in a live box died as a result of the spraying (Hoffman and Surber, 1948).

Caddisfly larvae were virtually eliminated from the tributaries of the Miramichi River in New Brunswick by an aerial spray of DDT in oil at a rate of .5 pounds of DDT per acre (Ide, 1957).

Several British Columbia streams were incidentally sprayed during budworm control with DDT in oil at the rate of 1 pound of DDT per acre. Spraying was done in June and by October caddisfly larvae were absent in the most severely affected streams. Losses of coho salmon fry, trout and yearling steelhead were heavy in most of the sprayed streams, however (Crouter and Vernon, 1959).

DDT has been demonstrated to be an effective caddisfly larvicide and it seems likely that it can be used without the subsequent loss of large
numbers of cyprinid, centrarchid and ictalurid fishes. It seems in order, however, to present further studies which concern the toxicity of DDT to fish. The toxicity limits of DDT are difficult to define because they are dependent upon many factors. The results of the following studies make this variability very evident.

Several studies illustrate that oil solutions of a given concentration are more toxic to fish than wettable powders. Surber and Friddle (1949) reported that a DDT wettable powder spray killed few fish in a woodland stream. An oil formulation, however, used the following year at the same dosage (1 pound per acre) killed six times as many fish. When a wettable powder DDT spray was applied to a West Virginia stream at 1 pound of DDT per acre, only 61 juvenile fish were reported killed. In a neighboring trout stream, however, a DDT oil formulation applied at the same rate killed large numbers of fish (Hoffman and Surber, 1948). DDT in a fuel oil formulation killed bluegills at 0.14 p.p.m. whereas wettable powder at the same rate killed none (Surber, 1948).

The results of the following studies illustrate clearly that no single set of toxicity limits may be set for all fish.

Goldfish did not seem to be affected when a DDT acetone suspension was applied at concentrations less than 0.2 p.p.m. When applied at a rate of 0.2 p.p.m. to 2.0 p.p.m., however, symptoms appeared in 1-6 hours and death ensued in 20-40 hours (Eide et al., 1945). Concentrations
of alcoholic DDT at 2.0 p.p.m. or greater killed goldfish within 24 hours and a 40% kill resulted in six days when a 0.1 p.p.m. treatment was applied (Ginsburg, 1945). Odum and Sumerford (1946) found that acetone-dissolved DDT in water killed goldfish at 0.01 p.p.m.

Bluegills were killed by concentrations as low as 0.04 p.p.m. DDT (oil solution) in concrete pools but four species of minnows were not killed (Surber, 1948). Large bluegills were scarcely affected by 0.1 p.p.m. emulsifiable DDT. Furthermore, adult bluegills, largemouth bass and buffalo fish were not killed in 45 days by 1.0 p.p.m. wettable powder DDT (Lawrence, 1950). Losses of 50% or more were reported among fingerling bluegills, black crappies and brown bullheads when ponds were sprayed with 0.04 p.p.m. DDT in oil (Surber and Hoffmann, 1949). A golden shiner population was not eradicated in a one-fourth acre earthen pond even though the pond was treated with 4.7 pounds of DDT per acre foot of water during a one-month period (Lawrence, 1950).

Apparently, some species of fish can survive great concentrations of DDT for short periods of time. Field tests revealed that concentrations of DDT (in oil) as great as 25 p.p.m. for 30 minutes had no noticeable effect upon walleye, common sucker or ling (Arnason et al., 1949).

Fry and fingerling salmonids have been severely affected by DDT in oil solution (Crouter and Vernon, 1959; Keenleyside, 1959; Alderice and Worthington, 1959). Eels also appeared to be severely affected,
but dace, shiners, fall fish and chubs were relatively unaffected by the DDT spray (Keenleyside, 1959).

It is possible that fish may be adversely affected by eating DDT-treated insects. Bluegills were apparently unaffected by eating caddisflies which had been treated by DDT at the rate of 1 pound per acre. Largemouth bass, however, were killed in one laboratory experiment when they were fed treated caddisflies (Surber, 1946). Mosquito larvae which had been killed by DDT at 1.0 to 0.05 p.p.m. were fed to goldfish. Although 100 larvae were fed to each fish over a 4-day period, none of the fish died (Ginsburg, 1947). When sprayed with equal amounts of DDT, insects sprayed with oil solution were more toxic to fish than suspension-sprayed insects. Furthermore, some fish were apparently killed by eating small numbers of sprayed insects while others gorged on them without effect. Large fish were less sensitive than small fish and well-fed fish were less susceptible to DDT than fish which were not well fed (Hoffmann, 1949).

In laboratory experiments, fish confined in small aquaria were more vulnerable to DDT at a given concentration than fish in a pond (Prevost et al., 1948).

Xylene, when used as a solvent, has been shown to be a source of toxicity (Everhart and Hassler, 1948).

Hoffmann and Linduska (1949) cite the following factors which modify the toxicity of DDT to fish: young fish are least resistant; poorly fed fish
are less resistant; insecticide formulations in order of toxicity—emulsion, oil solution, wettable powders; high temperature, reduced oxygen tension and soft water enhance the activity of DDT; turbidity of the water reduces toxicity; and when ingested, DDT is most toxic in oil. Rudd and Genelly (1956) list the following additional variables: species of the fish; and the depth, rate of flow, vegetation and bottom type of the water course. They conclude that suspended DDT in minute amounts is toxic to fish and that at 0.1 p.p.m. all fish will die within 12 hours; only a few fish will survive at 0.01 p.p.m.; and that many but not most of the test fish will be killed at .005 p.p.m.

The previously cited studies indicate that caddisfly larvae may be killed at concentrations of DDT which are not fatal to adult fish. As has been stated before, the nets of the hydropsychid caddisfly larvae probably concentrate wettable powders by their filtering action. It seems very possible that this filtering action can be taken advantage of in eradicating the larvae without injuring fish.

_Hydropsyche orris_ larvae, which were reared in an agitating aquarium in the laboratory, constructed normal catching nets and when bits of foreign material (e.g., crumbs of dry dog food) were swept into the larval net by the current they became lodged inside the antechambers of the larval tubes. The larva was usually able to wrestle the particles out of its tube, over the net and into the current to be swept away. While
struggling with the larger pieces, the larva was intimately in contact with them for prolonged periods (often several minutes). Hydropsychid larvae are constantly engaged in cleaning their nets. This activity becomes especially apparent when a larva dies, for its net very soon becomes heavily laden with algae, dirt and debris.

DDT applied to the river bottom in granular form may be concentrated by the caddisfly larval nets in sufficient quantity to kill the larvae. A relatively insoluble formulation would contribute very little DDT to the water, and since the water is always flowing the concentration would remain negligible. Such a formulation has been made previously.

Whitehead (1951) reported that Fuller's earth granules (15-mesh) were impregnated with dieldrin or parathion at a 2% concentration by weight. It was hoped that these granules would penetrate the vegetation of a rice field and reach the water below to control mosquito larvae. Although mosquito larvae were completely controlled by suspensions of both parathion and dieldrin at 0.1 pound per acre, identical concentrations of the pellets failed to give any measurable degree of control. Even after 2 or 3 days of soaking the granules remained firm and the evidence indicated that their failure to give mosquito control was due to their failure to release insecticides into the water.

Small pellets similar to those used by Whitehead may prove to be useful at Keokuk. Such pellets would sink rapidly, even in moving water,
and having done so many would probably be swept into caddisfly nets. The subsequent cleaning of the contaminated nets by the larvae may be sufficient to kill the larvae. Even if the insecticide fails to kill the larvae, it may cause them to detach and to be carried downstream. It is extremely doubtful if such pellets could render the water toxic to fish since the DDT is relatively insoluble. A mixture of assorted size granules may be best, the heavier granules settling in the fast current and the fine granules being carried farther with the current. A hand-operated alfalfa seeder would probably be adequate for spreading the insecticide.

Depletion of fish food. Hoopes (1959) has shown that the larvae of C. campyla and H. orris, which are the most abundant larvae in the tailwaters, are utilized but little by fish. Only one species of fish, the shovelnose sturgeon (Scaphirhynchus platorynchus) utilized caddisfly larvae extensively and these larvae were P. flava, which are most common in areas other than the tailwaters. It is doubtful, therefore, if a dearth of caddisfly larvae in the tailwaters would seriously affect the fish below the dam.

Change in species dominance. When an animal population is eradicated the void is sometimes filled by species which are less desirable than those which were exterminated. The following two studies clearly illustrate this point.

Caddisfly larvae were replaced by prodigious numbers of chironomid
larvae in the Miramichi River tributaries after DDT spraying. The alteration of the proportional representation of the two groups was thought to be because of the shorter life cycles among the Chironomidae and the lack of predators and competitors (Ide, 1957).

Davies (1950) sampled the emerging populations of black flies 5 years prior to and 3 years following the DDT treatment of a stream. No black flies emerged during the year in which spraying took place (1944). The emergence of these flies increased steadily in the subsequent years, however, and by 1947 the number was about 17 times the average emergence of the flies during the pre-spray years.

It seems doubtful that such a population change could occur for long below the dam at Keokuk even if one was caused by decimation of the larval caddisfly population. Repopulation by caddisfly larvae would most likely occur rapidly because of (1) the upstream migration of ovipositing females, and (2) the drifting of larvae downstream. If areas were repopulated by drifting larvae it is probable that *Cyrinellus marginalis* would replace *Cheumatopsyche campyla* for a time in the slower water areas. *Cyrinellus marginalis* has been shown previously to be a pioneer species.

**Application, dilution and pollution.** If DDT-impregnated pellets or granules are used they should be applied in two major areas: (1) at the water entrance to the power house and (2) in the tailwaters of the dam. The insecticidal pellets, when applied along the immediate upstream edge
of the power house would continue with the current through the water-conducting tubes of the power plant into the turbines, contacting larvae on the trash racks and in the water-conducting tunnels as they went. Continuing downstream the DDT granules, thoroughly mixed in the water by this time, would probably deal effectively with the _H. orris_ larvae in the tailrace below the power house. It seems probable, as mentioned before, that caddisfly larval nets will concentrate the granules.

The broad tailwaters which are below the dam (Fig. 1) constitute an area of slower, shallower water. As stated before, this area is populated predominantly by _C. campyla_, but _H. orris_ and _P. flava_ are also present in considerable numbers. During periods of low water (usually mid-summer, fall and winter) the average depth of the water in this area is about 4 feet and the current is moderate. For the most part the water moves less than 1 mile per hour. Channels of faster water course through the tailwater area, however, and the water in these channels attains a velocity of about 1.5 to 2 miles per hour.

Insecticide could be applied most effectively during July when the water is usually low. The larvicide would probably curtail the generations of _H. orris_, _C. campyla_ and _P. flava_ which would emerge from the tailwaters in late summer. If the granules are retained in caddisfly nets it is conceivable that they may remain as a residual poison in the net remnants and make the area relatively uninhabitable to the larvae for
several weeks.

Because the volume of flow of the Mississippi River is great, dilution would be a problem if liquid insecticides such as oil solutions or emulsions were used. Granular formulations may put this dilution factor to work since the dilution would prevent the insecticide from reaching concentrations toxic to fish. Before such an insecticide is applied to the tailwaters at the Keokuk dam, however, laboratory and field experiments should be conducted to determine the practicability of the operation. Such experiments should most certainly include aquarium experiments to determine the relative toxicity limits of hydropsychid caddisfly larvae and various species of river fish. Small scale applications should be tried, with controls, in the tailwaters before any large scale applications are attempted.

Adding insecticides to an already polluted river such as the Mississippi may seem outwardly to be a drastic, unwarranted measure. The amount of DDT which would probably be applied at Keokuk (approximately 1 pound per acre over 160 acres of river bottom) would be inconsequential, however, compared to the amount of insecticides which enter the river as run-off from agricultural lands and from Japanese beetle control programs.

It should be recognized that one insecticide application in the tailwaters of the dam will not permanently reduce the resident larval population. At least one insecticide treatment per year will probably be
required to give continued relief. It is extremely doubtful if any type of caddisfly control program at Keokuk could seriously affect the total caddisfly population in the river. As the larvae are killed in the tailwaters they will provide room for new larvae and with intraspecific competition thus reduced, the survival rate of newly hatched larvae will be greatly increased. Repopulation of the tailwaters by eggs and by drifting larvae should thus be completed in a very short time.
EPHEMEROPTERA

The Mayfly Problem

Invasions by vast numbers of mayflies (Hexagenia spp.) are familiar phenomena to people who live along the Mississippi River. On several nights each summer, some of the river cities are virtually blanketed by mayflies. 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-hourbugs, 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.

Burks (1953, p. 3) quotes the following Associated Press dispatch of July 23, 1940:

Sterling, Ill. -- Shadflies that in some places piled to a depth of four feet blocked traffic over the Fulton-Clinton highway bridge for nearly two hours last night.

Fifteen men in hip boots used shovels and a snow plow to clear a path. The bridge appeared to be covered with ice and snow. Trucks without chains were unable to operate until most of the flies had been shoveled into the Mississippi River.

The mayflies rest on terrestrial objects during the day and under their weight tree limbs become pendulous and even break (Fig. 11).

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. 12). The dead insects and their cast nympha1 eruviae form foul-smelling drifts where they are washed up along the shore.

Figley (1929) found that mayflies caused allergies along Lake Erie and reported four positive cases of mayfly hypersensitivity. The insect itself does not cause the allergy. Instead the cast subimaginal cuticle is the causative agent. Concerning this Figley (1929, p. 344) said:

Particles of the shed skin are readily wind-born and when one considers the millions of insects which take part in the annual Mayfly invasion, it is not difficult to obtain some comprehension of the amount of allergenic material given off by these insects.
Fig. 11.

Subimagoes of *Hexagenia bilineata* resting in the shade.

Subimagoes of *Hexagenia bilineata* weighting down a tree branch.
Hexagenia bilineata imagoes at a picnic site near Keokuk, Iowa.

Exposed portion of the bottom of the Mississippi River showing the nymphal burrows of Hexagenia bilineata.

Screened pail used to separate mayfly nymphs from mud.

Screen scoop used in reconnaissance sampling for mayfly nymphs.
He added that the most common mayflies along Lake Erie were *Hexagenia* spp. The most abundant mayflies along the upper Mississippi River also belong to this genus.

Parlato (1938) found that of 589 patients who had seasonal hay fever and asthma 19 reacted positively to mayfly extract. Of these 19, 7 or 1 per cent of the total number were definitely hypersensitive to mayfly emanations.

Figley (1940) found that 95 of 1,284 patients with seasonal hayfever reacted to mayfly antigens. He suggested that there is an antigen common to both the mayfly and the caddisfly, as well as species-specific antigens for both.

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 employed by the tow boats. These boats, with their barges, may be a quarter of a mile long and they depend entirely upon their searchlights at night to spot unlighted channel markers. Visibility is greatly reduced by the mass of insects in the beams of the searchlights and the crushed bodies of the insects render the decks, ladders and equipment of the boats slippery and dangerous. The tow boats must of necessity be completely hosed off with water after each encounter with a swarm of *Hexagenia*. 
Generalized Life History of *Hexagenia*

The following account is extracted wholly from Needham (1920), Needham *et al.* (1935), Burks (1953) and Hunt (1953).

*Hexagenia* usually emerges from the water at night and the newly emerged form is known as a subimago or dun. This sub-adult form is unique among insects and is peculiar to the Ephemeroptera. The sub-imago is a somber gray color and the appendages are relatively short and coarse. The cerci bear setae and the wings are cloudy and translucent. After emergence from the water the subimagos fly to trees along the shore and remain almost motionless during the day, usually moving only when disturbed or to keep themselves shaded (Fig. 11).

Eggs and sperm are mature by the time that the subimago stage is reached and stripped eggs may be fertilized in saline solution at this time. About 25 per cent of the body weight is lost, principally in the form of water, during the subimaginal stage.

During times of warm summer weather the subimago molts to the adult stage during the late afternoon and evening on the day following its emergence. The imago is noticeably more delicate than the subimago. 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 subimago is replaced by delicate shades of brown and cream.
Mating occurs principally at dusk and the males swarm in the lee of trees and other objects. The males perform a mating dance while in flight, spreading their cerci as balancers. Females which fly through the swarm are attacked by the males. The male approaches the female from beneath and grasps her thorax from below with his long eversible fore legs. 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 leaves the swarm to complete its 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 female usually returns to the water, flops awkwardly upon its surface and extrudes two packets of eggs. The packets fragment and the eggs sift downward to the river bottom. Usually, being unable to become airborne again, the female flops weakly until she drowns or is eaten by a predatory bird or fish.

The eggs which adhere to the substrate, hatch in about two weeks depending upon temperature. A "U" shaped burrow is constructed by the burrowing nymph in the river bottom and 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 and appears to gain its nourishment from the contained organic matter. The nymphal life is usually completed in about 1 or 2 years.

Development of the contained adult structures is virtually complete by the time the nymph terminates its last stadium and feeding is said to cease with the next to the last nymphal instar.

When ready to molt the mature nymph swims to the surface, the nymphal skin splits and the subimago quite rapidly pulls itself free from its nymphal exuviae. The complete process usually takes less than one minute. Mortality is high at this time due largely to predation.

The morphology of the winged stages differs markedly from that of the nymph in several respects. Adult antennae are reduced in size. Adult compound eyes, on the other hand, are extremely large compared to those of the nymph and 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. 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 from the adults. The familiar snapping noise which is heard when mayflies are stepped upon is caused by bursting of the air bladders.
Methods and Materials

Imagoes, subimagoes and nymphs were preserved in 75% ethyl alcohol and they were identified according to Burks (1953). The most satisfactory containers for storing both winged stages and nymphs were the previously described net-capped sections of glass tubing.

Adults were collected by means of an insect net and by hand picking. Quantitative nymphal collections were made by means of a 15.5 cm x 15.5 cm Ekman dredge and reconnaissance sampling was done with a large screen scoop (Fig. 6). Nymphs were separated from the muddy bottom material with a washing pail patterned after that of Rawson (1953) (Fig. 12). The pail, as described by Rawson, was modified by placing three screen windows in the sides and by mounting a stationary propeller beneath the screen bottom of the pail. The metal paddles which were mounted on the inside of Rawson's pail were omitted. The screen windows prevented the pail from becoming overfull of water as is often the case when mud plugs the screen bottom. The propeller functioned well and the pail had only to be whirled in the water.

Lockmasters at locks 18, 19, 20 and 21 and the bridge superintendent at Fort Madison were asked to keep records of the dates and times when large Hexagenia emergences took place. Two boat captains were also asked for aid, and envelopes which contained vials of alcohol and an instruction sheet (Fig. 13) were distributed to them by the personnel at Lock 19 as
Fig. 13. Mayfly information sheet and collecting vials which were distributed to ship captains on the Mississippi River in 1957 and 1958.
Dear Captain:

As a captain on the Mississippi River you have undoubtedly had experience with mayflies (also known as stoneflies, mayfly flies, etc.). The National Institute Fishmen is operating a 3-year research program to study the mayfly and other river insects. The results of this research will aid in determining if it is possible to control the mayfly.

One of the major difficulties I have encountered in my work has been the difficulty in collecting the insects. I am sure you are aware of the mayfly being common simultaneously at similar places along the river. I believe that the mayfly catches are the only people who can supply us with this much needed information.

The information I need will take less than a minute of your time. I have purchased a file of preserved mayflies, and am only able to get them at mail order house. Please order 10 mayfly flies to the address listed below. The order must be placed on the tag, The back markers at Reed's will take the mayfly flies when you pass through the gate. Again and again and again and again, if you need them.

If you have any questions, just send a letter to us at the address listed below. We are greatly appreciative of your cooperation.

Thank you very much.

[Signature]

Glen R. Fugman, Aquatic Biologist
Fisk State College, Ames, Iowa

[Diagram of mayfly]
the tow boats were locked through. The filled vials were returned at
Lock 19 the next time the boats were locked through. Whenever possible,
the aforementioned records were supplemented with personal observations.

**Hexagenia bilineata** (Say)

**History of Hexagenia bilineata occurrence in the Keokuk area**

_Hexagenia bilineata_ has been abundant in the Keokuk area for many
years. Walsh (1863, p. 199 and p. 202) stated:

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

On the whole, I am satisfied that at Rock Island we have only
two species of this group _Hexagenia_ - _bilinaeta_ and _limbata_ -
the former of which occurs in prodigious swarms and only on
the banks of the Mississippi, in the middle of July; the latter
occurs very sparsely and often as much as a mile from the
nearest river.

While working along the Mississippi River at Quincy, Illinois, Garman
(1890, pp. 179-180) also observed _H. bilineata_. He 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.

This _Hexagenia bilineata_ is the common brown Mayfly of
Illinois rivers and lakes. It occurs throughout the length of the
State, and often in such multitudes as to have acquired the name "mormom fly". It is commonly very abundant in the middle of July. In August, at Quincy, it was rare.

Needham (1920) summarized the data collected at Keokuk by Emerson Stringham in 1916. July was the principal month of emergence and the emergences took place in waves which reached their height about the 13th, 18th and 23rd of the month. Emergences took place simultaneously at Montrose and Fort Madison and smaller waves of emergence culminated on the 10th and 23rd of August. No relation could be found, by Needham, between time of emergence and meteorological conditions.

Coker (1929) also reported that _Hexagenia bilineata_ were very abundant in 1916 around Lake Keokuk. July 13, 14, and 17 were cited as being dates on which extreme emergences took place. He theorized that the abundance of mayflies in Lake Keokuk was possibly related to the great quantities of decaying land vegetation which had been inundated when the Keokuk dam was built.

In his list of the mayflies of Iowa, Thew (1956) lists the following species of _Hexagenia_ as having been reported by various workers along the Iowa portion of the Mississippi River: _Hexagenia bilineata, Hexagenia rigida_ and _Hexagenia venusta_. The frequency with which the various species were reported indicates that _H. bilineata_ and _H. limbata_ are much more abundant in that segment of the river than either _H. rigida_
During the present study, only H. bilineata and H. limbata were collected. Collections made by ship captains on the upper Mississippi River 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 primarily concerned with H. bilineata because it is the major problem species. H. limbata observations will also be included, however, because it, too, is relatively abundant.

Subimago

After the subimago has emerged from the water it flies to a resting place which may be almost any shady, sheltered object. Trees and shrubs are most often utilized as resting sites, but buildings and river boats are also host to large numbers of mayflies. The body color of the subimago is variable and it ranges from dark gray to a dull black.

During times of warm summer temperatures, H. bilineata subimagos usually begin molting at about 2 p.m. on the afternoon following emergence and molting continues into the evening with a peak being reached about 4 p.m. In times of cool weather, however, the insects remain longer as subimagos. 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 and although a few
of the subimagoes were seen to transform during the afternoon and
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
had, in effect, lived an extra day because of the cool weather. It is
interesting to note that thousands of subimagoes, often literally blanket
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 the surface area is even greater. The boats travel 24 hours a
day and they average about 10 miles per hour when downbound and approxi­
mately 8 miles per hour when upbound. During the aforementioned cool
weather emergence, many thousands of *H. bilineata* subimagoes could
have been transported over 350 miles downstream and over 250 miles
upstream before they transformed to imagoes and laid their eggs. During
periods of heavy *H. bilineata* emergence most of the towboats which
passed through the Keokuk lock were observed to carry cargoes of
subimagoes. Although the effects of this increased range are unknown,
its influence upon the gene pool of the species is interesting to contem­
plate.

*H. limbata* in southern Michigan usually remains in the subimaginal
stage for about 24 hours. During cold weather (minimum 49°, maximum
71° F.) subimaginal molts occurred from 36 to 49 hours after capture.
With refrigeration the *H. limbata* subimago stage lasted for 69-70 hours (Hunt, 1953).

The wings of *H. bilineata* subimagos seem to be very easily damaged and 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 subimagos lived as long as 36 hours in the laboratory before they died without molting successfully.

Hunt (1953) has described the subimaginal molt of *H. limbata* and his description fits that of *H. bilineata* very well. In *H. bilineata* a very reliable character was found which indicates when a subimago is about to molt. Normally the wings are held erect and their tips touch each other. Prior to a molt, however, the wings no longer touch, and they 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 during capture. Excellent photographs of the subimaginal molt have been presented by Jahoda (1950), Hintz (1952) and Hunt (1953).

**Imago**

The newly emerged *H. bilineata* imago is noticeably different from the subimago. Its wings are transparent, the body colors are distinct,
the forelegs are longer and more slender, the cerci also are longer and more slender and they no longer bear conspicuous setae. The imago is generally a trimmer appearing individual than the subimago and its powers of flight are much greater.

Occasionally the subimaginal cuticle remains 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_ has been described by many authors (Needham, 1927; Neave, 1932; Needham, Traver and Hsu, 1935; Spieth, 1940; Hunt, 1953). Since the behavior of the mating swarms of _H. bilineata_ apparently differs in several respects from other _Hexagenia_ species, however, the mating activity of _H. bilineata_ 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 _Hexagenia_, occurs at dusk, however, and the male imagoes at this time swarm in the lee of objects such as trees and buildings. Small swarms often occur at relatively low levels, sometimes at a height of about 6 feet. Small swarms usually
occur in the lee of relatively small objects while immense swarms are found higher and in the lee of gross objects such as a bluff or the edge of a line of trees.

Each male *H. bilineata* maintains a fixed position in the swarm. A distance of about 1 foot usually separates each member of the swarm and when relatively small swarms were observed they seemed to orient themselves by means of visual reference points such as the eaves of a building, the top rail of a fence, etc. The two widely spread cerci served as stabilizers. If a breeze was blowing, the hovering males faced into it. During times of calm, however, males often formed a continuous swarm completely encircling an object such as a small building. Unlike the males of *H. limbata* (Hunt, 1953; Lyman, 1955a), the males of *H. bilineata* were not observed to engage in a repeated upward flying movement with a subsequent planing downward. Instead, *H. bilineata* males remained in a fixed position in the swarm. Indeed, if a male at the edge of the swarm was touched so that it rapidly moved 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 a fixed position in the swarm (Cooke, 1952).

As a female flew through the swarm she was pursued by the males until copulation was affected. Copulating pairs flew clumsily from the swarm and usually separated in a matter of less than 30 seconds. It
seemed very doubtful if females were visually recognized as such by the swarming males. The following experiments illustrate that the males seem to be stimulated to copulate by the sight of a small 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 chased. 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 was a female, the swarm quickly recovered with 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 the 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. With the 6-foot long stick held erect the decoy was trailed behind while running through the swarm. 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 recognize only the flight
pattern of the females. Spieth (1940) observed male mayflies to attempt to mate with virtually any species of insect which passed through a mating swarm.

Another investigator (David T. Hoopes) at Keokuk observed females being attacked by males as soon as the females had flown from a wall on which they had completed their subimaginal ecdysis. It seems plausible that these mayflies have evolved a mating behavior pattern which best insures the males finding the females. The imago males may swarm near trees and buildings, not only because such locations are sheltered, but because these are the places where female subimagos have congregated after their emergence on the previous evening. As the females complete their subimaginal molt and attempt to fly away they are intercepted by the waiting males. Such a behavior pattern has been suggested by Lyman (1944, p. 209).

The location of swarms over land and the trees in particular is apparently correlated with the fact that the females, which are relatively cumbersome in flight owing to the weight of the egg packets, do not usually take part in the actual swarming activity which is carried on primarily by the males, are most numerous in the trees along the shore, and enter the swarming males only to mate.

The position which is assumed by Hexagenia mayflies during copulation has been described in detail by Spieth (1940) and Lyman (1944).

After they have mated, female *H. bilineata* return to the river to lay their eggs. Only a few observations were made of the oviposition
procedure and in these instances the females were observed to land on the water and then to struggle and release their egg packets. The body movements of the struggling female seem to aid in the expulsion of the egg masses. Females which are captured in spider webs extrude their egg packets as they struggle to free themselves.

_H. limbata_ also usually release their eggs after they have landed on the water. A few individuals which land lightly on the surface, however, are able to discharge a few eggs and to fly up again to repeat their performance. In four instances, individuals were seen to drop their egg packets from a height of 10-15 feet. _H. limbata_ females tend to extrude their egg packets after landing at a light or when they are picked up by the wings (Hunt, 1953).

When female _H. bilineata_ are attracted to a light, they extrude their egg packets before they die and the white packets are believed by many people to be maggots which have been generated in the decaying flies. When dead flies are removed from beneath a light in the morning, the dried and hardened egg packets remain.

Four _H. bilineata_ females were found to carry a total of 8,576, 8,936, 4,252, and 6,664 eggs. Two _H. limbata occulta_ which were examined by Neave (1932) carried 3,631 and 3,388 eggs. Hunt (1951) counted the eggs contained in 24 _H. limbata_ and found the number to average about 4,000 and to vary between 2,260 and 7,684.
Individual eggs of *H. limbata* have been shown experimentally to sink at an average rate of 1 foot in 80 seconds in calm water. Small clumps of eggs settled 1 foot in 60 seconds. Wave action and currents probably distribute the eggs widely before they come to rest under natural conditions (Hunt, 1953).

The eggs of *H. bilineata* adhere to the substrate when they come to rest. 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°-95° F., 18-22 days at 67°-81° F. and 20-26 days at 62°-73° F. *H. limbata* eggs were killed by freezing. It is interesting to note that the eggs of the white mayfly, *Ephoron album*, are capable of withstanding temperatures as low as -6.9° C. (Britt, 1950).

**Nymph**

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

In the Mississippi River, nymphs were taken at depths ranging from 1 to 25 feet. *H. bilineata* nymphs have been reported as quite abundant at depths of 0 to 30 feet in Lake Nipigon with greatest concentrations occurring between 9 and 15 feet (Adamstone, 1923, 1924; Adamstone and Harkness, 1923). Quite similar findings have been recorded for other
Hexagenia by Rawson (1930), Cronk (1932) and Hunt (1953). Miller (1938), in an Algonquin Park lake, found Hexagenia nymphs as deep as 70 feet. In all of these studies the nymphs were most abundant in soft mud and marl-mud bottoms. Soft mud was also the principal medium for H. bilineata habitation in the Mississippi River. In several instances, however, large numbers of nymphs were found in another type of bottom. 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 one-half inch in diameter.

Two-year life cycles have been reported for various species of Hexagenia by numerous authors (Hunt, 1953). One-year life cycles for H. bilineata in Tennessee and for H. limbata in southern Michigan have been reported by Lyman (1943) and Hunt (1953), respectively.

With regard to determining whether a 1- or 2-year cycle occurs, Neave (1932, p. 187) stated:

It is evident that if the nymphal period extends over one year only, there will be a season (at the time of swarming and during embryonic development) when only a few or no nymphs are available in the lake . . . . If, on the other hand, the life-cycle normally extends over two years or more, there would be medium or large size nymphs available at all times of the year, forming a continuous food supply.

It was soon obvious in Lake Winnipeg from the large numbers of nymphs present in August, just after the flight of the adults . . . . that the life cycle must extend over two years at least.
Lyman (1943a) found that *H. bilineata* in the Watts Bar Reservoir area, Tennessee, completes its life cycle in 1 year as evidenced by the fact that there were not two distinct size groups of nymphs in September.

Although systematic nymphal collections were not made in the Keokuk area at regular intervals, the following observations are considered as evidence of a one-year life cycle for *H. bilineata* at Keokuk.

Extensive bottom sampling above the Keokuk dam on August 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. This population emerged as subimagoes on the night of July 14 and again no nymphs could be found above the dam on August 20, 1958. Small nymphs were abundant above the dam again on December 6, 1958 and on March 15, 1959. If a two-year cycle were in effect at Keokuk there should have been various sized nymphs present during August in 1957 and 1958.

An excellent opportunity to examine a nymphal *H. bilineata* population in situ presented itself at Keokuk on July 9, 1958. On this date the guard gate at old Lock 19 was raised from the river bed. This 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 and its deck was uniformly covered with about 3 inches of soft mud. Since the gate was floated upward from a depth of 18 feet very slowly, the nymphs were not
disturbed. The mud layer atop the gate was heavily populated with _H. bilineata_ nymphs and its surface was uniformly pocked with nymphal burrows (Fig. 12). A smooth metal floor plate was chosen as a sampling site and all of the mud from its 10.5 square feet of surface was collected and screened. The mud 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 the chamber between it and the raised service gate was drained. The draining exposed a sub floor of the service gate. This sub floor is always at least 6 feet beneath the surface of the water and the mud upon its surface also contained a large nymphal population. The deck of the service gate shaded the water tight sub floor and the mud was slow in losing its water content. The mud remained a semi solid and most of the nymphs deserted their burrows to crawl clumsily about upon its surface. As the mud gradually lost its water content the nymphs became unable to move. The nymphal gills remained moist because they were in contact with the wet mud in the furrows which the nymphs had made when crawling. The mud on the head and thorax of each nymph became powder dry due to exposure to the air but the drying seemed to have no adverse effect on the nymphs and 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 sub floor, even though the mud had become very foul smelling.

The mud atop the deck of the guard gate was well drained and it was not shaded as was the mud on the service gate sub floor. Consequently, 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 due primarily to blackbird predation. When the clods of mud were broken open, however, viable nymphs were found in well-defined burrows. A bushel of the clods of mud was set aside in the shade and clods were examined again a week later. No live nymphs were found at this time although a few live chironomid larvae were observed.

A large number of nymphs were collected alive when the guard gate was raised and they were placed in tubs of water for observation in the laboratory. As stated previously, almost all of them were last instar nymphs. The following criteria enabled last instar nymphs to be identified with certainty. (1) The wing pads of mature nymphs were black. (2) The two cerci of mature H. bilineata nymphs were dark while the caudal filament was hyaline. The caudal filament is small in the
subimago, hence the caudal filament is hollow and hyaline in appearance. The cerci of the subimago, however, are black and they are covered with setae. These cerci caused the nymphal cerci (which contained them) also to appear dark. The latter observation is easily verified by sliding out the ensheathed portions of the cerci of a mature nymph. All three filaments then appear hyaline. (3) Careful observation revealed that the subimaginal legs could be seen inside the legs of the last instar nymphs.

**Emergence**

The nymphs mentioned were collected at a most opportune time because their emergence in the laboratory coincided with an emergence from the river just 5 days after the nymphs were collected. This fortunate circumstance allowed detailed observations of emergence to be made in the laboratory while an emergence of the intact population occurred simultaneously from the river.

At 6:30 p.m. (July 13, 1958) a subimago was observed in the river as it attempted to free itself from its nymphal cuticle. The mayfly was captured and was placed in a container of water in the laboratory where it completed its emergence. This single specimen was an indicator of a minor emergence which was to occur during the night, for a number of *H. bilineata* subimagoes were observed at the lock on the following morning (July 14). Six subimagoes had emerged during the night from
the tubs in the laboratory and two more emerged in the laboratory at about 10:30 a.m. July 14.

At 3 p.m. (July 14) a subimago was seen emerging from the river beside the laboratory and between 7 and 7:30 p.m., 10 more subimagoes were observed with binoculars to emerge from the river. In the same interval three subimagoes emerged in the laboratory. It rained hard during the earlier part of the evening and the temperature was quite low all night. Nevertheless, a large emergence of H. bilineata occurred from the river during the night and 20 subimagoes emerged in the laboratory. The emergence in the laboratory was known only to take place sometime after 9 p.m.

In the laboratory, 10 subimagoes emerged at intervals during the morning and afternoon on the following day (July 15) and 15 additional specimens emerged between 4:30 p.m. and 7:15 p.m. Ten more subimagoes emerged during the night in the laboratory and relatively few subimagoes emerged from the river.

By 8 a.m. on July 16 all of the mature nymphs in the laboratory had either transformed or died and no emergence was observed to take place from the river during the next 8 days. Evidently, moving the nymphs from the river to the laboratory had not disrupted their normal time of emergence.

Although the emergence of subimagoes took place during three days'
time, it definitely reached a peak sometime after 9 p.m. during the night of July 14. This emergence was the heaviest one experienced at Keokuk during the entire summer. It is interesting to note that 31 other large emergences were reported by cooperators during this brief 3-day period in the area from Louisiana, Missouri, to Winona, Minnesota (Fig. 14).

The large number of $H. \ bilineata$ nymphs which transformed in the laboratory enabled detailed observations to be made of the process. The process of transformation in $H. \ limbata$ has been described in considerable detail by Hunt (1953) and the following account substantiates as well as supplements his observations.

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 the nymphs which swam at the surface were noticeably silvery in appearance. This silver appearance was caused by an air space which formed between the nymphaal and subimaginal cuticles prior to molting. Close observation revealed that the grooves in the wing pads of the nymphs first became silvery while the nymphs were still swimming along the bottom. The nymphs were watched closely and the grooves of
Fig. 14. Locations and dates of *Hexagenia bilineata* emergences which were reported on the Upper Mississippi River during 1958.
REPORTED HEXAGENIA BILINEATA EMERGENCES IN 1958

MILES ABOVE THE CONFLUENCE OF THE OHIO AND MISSISSIPPI RIVERS
silver gave way to patches of silver which slowly became larger. 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. The air space which is trapped between the integuments undoubtedly accounts for the buoyancy of the surface-swimming nymphs. Indeed, it seemed doubtful if the buoyant, transforming nymphs must of necessity swim to the surface at all. Molting was initiated at the bottom of the tub in all observed instances and the nymphs seemingly attempted to remain at the bottom. When they became too buoyant, they rose, still swimming, to the surface. By the time each nymph was ready to transform its whole thorax was silvery and finally the abdomen also assumed a silver appearance.

Nymphs in the laboratory seemed to molt more slowly than those in the river. The following hypothesis is suggested as a reason for this. The trapped gasses between the nymphal and subimaginal integuments are obviously 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 and this expansion probably aids in the separation of the integuments. If this be the case, it would follow that the transformation of the nymphs rising from the greatest depths would be facilitated the most.
Once the nympha! cuticle between the wing pads was split, transformation was quite rapid. The thorax of the subimago was pushed up and forward and it protruded progressively farther through the split. The abdomen, which had become silvery in appearance, contracted rhythmically and the subimaginal abdomen and cerci were pulled free from, but were not yet pulled out of, those of the nymph.

Subimagines which successfully emerged from their nympha! exuviae always kept their feet on their shed nympha! 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 consequently they were unable to pull their filaments and wings from the nympha! skin. This accident, which was always fatal, was observed in eight instances. The wings were ready for flight as soon as they were pulled from the nympha! wing pads. The wings of subimagines which had difficulty in freeing their wings invariably became crippled and the subimagines never attained the imago stage.

Those subimagines 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 subimagines, both male and female, expelled one to three large drops of an amber-colored, water-soluble
fluid from their anus and quivered their outstretched wings for an instance before they became airborne.

During the summer months of 1958, 150 observations were made of mayfly emergences by ship captains, lock personnel and by the bridge crew at Fort Madison. The letter of instructions and the specimen vials which were supplied to these cooperators are illustrated in Fig. 13 and the time and place of the observations which were made during 1958 are plotted in Fig. 14. 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 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 of subimagoes were reported between the hours of 1 and 4 a.m. _H. limbata_ emergence, on the other hand, always reached a peak from 1 to 2 hours after the fall of darkness and was usually over by 11:00 p.m. E.S.T. in the three southern Michigan lakes studied by Hunt (1953). Hunt never observed subimagoes emerging during the day or early morning.

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.
H. limbata, however, in southern Michigan emerges in greatest numbers in June (Hunt, 1953). In Lake Winnipeg, H. limbata first emerges about June 20 and its numbers increase fairly steadily until the middle of July, when a large emergence marks the height of the swarming season. After a few days the numbers may drop to almost zero but lesser swarms and scattered individuals appear at intervals until the latter part of August (Neave, 1932).

Hexagenia rigida was also reported as common in Lake Winnipeg and it too appeared late in June or early in July. The emergence peak of H. rigida occurred about a week earlier than that of H. limbata and no H. limbata were observed while the largest H. rigida emergence took place (Neave, 1932).

In the Keokuk area, H. limbata were collected in small numbers as early as May 23 and as late as August 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 and 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 observed rarely at Keokuk but they are quite common at Fort Madison 15 miles to the north. No specimens of H. limbata were observed or collected south of Keokuk. Apparently this species becomes increasingly abundant northward.

The pattern of H. bilineata emergences as shown in Fig. 14 clearly indicates they 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. In the period of time which included July 11-17, however, 39 observations were made and 30 of these were made during a brief three-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 mid-summer.

Particular attention was given to the H. bilineata emergences at Keokuk, Iowa, because field operations were centered there. Daily air temperatures 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 generally is 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 degrees. Similarly, no correlation was evident between emergence and water temperature nor between emergence and fluctuations in water level. Needham (1920) also failed to find any correlation between emergence and air temperatures at Keokuk during the summer of 1916.

A rhythm of emergence obviously existed along the upper Mississippi River in 1958, however, with waves occurring at intervals of about 6 to 11 days. As stated before, Needham (1920) noticed that _H. bilineata_ emergences occurred in waves at Keokuk during 1916. There did not seem to be a 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 the same interval of time throughout the entire river segment.

A similar phenomenon has been reported from Lake Winnipeg, where Neave (1932) observed that _H. limbata_ did not emerge earlier in the southern end than in the northern end of that elongate body of water. He stated (p. 184):

The greatest numbers of imagines do not appear simultaneously at all points on the lake. Nevertheless, the maximum does not necessarily occur later in the more northern localities, as might be supposed. In 1930, for instance, the height of the
swarming at Gimli, near the south end of the lake, occurred from July 15 to 17. At Limestone bay, 220 miles further north, the maximum was passed before the 14th, as attested by the great numbers of dead and dying flies which were present on this date.

During August 7-9, 1957, ten transects were established across the Mississippi River in the area from Keokuk to Lock and Dam 18 near Burlington, Iowa. The transects were established at approximately 4-mile intervals in this 45 mile river segment. Four stations were sampled along each transect and two Ekman dredge samples were taken at each station.

Eighty samples, most of which were taken in muddy bottoms, yielded only 106 Hexagenia nymphs. No last instar nymphs were collected. The majority of the nymphs were very small and they averaged about 8-10 mm. in length (from the anterior tip of the frontal process to the end of the last abdominal segment). Progressing upstream from Keokuk, the following numbers of nymphs were taken in the transects: 0, 0, 1, 1, 8, 13, 4, 0, 11 and 70.

About one year later, on August 20 and 21, 1958, a series of qualitative samples were collected in the area from Keokuk to Burlington, Iowa. No attempt was made to sample by means of transects as was done in 1957. Instead, 14 sampling stations were subjectively chosen at intervals along the river. An effort was made to choose sampling stations which seemed similar and which were judged to be potentially good Hexagenia
habitat. The water depth at these locations varied from 2 to 5 feet and the bottom was usually composed of mud or a mixture of mud, sand and detritus. Twelve Ekman dredge samples and five hauls with the screen scoop were taken at each station. The 168 Ekman dredge samples and 70 screen scoop samples collected a total of 423 Hexagenia nymphs. As in August, 1957, no last instar nymphs were collected and most of the nymphs were about 9 mm. long. Extreme variability was the rule in the number of nymphs collected at the 13 sampling stations. Progressing upriver from Keokuk to Burlington the numbers of nymphs per station were 2, 19, 10, 1, 2, 3, 4, 29, 5, 10, 10, 112, 165.

The sampling procedures which were employed in August 1957 and August, 1958 were not designed to collect early instar nymphs and it is almost certain that unsampled populations of early instar nymphs existed at the stations where no nymphs were collected. If sampling had been done in late fall or late spring, large numbers of nymphs would most likely have been collected at all of the sampling stations, since all of the nymphs would have been sufficiently large to be sampled at that time.

It follows, then, that if large nymphal collections were made in June at the stations which were sampled in August, a considerable variance would be evident between the length frequency distributions of the nymphs between stations.
In instances where large numbers of nymphs were collected there appeared to be a predominance of nymphs of a given size. A prime example of this was the population of last instar nymphs which was observed at Lock 19 in July, 1958. It seems evident that such nymphs are of the same age, having been laid as eggs at the same time. Intraspecific competition may partially account for the obvious uniformity in size of the nymphs in such an area. An existing nymphal population may exclude, by predation or some other means, the successful inhabitation of the area by eggs or younger nymphs.

Having been laid as eggs within one or at most two days of each other, the dominant nymphal population should obviously emerge at approximately the same time. When such a mass emergence occurs, the nymphal habitat at the river bottom will be left almost vacant of nymphs for a short time and intraspecific strife will be negligible. Such a substrate is left open then to recolonization by mayfly eggs. The mayflies which emerge from a given area most likely also repopulate it with their eggs. This hypothesis may account, in part, for the spontaneity of _H. bilineata_ emergences.

Thus, it seems that the waves of _H. bilineata_ emergence which occur along the upper Mississippi River are most likely caused by the emergence of a series of dominant age groups. Limited bottom sampling has indicated that the various age groups are not uniformly intermingled, but that
certain areas contain mostly nymphs of one brood while adjacent areas may harbor predominantly younger or older nymphs.

Since the adults of *H. bilineata* are very short-lived, the subpopulations are sexually isolated by time. Furthermore, individuals which emerge at times of low adult abundance are selected against because they are more subject to predation and stand less chance of finding a mate. Conversely, natural selection would tend to favor individuals which emerged with the bulk of the population. The aforementioned selection factors, and probably many others, have apparently succeeded in molding subpopulations of individuals which are very similar genetically and which thus tend to emerge simultaneously.

Hartland-Rowe (1955) reported that *Povilla adusta*, a burrowing mayfly which is widely distributed in central and southern Africa, appears to swarm principally within 5 days of a full moon, with the greatest number of swarms on the second night after the full moon. At Keokuk, no correlation was evident between moon phases and emergence peaks.

Diurnal rhythm in mayfly nymphs has been effectively demonstrated by Harker (1953). By painting luminous spots on the nymphs of *Ecdyonurus torrentis*, *Heptagenia lateralis* and *Baetis rhodami*, she found that diurnal peaks of activity occurred for all three species under conditions of natural daylight and darkness. Neither continuous light, continuous darkness, reversal of day and night, nor constant temperature altered
the diurnal activity of the nymphs. No rhythm developed in nymphs which had been constantly illuminated for 7 months subsequent to hatching. Exposure of the nymphs to natural daylight and darkness for a single day, however, was sufficient to impress a diurnal rhythm upon them. Experimental evidence suggested that the original rhythm of light and darkness to which the eggs and nymphs were exposed determined the rhythm of activity.

The burrowing nymph, *Povilla adulta*, shows a marked diurnal rhythm, swimming freely at night but remaining in its burrow during the day (Hartland-Rowe, 1955).

*Hexagenia* nymphs, however, were not observed by Lyman (1943) to leave their burrows or to come to the surface of the mud during either day or night.

Leonard (1947) found *Hexagenia occulta* to occur steadily in rainbow trout stomachs. He felt that *H. occulta* nymphs either leave their burrows occasionally or at least come near enough to the surface of the lake bottom to fall a consistent prey to the bottom-feeding trout.

**Parasites of Hexagenia bilineata**

Large numbers of trematode metacercariae have been observed in the nymphs, subimagoes and imagoes of *Hexagenia bilineata*. Parasitized *H. bilineata* from the Keokuk area were also observed by Needham (1920, p. 281) who wrote:
I found a large nematode worm filling the body cavity of one Mississippi River specimen \textit{[Hexagenia bilineata]}, and most of the nymphs have their gills thickly beset with the cysts of some parasite unknown to me.

The trematode cysts in \textit{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 elsewhere in the body of the insect and 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. A heavily infected \textit{H. bilineata} female imago was dissected so that the metacercariae could readily be seen. The insect was passed through a series of alcohols to 100% alcohol to harden it. It was then split sagitally with a razor blade, passed down through the alcohols to 70% alcohol and the viscera and eggs were dissected from the abdomen. After the insect had been passed upward through the alcohols to absolute once more, it was cleared in terpineol. A permanent slide mount of the insect was made and it was photographed. Fig. 15 shows the metacercariae present in one half of the adult abdomen. The metacercariae are round and are usually quite dark. A few mayfly eggs are also visible in the photograph but they are readily distinguished from the metacercariae by their barrel shape.

The number of metacercariae varied with the age of the host. Small nymphs (13 mm. long) contained an average of three metacercariae per
Fig. 15. Female *Hexagenia bilineata* imago which has been sectioned, eviscerated and cleared 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. Photograph by Louis Facto.
Last instar nymphs were most heavily parasitized, often bearing as many as 185 metacercariae. Adults carried fewer metacercariae than nymphs due to losses of 10-20 of them during the shedding of the nymphal exuviae. No metacercaria-free adults or large nymphs were observed during this study. The variation in the relative thickness and darkness of the cyst walls indicates that the infection is an accumulative one.

Metacercariae in viable or recently dead mayflies were fed experimentally to day-old chicks, ring-neck 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 and Crepidostomum cooperi 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.
Neave (1932) found as many as 92% of the nympha] Hexagenia limbata which he collected at Lake Winnipeg to carry trematode cysts. The cysts were found in both the gills and abdominal musculature and were thought to be those of Crepidostomum (= Megalgonia) ictaluri. He found the distribution of the parasite to be sporadic, nearly all specimens from certain localities being infected, while in other places very few or none showed any cysts. H. limbata adults which were collected near Keokuk were also hosts to metacercariae, but they seemed to carry considerably few of them than H. bilineata.

Mayfly Control

The following three reports deal with attempts to control bottom-inhabiting insect populations in lentic habitats.

TDE emulsion at the rate of 0.02 to 0.01 p.p.m. was applied to Clear Lake, California, to control a large gnat (Chaoborus astictopus) population (Lindquist et al., 1951). A total of 14,000 gallons of 30% TDE was applied to the 41,600-acre lake. The gnats were completely controlled and other aquatic organisms, including insects, were apparently unharmed. The TDE was thought to be effective against C. astictopus because the larvae migrated upward from the lake bottom each night. The insecticide was reported to be ineffective in the mud.

In Florida, too, gnat populations have been controlled with larvicides.
The most troublesome species in Polk County is *Glyptotendipes paripes* whose larva is a burrowing form. Dramatic temporary relief was achieved around many Polk County lakes which were treated with wettable powder, gamma isomer of benzene hexachloride at a rate of 0.16 to 0.20 lb. per acre. After several months, however, the midge larvae developed considerable resistance to BEG. Since then, EPN at dosages of 0.1 to 0.125 lb. per acre has also been used. Larval resistance to EPN was also encountered and neither doubling the usual dosage of EPN nor a combination of BHC-EPN gave satisfactory control after resistance was established (Lieux and Mulrennan, 1956).

*Hexagenia munda orlando* has been reported as emerging in great numbers from Bear Gully Lake, Florida, at approximately weekly intervals during the summer months (Lieux and Mulrennan, 1955). Dredging indicated that a population of about 125,452,800 nymphs was present in that 200-acre lake. The lake was treated on April 13, 1954, with 0.24 lb. of wettable powder BHC (gamma isomer) per acre. No living nymphs were found in the lake 23 days subsequent to treatment and not a single adult mayfly was observed at the lake during the year of 1954. No apparent damage resulted to fish or other aquatic wildlife as a result of the chemical treatment.

It is apparent from the previous studies that bottom-dwelling insects are not invulnerable to insecticides. In fact, *Hexagenia* appears to be
very susceptible.

Outwardly it would seem that the previously mentioned aquatic habitats are very dissimilar to the Mississippi River. It must be remembered, however, that Hexagenia bilineata nymphs do not inhabit the main channel of the Mississippi River to any great extent. Instead, they occur primarily in the silted, shallow areas of the river where the current is very slight. In these areas the nymphs should be very vulnerable to applications of wettable powders and granular formulations which would sink to the river bottom. Such applications could be readily made by boat or even by aircraft, in some cases, since the river is so large.

A control program would be very feasible at Keokuk for several reasons. Keokuk, for the most part, lies just below the site of a large dam and, as a result of the turbulence and the subsequent lack of siltation below the dam, few Hexagenia nymphs are found there. For this reason most of Keokuk, in particular the business district, receives far fewer Hexagenia adults than most other river cities. The northeast section of Keokuk, however, lies along the area which is impounded by the dam. This area is heavily silted and the current is very moderate except in the main channel. Consequently, large Hexagenia populations exist in that area and when they emerge they create a problem along the shore. The impounded segment runs in a north-northwesterly direction and the nuisance which the mayflies cause is dependent upon vagaries of
the wind. Mayflies are most heavily concentrated along the Iowa shore when an east or north wind blows during emergence and downtown Keokuk only receives quantities of Hexagenia from northeasterly winds. Conversely, heaviest concentrations at the Hamilton, Illinois, Yacht Club (on the opposite shore) occur during times of westerly winds.

It is doubtful if many Hexagenia adults fly more than three miles upstream or downstream from their place of emergence and Keokuk receives virtually all of its Hexagenia from the impounded area immediately above the dam. Only about 3 miles of river would have to be treated at Keokuk, then, because most of the city lies along the tailwaters of the dam where only a meager population of nymphs is found.

Many river cities receive more frequent and more severe Hexagenia swarms than Keokuk. Fort Madison is typical of these cities. Fort Madison lies entirely along an impounded, silted expanse of the Mississippi River which abounds with Hexagenia nymphs. Furthermore, large populations of nymphs occur both upstream and downstream from the city. Thus Fort Madison may receive concentrations of adult Hexagenia from any one of three directions depending upon the wind.

Fort Madison could greatly alleviate its mayfly problems, therefore, by applying wettable powder or granular insecticides to the river shallows which are within a 3-mile distance from the city limits. Fort Madison borders the river for about 5 miles and approximately 11 miles of river
would thus require treatment.

Insecticides would be most effectively applied in mid-June, prior to the first large emergences. One application would probably suffice for the entire season because the life cycle of the insect is about 1 year. Treatment would be required yearly, however, because the area would be rapidly repopulated by drifting eggs and larvae and by ovipositing females which could fly or be transported into the area. Since intra-specific strife would be lessened in the depopulated area, the survival rate of eggs and newly hatched larvae would be greatly increased, thus further hastening repopulation by Hexagenia.

Control of Hexagenia mayflies seems to be both possible and practicable, but before control measures are initiated, the desirability of such programs should be carefully considered. A companion study by Hoopes (1959) revealed that Hexagenia spp. nymphs comprised over 50 per cent of the food of channel catfish, freshwater drum, mooneyes, goldeyes and white bass and over 40 per cent of the food of paddlefish and white crappies. The nymphs were also eaten by shovelnose sturgeon, bluegill sunfish, black crappies and black bullheads.

Hoopes adds that about 1, 168,000 pounds of fish are taken each year from Pool 19 by commercial fishermen and that these fish represent a total annual income of about $171,000 for the fishermen. Pool 19 also provides over 50,000 man hours of recreation to sport fishermen.
These data indicate that large scale control of *Hexagenia* nymphs may adversely affect the fish populations upon which a valuable fishery depends.

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.

It is doubtful if control of adult *Hexagenia* could affect the total population to any appreciable degree. Consequently, programs directed at the imagoes should not be considered as a means of eradicating the insects but as a means of lessening the intensity of the nuisance which they cause.
SUMMARY

Trichoptera

The principal nuisance species of caddisflies at Keokuk, Iowa, are *Hydropsyche orris* Ross, *Cheumatopsyche campyla* Ross and *Potamyia flava* (Hagen). The larvae of these allergy-causing, hydropsychid species require considerable current so that food may be carried into the nets which they construct upon submerged rocks and other silt-free structures. Keokuk lies along the tailwaters of the largest dam on the upper Mississippi River and the current and subsequent lack of silting create a large area which is favorable for hydropsychid larval habitation. Consequently, Keokuk is host to more caddisflies than the other river cities.

*H. orris* larvae build rigid catching nets and they are most abundant in the fastest currents. *C. campyla* larvae construct loose, voluminous nets and they are most abundant in the tailwaters and other areas where the current is moderated. *P. flava* larvae also build loose nets but they are found most frequently in the rock and sand areas of the main channel of the river. Hydropsychid larvae are capable of populating areas by drifting with water currents.

Ovipositing females of the three species were collected beneath the surface of the water with an underwater light trap. *P. flava* females were collected as deep as 20 feet and *H. orris* and *C. campyla* as deep as
12 feet. Females may re-enter the water several times and emergence traps captured many more females than males. Experiments with a vertically-floating pole indicated that oviposition was most concentrated at a depth of 3 to 4 feet. C. campyla and P. flava oviposition was observed in the laboratory and adult females were seen to remain submerged for several hours.

An analysis of the numbers of caddisflies which were captured nightly at a downtown cafe window indicated that H. orris, C. campyla and P. flava are bivoltine species and that they reach peaks of abundance in early and late summer. Size-frequency distributions of H. orris larvae collected from navigation buoys also indicated that H. orris completes two generations per year. C. campyla were reared from eggs to adults in 51 days in the laboratory.

A blacklight trap was developed and it may serve as a caddisfly abatement device at Keokuk. Insecticide space sprays applied to H. orris swarming areas hold promise, as do residual sprays applied to riverside foliage where the caddisflies rest during the day. Granular larvicides applied to the tailwaters may control local larval populations temporarily. Low solubility of the granular formulation may prevent fish from being injured. A loss of caddisfly larvae in the tailwaters should affect the fish very little since fish scarcely utilize the hydropsychid caddisfly larvae in this area.
Ephemeroptera

_Hexagenia bilineata_ and _Hexagenia limbata_ 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 size nymphs in late summer indicated that _H. bilineata_ completes a generation in one year in the Keokuk area. _H. bilineata_ nymphs live in burrows in the river bottom and they 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 such as Fort Madison, Iowa, which lie entirely along silted areas receive greater quantities of adult _Hexagenia_. 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 somewhat.
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Lyman, F. Earle  


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McLachlan, Robert  

Miall, Louis C.  

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192

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Roos, Tage

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Wesenberg-Lund, Carl Jorgen


Whitehead, F. E.
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My major professor, Dr. Kenneth D. Carlander, initiated this investigation and provided guidance throughout the study and the preparation of this thesis. My fellow student, David T. Hoopes, was a constant assistant and companion 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 U. S. Army Corps of Engineers, Lockmaster Donald Pullin and the personnel of Lock 19 provided laboratory space, allowed the use of their facilities, served as advisors on many construction problems distributed collection materials to towboat captains, and made daily observations of insect activities. The U. S. Coast Guard, Captain Donald Meyers and the crew of the Lantana assisted in sampling and provided lodging, transportation and companionship during several extensive collecting trips on the Mississippi River. Pay Buchan, Power Plant Superintendent, allowed the use of the facilities and data of the Union Electric Company at Keokuk. My wife,
Arlayne, often served as laboratory assistant and typed the first drafts of this thesis. Many observations and collections of insects were made by the captains and crews of the tow boats which navigate the upper Mississippi River. Observations and collections were also made by Lockmasters Frank Fiedler, Robert Cook and Thomas McKittrick at Locks 17, 18 and 20, respectively, and by Fort Madison Bridge Superintendent, F. J. Moore. Dr. Herbert H. Ross of the Illinois Natural History Survey identified caddisflies and offered many valuable research suggestions. Technical advice was received at Iowa State College from Drs. Jean Laffoon, Martin Ulmer, Edwin Hibbs and John Lilly. Thomas Thew of the Davenport Public Museum identified many mayflies. Mr. H. E. Thompson, past President of the Fort Erie, Ontario, Lions Club offered valuable information concerning the caddisfly control program at Fort Erie. Excellent publicity was given this study by the Keokuk Daily Gate City and by Charles Fugate in particular. My fellow graduate students James Schmulbach, Fred Meyer, Robert Johnson and Clarence Carlson assisted at various times in the field.

This investigation has been sponsored by a National Science Foundation grant.
Table 6. Number of males and females of 3 species of caddisflies collected at 3 sources of light at the Keokuk dam. The relative position of each light is indicated by the letter L, R and C for left, right and center.

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<th>P. flava</th>
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