

# Seasonal Movements of the Mayfly *Leptophlebia cupida* (Say) in a Brown-water Stream of Alberta, Canada

WORTH HAYDEN<sup>1</sup> and HUGH F. CLIFFORD

*Department of Zoology, University of Alberta, Edmonton, Alberta, Canada*

**ABSTRACT:** The seasonal movements of the ephemeropteran *Leptophlebia cupida* (Say) are reported from a brown-water stream of Alberta. Nymphs of the new generation appear in the main stream during autumn, usually first in riffle regions. As winter progresses, the nymphs move from riffles to pools. For a short period after the ice breaks up in the spring, the nymphs move from pools to the bank and then upstream following the shoreline. The initial movements are associated with a rise in water level. The upstream movements take place during the daylight hours, and this day activity considerably modifies the typical night-active drift pattern of this species. Nymphs move upstream at an average rate of 10 m/hr. By following the shoreline, which will bend in towards the tributaries, the nymphs will move into both vernal and permanent tributaries. The nymphs continue to be day-active as they move through the tributaries. Eventually the nymphs will be extensively dispersed in the marshy areas drained by the tributaries. Emergence takes place mainly from the marshy areas. The female imagoes then fly back to the main stream to oviposit. It is suggested that the springtime movements allow *L. cupida*, which is morphologically poorly adapted to the lotic environment, to maintain a population in that environment.

## INTRODUCTION

Stream invertebrates move downstream via drift in considerable numbers. Some immature insects, especially ephemeropterans, plecopterans and simuliids, exhibit behavioral drift, with the greatest drift rates usually being at night. If there were no compensatory mechanisms for the downstream movements and assuming that all individuals drift, upstream areas could be completely depopulated of certain immature insects. Two possible ways that drift-prone stream insects might maintain upstream populations are via upstream ovipositing flights of the imagoes (Roos, 1957) and upstream movements of the immature insects. However, the movements of most adult amphibiotic insects appear to be mainly controlled by local wind conditions (Elliott, 1967; Bishop and Hynes, 1969a), and the few quantitative studies concerned with the upstream movements of immature insects indicate that the number of insects moving upstream cannot compensate for the much larger number of insects moving downstream in the drift (Bishop and Hynes, 1969b; Elliott, 1971). Immature insects can move upstream on top of the substrate or at varying depths in the substrate; they might move upstream near the bank or in the middle of the channel. Various types of traps are usually used to estimate the number of animals

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<sup>1</sup> Present address: Department of Mines, Resources and Environmental Management, Winnipeg 29, Manitoba.

moving upstream, and it is difficult to design and position the traps in such a way that one is certain all the insects in the trap were moving upstream instead of perhaps being caught in the trap while performing nonoriented movements. It is usually necessary to rely on indirect estimates without being able to see the animals moving upstream.

For a short period after the ice breaks up in spring, northern populations of *Leptophlebia cupida* (Say) (Ephemeroptera: Leptophlebiidae) nymphs move to the banks of streams and then upstream by following the shoreline. These movements result in a rather spectacular "en masse migration" of the nymphs. One can see the nymphs with the unaided eye. Hence direct counts can be made, individual movements can be timed, etc.; it is not necessary to rely on indirect estimates. The springtime *L. cupida* movements were first reported from a Manitoba stream by Neave (1930); subsequently, movements have been reported from streams in Alberta (Clifford, 1969), Ontario (Hynes, 1970) and southern Michigan (K. W. Cummins, Mich. State Univ. pers. comm.).

Our study was concerned with the seasonal movements of *L. cupida* in a brown-water stream, the Bigoray River, of W-central Alberta. The objectives of the study were: (1) to determine the nature and extent of the upstream movements and the possible factors responsible for the springtime movements; (2) to describe the downstream movements of this species; and (3) to document the more subtle seasonal movements taking place within a restricted area of the stream.

#### DESCRIPTION OF THE STUDY AREA

Physical and chemical features of the Bigoray River have been described by Clifford (1969). The stream (53°24'N, 115°07'W) is part of the Arctic Ocean drainage and drains extensive muskeg-type terrain. The pH of the water is, however, usually above 7.0; water temperatures are near 0°C for about 6 months of the year, and the stream is completely ice-covered for about 5 months. The stream is fed by a large number of small, mainly intermittent tributaries draining the marshy areas. The tributary studied in respect to the upstream movements of *L. cupida* has, from its confluence with the Bigoray River to where it blends imperceptibly with the water of the marsh, a lotic channel of about 50 m in length. In some years the tributary may flow during the entire ice-free season (late April through October), but in years of normal precipitation the channel is usually dry by early September. Water that might be in the channel when freeze-up occurs will freeze into the substrate; there is never water in the tributary during winter. Flow values of the tributary range from zero in winter to about 10 liters per sec when the snow melts in late April or early May. The tributary drains a marshy area of approximately 15,000 sq m. During the ice-free season the water in the marsh has an average depth of about 30 cm, but in places the water is much deeper. The major plants of the marsh are *Carex*, *Equisetum* and *Sphagnum*.

## METHODS

Number of nymphs moving upstream per unit time was determined by visual counts of nymphs moving across a line per minute. Usually, 10 counts, each of 1 min duration, were made during each observation. The rate of nymphal movement was estimated by timing individual nymphs of various sizes over distances of 0.5 m; these distances encompassed various current and substrate conditions. When the nymphs were moving through the tributary and marsh, the leading edge of the population was established by collecting nymphs with a dip net having a mesh size of 320  $\mu\text{m}$ . Emergence of *L. cupida* from the river, tributary and marsh was monitored with three-sided emergence traps, each trap having an effective sampling area of 0.14 m<sup>2</sup>.

To make semiquantitative comparisons of *L. cupida* numbers from different types of habitat—e.g., riffles, deep pools, shallow lotic channel of the tributary and heavily vegetated marshy areas—we used a 1 m length of stovepipe having a 20 cm diam opening at each end. The pipe was pushed as far as possible into the substrate; a section of rubber hose was inserted into the pipe, and then the substrate material and water column were pumped out using a hand-operated, 10 cm diaphragm pump with an overpour discharge. Holes were drilled in the lower 40 cm of the pipe and covered with fine-mesh brass screening (pore size: 700  $\mu\text{m}$ ). This allowed water surrounding the pipe to flush the area being sampled. The material passing through the hose was caught in a 720  $\mu\text{m}$  mesh bag at the pump discharge. The pump was mounted on a metal sled and worked well in both winter and summer; a disadvantage was that the pump would not maintain its prime in water less than about 20 cm in depth.

The downstream movements of *L. cupida* were studied by using drift nets; the drift methods for both the main stream and the tributary are described in detail elsewhere (Clifford, 1972 a & b), and only a brief summary is given here. Each drift net in the main stream had a mouth aperture of 9  $\times$  9 cm and a mesh size of 320  $\mu\text{m}$ . Two nets, one on top of the other, were attached to a pair of steel rods; the lower net was positioned with its lower edge 3 cm above the substrate, and the upper net sampled the surface water to a depth of 7 cm. Seven samples of 1 hr duration each were taken in the main stream at evenly spaced intervals during each 24-hr period. The tributary flows over a waterfall 5 m before entering the main stream. A plankton net, having a mesh size of 76  $\mu\text{m}$ , was placed beneath the fall and the entire flow of the tributary passed through the net. Seven samples of 20 min duration each were taken in the tributary at evenly spaced intervals during each 24 hrs.

The upstream movements of *L. cupida* were studied in detail from April 1969 to May 1970 and the downstream movements from May 1970 to May 1971; hence the two aspects of the study were not carried out concurrently. However, observations on *L. cupida* movements and studies of the species ecology and life cycle have been carried out since 1966. The movements are recurring and predictable, and the

results of the upstream and downstream studies will be reported here as one generalized study.

### RESULTS

Detailed description of the life cycle and growth of *L. cupida* in the Bigoray River have been reported (Clifford, 1969; Clifford, 1970). There is one generation a year. Nymphs of the new generation first appear in large numbers in the main stream in August and September. They grow rapidly during the remainder of the ice-free season, but very little in winter, which extends from November through most of April. There is, however, a continuous influx of small nymphs into the population through December, indicating delayed hatching. In late April or early May, when the ice breaks up, most of the nymphs move from the main stream into small, usually vernal, tributaries and then into the marshy regions drained by the tributaries. Most of the nymphs transform and emerge from the marshes in May and June. The female imagos fly back to the main stream to oviposit.

*Movements during autumn and winter.*—The small nymphs of the new generation are usually found first in riffle regions of the main stream (Clifford, 1969). By late autumn some of the nymphs have moved into the pools, although the majority is still found in riffle regions (Table 1). In winter there is a tendency for the nymphs to congregate in deeper pools. By March, which is about 1 month before the ice goes out, almost all the nymphs are found in pools. By this time, water has frozen into the substrate of many of the riffle areas.

During the autumn and winter when the nymphs are in the main stream, they move downstream, exhibiting the nighttime behavioral drift pattern typical of mayflies (Fig. 1). In fact, in autumn and winter (August through March) there is no downstream drift at all during the daylight hours, the night-active pattern persisting even in winter when the stream is completely covered with a thick layer of ice and up to a meter of snow. Drift densities of the new generation were initially greatest during the 2400-hr sampling period; but by early October, when day lengths were shorter, the maximum downstream

TABLE 1.—Average percentage of *L. cupida* nymphs in two riffles and two pools of the main stream during autumn and winter, 17 October 1969 to 27 March 1970

	Riffles	Pools	Total number
1969			
17 October	69	31	103
29 November	86	14	45
27 December	26	74	29
1970			
25 January	36	64	50
28 February	26	84	47
27 March	15	85	34

movement was at the 2000-hr sampling period, and maximum drift densities remained at 2000-hr throughout the winter.

*Springtime upstream movements.*—During, and for a short period after, the breakup of ice in the spring, the nymphs move out of the pools to the shore, and then they follow the shoreline upstream. In 1969, the movements were first observed on 9 April. At this time there was still some ice on the stream, but it was breaking up; the water was quite turbulent, surging up and down through large open areas of the stream. The nymphs moved upstream along the bank of the river (Fig. 2). Usually the nymphs stayed in contact with the substrate as they crawled upstream, but in quiet water regions they swam upstream. Male and female nymphs of all sizes were observed moving on both sides of the main stream along most of the river's course; hence the movements appeared to be general for the entire *L. cupida* population of the river.

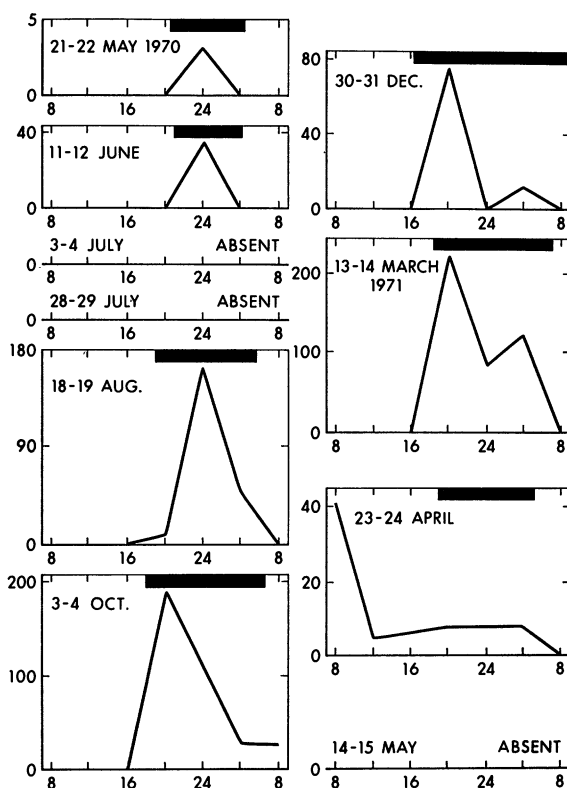


Fig. 1.—Drift densities of *L. cupida* in the main stream for the seven 1-hr sampling intervals of each 24-hr period. Ordinate values are numbers per 100 m<sup>3</sup>; the black bars indicate the periods between sunset and sunrise

Before, during and after the springtime movements, we measured several chemical and physical constituents, *i.e.*, dissolved oxygen, *pH*, turbidity, color, total iron, ortho-phosphate, alkalinity and specific conductance. On two occasions during the movements the constituents were measured every 3 hr in 24. Although the concentration of certain chemical constituents changed greatly during the spring breakup, none could be associated with the initiation or termination of the *L. cupida* movements. Also water temperature was constant and near 0 C when the movements started.

Our data indicate that the stimulus for the initial *L. cupida* movements in the main stream is at least casually associated with a rise in water level (Fig. 3). In 1969 the nymphs were first observed moving upstream on 9 April, when the water level had risen to 100 cm. The water level rose to 119 cm on 14 April and then started to subside. The number of upstream-moving nymphs tapered off as water level dropped, and by 21 April, with the water level at 76 cm, the movements ceased. Three days later rain and snow caused the river to rise again, and on 25 April movements were again observed. They ceased for the second time on 29 April when the water level had dropped to

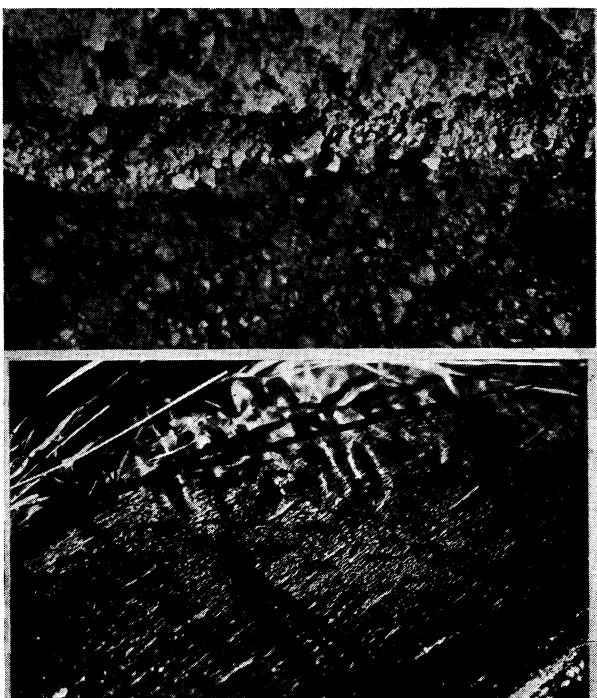


Fig. 2.—Upper: *L. cupida* nymphs moving upstream along the bank.  
Lower: *L. cupida* nymphs moving through the tributary

85 cm. On 5 May, following more snow and rain, the river rose for the third time, and upstream movements were again observed. Hence, in 1969 there were three periods of upstream movements. Field notes compiled since 1966 and subsequent observations in 1970 and 1971 support our suggestions that the initial movements are related to a rise in water level.

It is believed that an increase in turbulence during the periods of high water is a key factor in initiating nymphal movements. Movements ceased in the main stream when the water level dropped, and hence when the turbulence—accentuated by ice conditions in the river—had decreased to the point where the nymphs could maintain their position in their preferred stream habitats. These habitats were at the edges of pools where vegetation was present.

The upstream movement of *L. cupida* in the main stream is mainly a day-active event (Fig. 4). Figure 4 is based on counts made at various times over a 3-day period, 26-28 April 1969, at a site 5 m downstream from the tributary described above. Although other counting sites on the river displayed different daily patterns, movements at all sites appeared to be restricted to the daylight hours. However, it was difficult to determine accurately movements at night because the nymphs are dark and the water at this time was quite turbid. Using a flashlight, we would observe no movements of nymphs for the first 2 or 3 min, but thereafter the nymphs would start to move, appearing to circle around the light beam. All nighttime counts were considered to be zero. Even if some upstream movement did take place at night, it would be of a relatively small magnitude when compared to move-

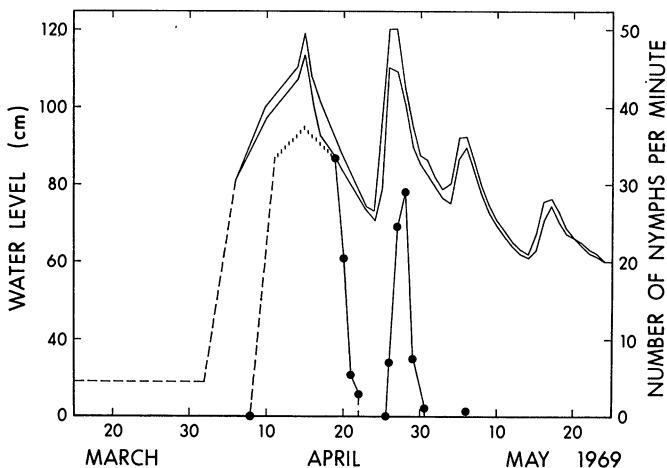


Fig. 3.—Water level and average number of nymphs moving across a line in 1 min. The upper two lines indicate daily maximum and minimum water levels; the lower line indicates nymphal activity. For water level, the broken line indicates a period of no observations; for nymphal activity, the broken line indicates the period before the counting procedure was standardized

ments during the daylight hours. Nymphs moved upstream at an average rate of 10 m/hr. By timing 28 nymphs subjectively classed as small, medium and large, the speed of each class was found to be 7.2 m/hr, 9.0 m/hr, 18.8 m/hr, respectively. Female nymphs are larger than males of a comparable age and, hence, can move faster. Rate of movement did not appear to vary with the time of day, the speed being uniform throughout the daylight hours.

The day-active movements are surprising, since the nymphs normally exhibit a nighttime behavioral drift pattern. But when the nymphs are moving upstream in the spring, they exhibit a day-active drift pattern (Fig. 5). The data used to construct this graph were obtained on 15 and 16 April 1970, during the height of the upstream movements. The lines represent drift rates obtained from drift nets placed in various places of the stream. The day-active drift pattern during the springtime movements is also evident from Figure 1, where the main stream drift data are plotted as drift densities throughout the year. The May and June drift samples were taken after the nymphs had ceased moving in the main stream, and the drift pattern is the typical night-active type for these dates. The new generation also exhibits the night-active pattern, continuing through the winter. The April 1971 sample was taken when the nymphs were moving upstream and, as found in the spring of 1970, drift was again greatest during the day.

*Movements in the tributaries.*—The nymphs continue to follow

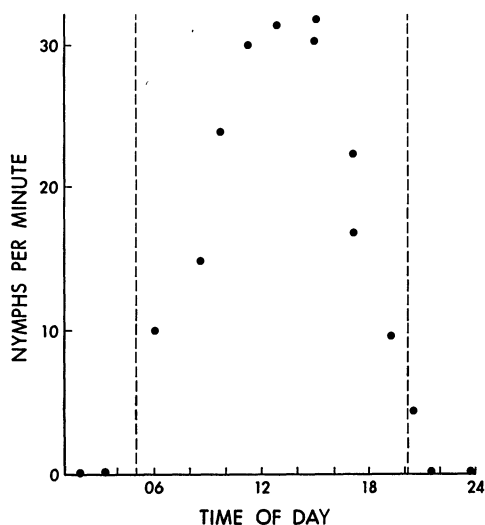


Fig. 4.—Daily movement of nymphs in the main stream. Points are the average of 10 1-min counts of nymphs moving upstream over a line and encompass a 3-day period from 26-28 April 1969. The vertical broken lines indicate sunrise and sunset



the shoreline upstream until they come to a tributary. The contour of the stream bank will bend in towards the tributary, leading the nymphs into the tributary and away from the river. There was no indication that any factor other than the shape of the shoreline influenced the movements out of the river. Water temperatures of several tributaries were monitored during the movements. Some were warmer, some were colder, and others had the same temperature as the main stream; the nymphs moved up all the tributaries with seemingly no preference. Our remarks here will be confined to the tributary previously described.

In 1969 the nymphs started moving up the tributary on 8 April. The leading edge of the "migrating" population was located and, via visual observations and dip net samples, was followed for several days. Five meters from the main stream the nymphs encountered a waterfall, which is 1.5 m in height. Nymphs ascended the fall by climbing up the near vertical face of ice extending out on both sides of the water flowing over the precipice. Later, when the ice had melted, the nymphs negotiated the fall by climbing up wet vegetation hanging over the edges of the fall. By 9 April some nymphs had moved 58 m up the tributary (Fig. 2). Thereafter, the vanguard of migrating nymphs advanced through the marshy area at a rate of about 100 m/day. By 15 April, the nymphs had moved about 750 m away from the main stream, and by early May some of the larger nymphs were found near the hydrographic divide, 1200 m from the river.

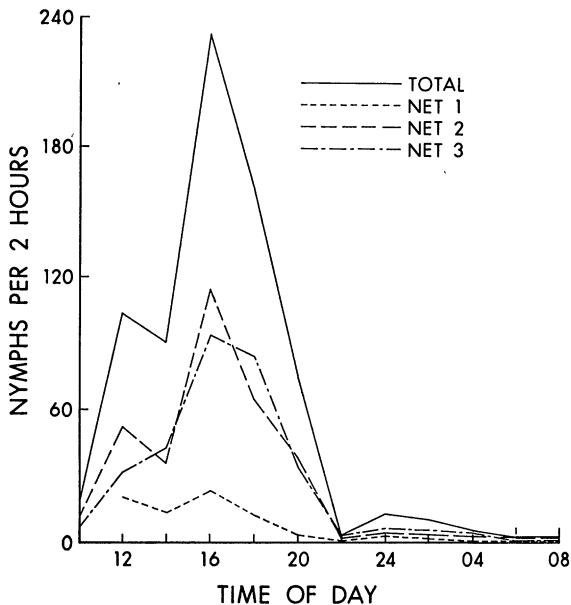


Fig. 5.—Drift rate of nymphs in the main stream during the period when they were moving upstream, 15-16 April 1970

The movements into the tributaries affect the density of the river population. In late March 1969, before the exodus from the main stream, the *L. cupida* population was estimated to comprise (by numbers) 30% of the total macroinvertebrate fauna (excluding Chironomidae) in the river; in late March 1970, also before the movements, *L. cupida* comprised 19% of the total river fauna. When movements out of the river had ceased, in early May of both 1969 and 1970, the *L. cupida* population was estimated at about 4% of the total macroinvertebrate fauna of the river.

Although we did not count the number of nymphs moving across a line for an entire 24-hr period in the tributary, visual observation and tributary drift data indicate the nymphs, at least initially, continue to be day-active as they move up the tributary (Fig. 6). The May 1970

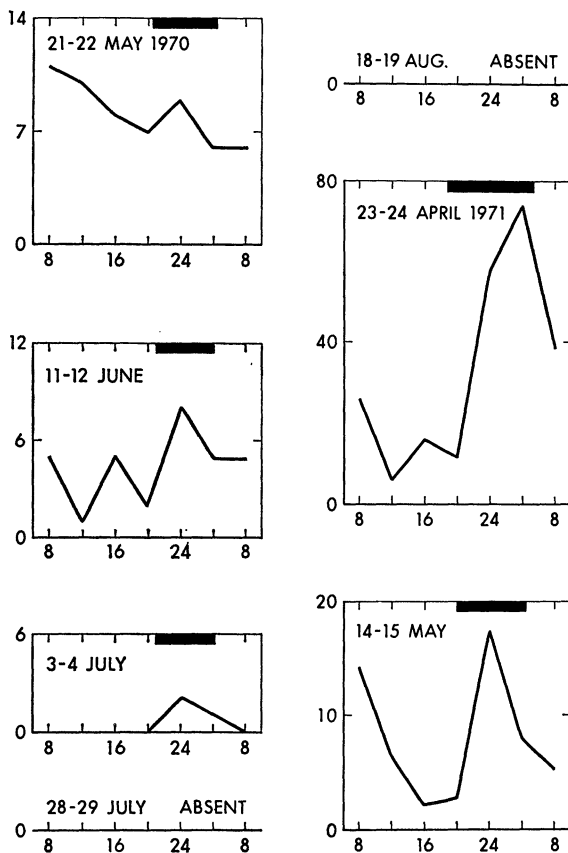


Fig. 6.—Drift rates of nymphs in the tributary for the seven 20-min sampling intervals of each 24-hr period. Ordinate values are numbers per 20 min; the black bars indicate the periods between sunset and sunrise

drift sample was taken when nymphs were moving up the tributary; their daytime movements considerably modified the typical nighttime behavioral drift pattern. In June and especially July, when the nymphs had ceased moving up the tributary, the nighttime drift pattern was more prominent. Again in April and May 1971, the nighttime drift pattern was considerably modified by the nymphs moving up the tributary during the day.

*Dispersion and emergence in the marsh.*—Usually by late May or early June of each year, the nymphs are dispersed throughout the entire marshy region. At least for a time, the nymphs are larger and there are more female nymphs in marshy areas farthest from the river. This would be expected since the females are larger than the males of a comparable age and can move faster. In the middle of May 1969, using the pump sampler, we estimated there were 200 nymphs per m<sup>2</sup> of marsh, which comprises a total area of about 15,000 m<sup>2</sup>. For the same area in the middle of May 1970, we estimated there were 180 nymphs per m<sup>2</sup>.

Most of the nymphs complete development and transform in the marshy region. In 1969, emergence of subimagos was monitored daily for 16 days and sporadically thereafter (Fig. 7). The first subimagos, including both males and females, were collected on 20 May from

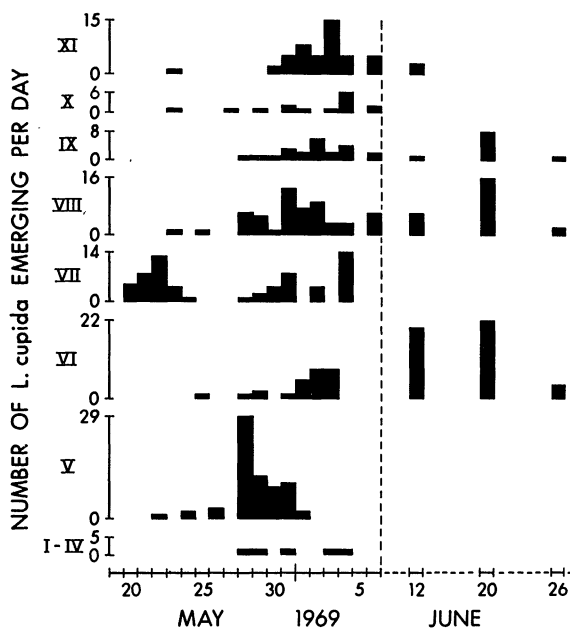


Fig. 7.—Number of *L. cupida* subimagos caught in emergence traps at various sites in the study area. Roman numerals I-IV indicate traps in the main stream; V indicates a tributary trap; VI-XI indicate traps at various sites in the marsh, XI being farthest from the main stream

about the middle of the marsh. There was no discernible day-to-day spatial pattern of emergence from the marsh, although we expected a spatial pattern considering the initial size distribution of the nymphs in the marsh. However, subimagos did emerge earlier from the marsh and the tributary than from the main stream. There was relatively little emergence from the river, and after 5 June subimagos were caught only in the traps of the marsh.

The subimagos were airborne within 2 or 3 min after transforming, dispersing in all directions, some towards and some away from the river. We spent considerable time looking for the mating swarms of the imagos, but without success. On 23 May 1969, 3 days after the first emergence from the marsh, female imagos were first observed ovipositing in the main stream. We never observed *L. cupida* ovipositing in the marsh or tributaries, and in the autumns of 1969 and 1970 we found, in the marsh, only one nymph of apparently the new generation despite thorough monthly sampling.

#### DISCUSSION

We associated the control of nymphal movement in the main stream with a rise in water level. The upstream movements of the nymphs along the bank of the main stream are probably accounted for by the nymph's shape and a positive rheotactic response to current. Neave (1930) found that even when dead nymphs were subjected to water flow they always came to rest facing the direction of the current. This was true regardless of the initial angle of the current to the nymphs. During the spring breakup in 1970, nymphs of the Bigoray River were observed climbing up through melt-holes near the bank. As the nymphs moved through the holes into the thin layer of running water covering the ice, they turned to face the current and, once free from the melt-hole, began to crawl upstream. Nymphs that were dislodged from the ice maintained their head-upstream orientation as they drifted downstream. As soon as they again contacted the ice substrate, they began once more to crawl upstream. The general movements from the pools to the shore in the spring are probably related to rheotactic response and catastrophic drift and, therefore, would be a passive phenomenon, the nymphs losing contact with the substrate of the pools, being swept downstream, and eventually being distributed to the banks where current is less and where they can again make contact with substrate. There is no discernible current when the nymphs reach the marshy area; and yet they continue to move, dispersing away from the river. Temperature gradients had no discernible effect on the direction or extent of movement, for nymphs moved successively through cooler, then warmer, then cooler areas of the marsh. It is possible that chemical gradients in the marsh are important in the movements and route of dispersion in the marsh; but combined field and laboratory work would be needed to substantiate this.

The general upstream movements of immature insects would have adaptive value by compensating, at least in part, for the large number of immature insects drifting downstream. However, the "en masse"

springtime movements of *L. cupida* are seasonally restrictive, and the nymphs move upstream only to the first tributary. This would compensate very little over the long run for the number of nymphs drifting downstream. The movements of *L. cupida* are more comparable to the springtime movements of certain mayfly species found in lakes, where the nymphs move towards the shore of the lake, usually at a time when the level of the lake is rising (Moon, 1935; Lyman, 1956). *L. cupida* nymphs, especially the larger ones, are morphologically poorly adapted to the lotic environment; the nymphs have large laterally extended gills and, in general, resemble mayfly species of lakes and ponds. In fact, *L. cupida* is often found in and migrates from (Neave, 1930) ponds and lakes. We suggest that the springtime movements of *L. cupida* allow this species to maintain, in the broadest sense, its position in the stream or, more properly, the watershed. Specifically, the movements would allow *L. cupida*, which is morphologically poorly adapted to the lotic environment, to maintain a population in the lotic environment.

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