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# The Summer Standing Crop, Growth and Distribution of *Chironomus Plumosus*, in Lake Itasca, Minnesota

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**ABSTRACT**— During the period 15 June to 3 September 1965, 626 Ekman dredge hauls were made in Lake Itasca, Minnesota. The numbers and weights of *Chironomus plumosus* L. at 6 m, 7 m, 8 m, Siefert's Hole (9.5–10.4 m), and Peace Pipe Vista (11.5–13.7 m) depression were determined. In addition, the numbers and weights of several other benthic dipteran larvae, *Cryptochironomus*, *Palpomyia*, and *Procladius*, normal associates of *C. plumosus*, were determined. A loss of 98,407 larvae/ha/day occurred in the 6–9 m stratum during the 12 weeks. There was a decrease in numbers of larvae of 79.3% and 84% at Siefert's Hole and Peace Pipe Vista depression, respectively. The summer decrease in biomass was 4.23 kg/ha/day in the 6–9 m stratum, 1.72 kg/ha/day in Siefert's Hole, and 0.98 kg/ha/day in the Peace Pipe Vista depression. The individual larvae were gaining weight during the 12 week period when the biomass was decreasing. The ANOVA of numbers of larvae during the last seven weeks of the sampling period showed significant effects of depth and time on numbers, but no significant interaction. Fisher's coefficient of dispersion was used to determine the distributional patterns of larvae at the various sampling depths; few collections varied significantly from random distribution, in several samples from Siefert's Hole and the Peace Pipe Vista depression the larvae showed a clumped distribution. The number of larvae surviving to 3 September were estimated to represent a potential pupal crop of 87.31 kg/ha in the 6–10.5 m stratum.

In 1964 a peak in numbers of larvae of the midge, *Chironomus plumosus* (L), occurred at 7 m which was at the boundary of aerobic and anaerobic water toward the end of the summer (Cole and Underhill 1965, fig. 2 & 3). This classical picture of a lower sublittoral-upper profundal zone during the summer (Eggleton 1931) invited investigation concerning its mode of formation and a study with this purpose was initiated on 15 June 1965. The standing crop of profundal and sublittoral benthos in Lake Itasca, Minnesota, was extremely high during the period 10–22 July 1964 (Cole and Underhill 1965). The two most abundant animals, in 1964 and again in 1965, were *C. plumosus* and the phantom larvae, *Chaoborus punctipennis* Say. The two were roughly equivalent in numbers, but *C. plumosus* made up more than 90% of the formalin weight of the total biomass.

The summer of 1965 was unusually cool at Lake Itasca and stratification comparable to that of 1964 did not occur. The water about 9.5 m did not become anaerobic and there was always at least 2 mg/liter dissolved oxygen at 7 m (fig. 1). Because the sampling regime centered around 6 m as the potential lower sublittoral, 7 m as the concentration zone, and 8 m as the upper profundal depths, the planned project was not feasible. The sampling included 626 Ekman dredge hauls, however, and continued for a 12-week period until September

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1965, yielding numerous data reported here on growth, mortality, distribution, etc. of *C. plumosus* and certain of its benthic associates.

Environmental features of the hard-carbonate Lake Itasca have been presented in some detail (Cole and Underhill 1965) and the same physical and chemical methods described for 1964 were utilized during the summer of 1965. Figure 1 shows the results of many analyses from different stations and probably represents a useful portrayal of some physico-chemical conditions in the north arm of the lake during the study period.

An Ekman dredge covering an area of ca. 233 cm<sup>2</sup> was used to collect benthos and a No. 20 sieve (mesh opening ca. 0.83 mm) was used immediately to screen the collected sediment. Fifty collections were taken from the north arm of Lake Itasca (see Cole and Underhill 1965, Fig. 1) and five were taken from the deepest part of the lake, the Peace Pipe depression, 11.5–13.7 m, in the southeast arm. In the north arm, twelve collections were from the sublittoral depth of 6 m; 12 were from 7 m; 10 were from 8 m; 15 were from the profundal Siefert's Hole depression (9.5–10.4 m); and one was taken from 9 m. Fifty-one collections included 11 Ekman-dredge hauls; two included 20 dredges; one included 15 dredges; and one consisted of 10 dredges. The dates of collection are indicated in Fig. 2.

Each of the 626 dredges was treated separately. All *C. plumosus* larvae were counted, blotted on filter paper and weighed alive with a Mettler electric balance. Each collection was then preserved in 10% formalin. Dead and moribund larvae were tallied also, but the dead larvae were not included in the counts and weighing. Pupae were also counted and weighed.

In October, 10 preserved collections amounting to 111.34 g fresh weight were weighed again and oven dried for three days at about 60° C to determine dry weight. Formalin weight was 94.3% of the live weight

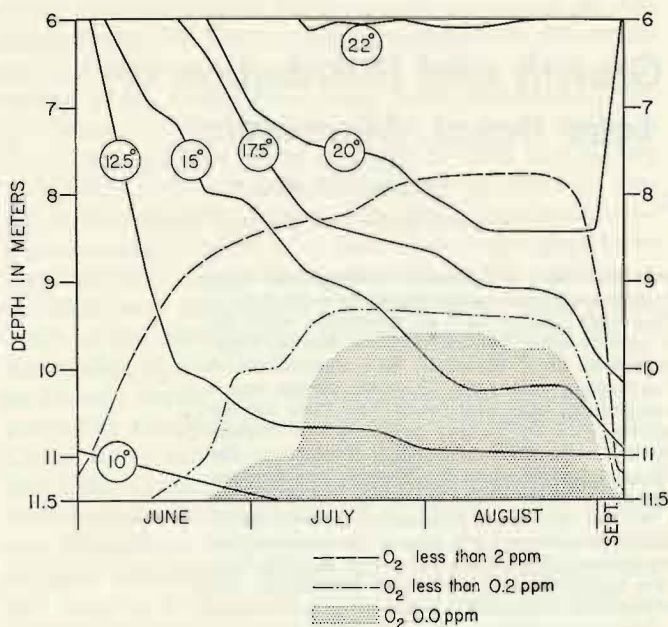


FIGURE 1. Temperature and oxygen concentrations in Lake Itasca during the summer of 1965.

and the dry weight of the preserved larvae was 7.85% of the original live weight. During late June and early July, larvae from 20 samples of 11 Ekmans each were oven dried at 105° C to determine the dry weight. The dried weight of the larvae was  $11.8 \pm 0.4\%$  (range 8.2-14.6%) of the original live weight. Moreover, the ash free wet weight averaged  $99.3 \pm 0.08\%$  (range 98.8-99.7%) of the wet weight, and the ash free dry weight averaged  $9.4 \pm 0.7\%$  (range 87.4-97.2%) of the dry weight. Formalin preserved samples provide conservative estimates of *Chironomus* production and apparently are less reliable than estimates based on unpreserved larvae.

All preserved larvae were measured for total length.

Additional calculations gave data on total numbers and weights per m<sup>2</sup> or ha, Fisher's coefficient of dispersion  $s^2/\bar{x}$ , mean weights per larva and pupa, and frequency of dead, moribund and pupal individuals.

#### Benthic Animals Other Than *C. plumosus*

*Chaoborus punctipennis* is numerically comparable to *C. plumosus* in Lake Itasca (Cole and Underhill 1965), but we collected no data on it during the summer of 1965. Furthermore, the benthic clam, *Pisidium*, was ignored. Other dipterous larvae, *Cryptochironomus*, *Palpomyia* and *Procladius* were studied, however, particularly during the second six weeks.

*Cryptochironomus* was more abundant than it was during the 10-22 July period in 1964 (Cole and Underhill 1965). It was encountered at all depths although especially common at 6 and 7 m; the mean frequencies were 0.67 and 0.12 for these two depths respectively. At least once it was found in all eleven dredges from a 6-m collection. Below 7 m its mean frequency was 0.02. Maximum populations, in early August, were inferred to be 78.6/m<sup>2</sup> at 6 m. Mean populations for the second

half of the summer were 54.45/m<sup>2</sup>, 5.05/m<sup>2</sup> and 0.56/m<sup>2</sup> at 6, 7, and 8 m, respectively. Maximum wet weights were 8.68 kg/ha at 6 m. The animals grew from about 6 mg in the first half of the summer to 10 mg toward the end of the 12 weeks. Pupae were observed on 31 August.

The ceratopogonid *Palpomyia* showed highest mean frequencies in the 6-m collections, 0.53. At 7 m its frequency was 0.23, and at 8 m, Siefert's Hole and Peace Pipe Vista the frequencies were 0.17, 0.23, and 0.02, respectively. Mean populations were 50.3/m<sup>2</sup>, 14.6/m<sup>2</sup>, 7.9/m<sup>2</sup>, 4.7/m<sup>2</sup> and 0.8/m<sup>2</sup> at the five depths. The greatest populations at 6 m weighed about 3.9 kg/ha. Individual larvae ranged from 4.4 mg to 6.0 mg. The greatest abundance of *Palpomyia* during 1964 was also at sublittoral depths (Cole and Underhill 1965, Fig. 4).

The mean frequencies of *Procladius* in the collections were 0.40, 0.63, 0.69, 0.45, and 0.05 at 6 m, 7 m, 8 m, Siefert's Hole and Peace Pipe Vista, respectively. Mean populations at these depths during the second six weeks were 20.1, 104.4, 140.9, 29.9, and 2.4/m<sup>2</sup>, respectively. The greatest mass was encountered at 8 m, amounting to 12.9 kg/ha. These numerical and mass distributions are much like those encountered in July 1964 (Cole and Underhill 1965, Figs. 4, 5). Individual larvae ranged from 4.1 mg to 5.7 mg, with a mean weight of 4.7 mg.

Except for one worm dredged from 6 m and one from 9 m, tubificids were limited to the Siefert's Hole depression, where they were infrequently found. The greatest population was 35.4/m<sup>2</sup> and the mean population of oligochaetes in Siefert's Hole during the second six weeks of collecting was 6.7/m<sup>2</sup>. Individual worms weighed about 2.4 mg.

#### Frequency, Pupation and Mortality of *C. plumosus*

The frequency of *Chironomus plumosus* was 1.0 in the 11 or more samples representing each collection during the first six weeks, but the 26 July and the 5, 12, and 26 August samples from the Peace Pipe Vista depression revealed frequencies of only 0.73, 0.91, 0.64, and 0.73, respectively. Also the 23 and 30 August samples from Siefert's Hole showed larval frequencies of 0.82 and 0.91. We believe these reductions were caused by mortality rather than emergence of adults. No pupae were collected at those depths and other pupal data suggest that the emergence commenced farther up the slope in the lower sublittoral.

The first pupa, a single individual, was encountered at 6 m on 18 July. On 27 and 31 August, 6.6% and 5.6%, respectively, of the population was pupated at that depth. The only other pupae observed were at 7 m and 8 m (7.1% and 5.1% of the populations) on 2 and 3 September, respectively. From these limited data it appears that a wave of pupation progressed down the basin slope, and that the larvae matured earlier in the shallower depths. There was evidence, however, of some swarming as early as mid-August (Fig. 2). Perhaps some pupation occurs above the sediments; Hilsenhoff (1966) reports *C. plumosus* sometimes becomes limnetic in the fourth instar.

Dead chironomids were found in all 55 collections, but relatively more were present in the collection from deeper water. Thus at the different depths the mean percentages of dead larvae in a collection were as follows: 3.8% at 6 m; 3.5% at 7 m; 4.2% at 8 m; 5.8% in Siefert's Hole; and 27.6% in Peace Pipe Vista.

The data on moribund larvae are less reliable. The first collection from the Peace Pipe Vista depression implied 157,200/ha which was more than 6% of the total population there. The mean moribund larvae in the 6-9 m stratum for weeks, II, IV and V was 110,082/ha; and the mean in Siefert's Hole was 80,550/ha for weeks III and V, roughly two per cent of the total. This was relatively greater than in the 6-9 m stratum.

### Numerical Changes of *C. plumosus* at Individual Sampling Depths

Figure 2 shows densities of *Chironomus* populations at different depths during the sampling period, 15 June-3 September. We hoped the relative pattern of density at 6, 7 and 8 m would change as the summer progressed until the 7 m population became more abundant than those at 6 m and 8 m as it was in 1964. The first indication that this might occur was when the 6 m population was reduced precipitously during the first half of July, becoming, briefly, smaller than that at 7 m (Fig. 2). A slight increase at 7 m may have occurred then but in no way matched the sublittoral decline. Stomach analyses from yellow perch (*Perca flavescens* L.) showed they were feeding on *C. plumosus* larvae at that time, and predation may have accounted for the decline, first at 6 m and slightly later at 7 and 8 m (Fig. 2). Also, examination of the stomach contents of 183 *Coregonus artedii* LeSueur showed that 23.5% had been feeding on *Chironomus*. All these whitefish were from the Peace Pipe Vista depression in the southeast arm, however, and there was no evidence that *Coregonus* was present at Siefert's Hole in the north arm of the lake.

With the sharp population decline at 6 m we hoped that one mechanism effective in the formation of the concentration zone had been revealed—fish predation in aerobic water. Because dead and moribund larvae were most abundant in the deeper, anaerobic zones and popu-

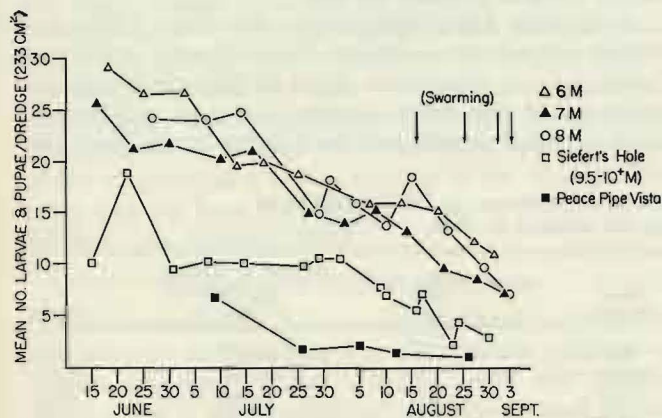


FIGURE 2. Mean numbers of *C. plumosus* larvae per Ekman dredge sample at the five sampling depths in Lake Itasca.

lations were relatively depauperate there, we suspected that an oxygen profile similar to that of 1964 would bring about a decline in the larval numbers below 7 m. Thus, predation in the lower sublittoral and increased mortality in the anoxic, upper profundal could leave a peak at the boundary of aerobic and anaerobic water. This, of course, did not occur at the depths we had selected for sampling (see Fig. 3).

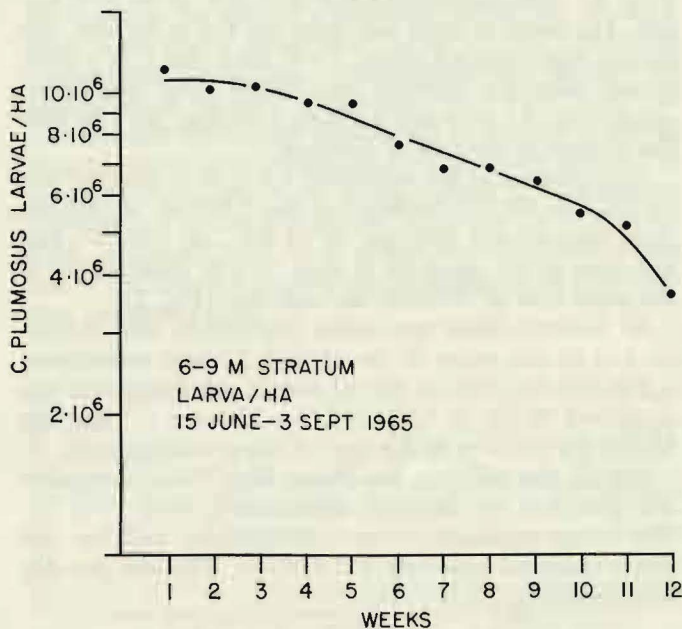


FIGURE 3. Numbers of *C. plumosus* larvae per hectare in the 6-9 m stratum during the period 15 June to 3 September 1965.

There is no way to be sure from trends in Fig. 2 whether or not decreases at one depth were accompanied by meaningful increases at other depths. The analysis of variance of numbers of larvae taken in 231 Ekman samples during the last seven weeks of the sampling period (Table 1) shows significant effects of depth and time on numbers of larvae. The F value for interaction has a probability greater than 0.20 and there is little ground for suspecting interaction. The somewhat surprising absence of interaction has been interpreted to mean that the additive effect of depth upon numbers of larvae per sample remained constant through time; and, likewise, the variations in numbers per sample through time was constant across depths. Therefore, if migrations do occur, the losses or gains appear to be compensated for by the environmental changes that accompany the shift in

TABLE 1. Analysis of variance in numbers of larvae of *Chironomus plumosus* at 6, 7 and 8 meters, 20 July-3 September 1965, in Lake Itasca.

Source	Sum of Squares	d.f.	Mean Square	F
Depth	437.94	2	218.97	13.73*
Time	2198.59	6	366.43	22.97*
Interactions	275.58	12	22.96	1.44
Deviations	3350.96	210	15.95	
TOTAL	6262.57	230		

\* P < 0.005

depth or perhaps differential mortality or emergence is compensated for by migrations.

The 18.6 ha that make up the 6-9 m stratum can be treated as a unit by multiplying individual areas of the 6.0-6.99 m, 7.0-7.99 m, and 8.0-8.99 m strata by the larvae in each area, summing and dividing the total by 18.6. In this broad stratum, the larvae decreased from 11,454,860/ha to 3,680,690/ha during the 12 weeks (Fig. 3). This represents a loss of 67.9% or 98,407/ha/day. The week to week loss from the 6-9 m stratum was erratic, but averaged about 7.4% until the 11-12 week period when the decrease was 29.7% (Fig. 2). Emergence (Fig. 2) probably accounted, in part, for this sudden change in the rate of decrease.

The decrease in the sublittoral 6.0-6.99 m stratum was 61.3%, or 65,323/ha/day; in the 7.0-7.99 m stratum there was a total decrease of 71.6%, or 101,777/ha/day; and in the 8.0-8.99 m area 71.1% disappeared at the mean rate of 109,230/ha each day (Fig. 2).

In Siefert's Hole the initial population was considered to be the mean of the 15 and 22 June collections, 6,268,350/ha (Fig. 2). By 30 August this population had decreased 79.3% to 1,296,900/ha. The loss per day was 65,414 for each ha in this part of the profundal zone.

During the 48 days the Peace Pipe Vista depression was observed, the decrease amounted to 84% (Fig. 2). The initial population was 2,947,500/ha and the last count observed was only 471,600/ha. The loss per day was, therefore, 51,581/ha.

#### Summer Decrease in Biomass of *C. plumosus*

The total, live weight biomass contributed by *C. plumosus* that disappeared from the 6-9 m stratum during the 12 weeks was 334.54 kg/ha, a 59.8% loss from the original 558.99 kg/ha (Fig. 4). This amounted to a mean daily loss of 4.23 kg/ha.

The 6.0-6.99 m level changed 58%, or from 608.07 kg/ha to 352.86/ha. At 7.0-7.99 m the original population weighed 509.12 kg/ha and decreased 69.4% and at the 8.0-8.99 m stratum the first collection implied 461.29 kg/ha, but decreased 64.3% to 296.62 kg/ha. The loss each day was more than 4 kg/ha at each of the three levels.

In Siefert's Hole the original population, based on the mean weights of 15 and 22 June, was 190.11 kg/ha and it decreased to 59.54 kg/ha. This was a 68.7% loss in biomass that amounted to 1.72 kg/ha/day.

The original wet weight of larvae in the deeps of the Peace Pipe Vista hole was 68.13 kg/ha. Forty-eight days

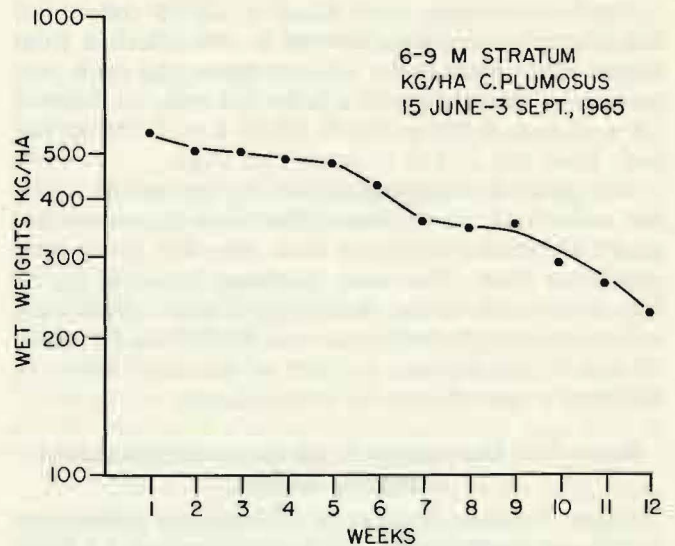


FIGURE 4. Weight of *C. plumosus* larvae in kg/ha in the 6-9 m stratum during the period 14 June to 3 September 1965.

later it was 21.30 kg/ha, a loss of 68.7% at the mean rate of about 0.98kg/ha/day.

#### Growth, Weights and Lengths of Individual Larvae

Individual larvae were gaining weight during the 12-week period (Table 2) when total biomass was decreasing. At 6, 7, and 8 m each larva increased at the mean rate of about 0.1 mg/day. In Siefert's Hole the mean weight increase was 0.18 mg/day for each larva, and the percent of increase was almost three times that of the larvae at shallower depths. During the 48 days covering observations at Peace Pipe Vista each larva increased over 95%, gaining weight at the mean rate of 0.46 mg/day. Table 2 shows that the average larva from the two deep depressions, when last observed, had about the same mass as those at 7 m in mid-June. Their greatest gains were made during the last week or ten days, however, and they may well have attained weights comparable to those at shallower depths very soon after we stopped collecting. This rapid spurt of growth seen in the larvae from the deeper profundal areas is difficult to explain, but it served to nearly synchronize emergence of adults from all parts of the lake.

Data from Lake Winnebago, Wisconsin (Hilsenhoff 1966) suggest the combined mean of male and female larvae prior to pupation is about 60 mg, which is greater than any of our mean weights. Our final weights may have included second and third instar larvae from mid-

TABLE 2. Mean larval weight increase of *Chironomus plumosus* at different depths in Lake Itasca, Minnesota, during the summer of 1965.

Depth (Meters)	Date of First Observation	Days of Observation	Initial Weight	Final Weight	Increase in Weight		
					Total mg.	Per Day mg.	Percent
6	June 18	74	48.5	56.3	7.8	0.105	16.1
7	June 16	78	45.9	53.5	7.6	0.097	16.5
8	June 27	68	50.9	57.4	6.5	0.095	12.8
9.5-10	June 15	76	32.1	45.9	13.8	0.181	43.0
11.5-12.5	July 9	48	32.1	45.2	22.1	0.460	95.5

August oviposition, serving to make our estimates of individual growth too small.

The weight of an average pupa at 6 m was 35.3 mg which was roughly 63% of the weight of a larva just prior to pupation.

On the first sampling date at each depth the following modal and maximum length prevailed: 6 m, 26 and 30 mm; 7 m, 25 and 30 mm; 8 m, 24 and 30 mm; Siefert's Hole, 23 and 28 mm; Peace Pipe Vista, 20 and 26 mm. During the course of the summer, the largest larvae (31 mm) were found only at 6 m and 7 m. All the above dimensions are those of 4th instar larvae, but third and perhaps second instar larvae were taken in some of our samples.

Previously we (Cole and Underhill 1965) considered *C. plumosus* to be univoltine in Lake Itasca. There were, however, some third instar larvae in the first few samples we took during June, and it is doubtful that these wintered in this stage. Hilsenhoff (1966) found that this midge winters over in Lake Winnebago, Wisconsin, in the 4th instar. There is, therefore, probably an Itasca emergence, followed by oviposition in late spring, perhaps early May, which we missed. The larvae we started sampling in June were derived from this flight, and the species probably has two generations a year in Lake Itasca.

Probably the larvae below 14 mm long were not fourth instar and those 6 mm long may have represented the lower limit of the third instar. During the first six weeks of collecting, samples from the 6 m depth included some third instar larvae once, and the same was true for 7 m; the three collections from 8 m, the one from 9 m, and all five from Siefert's Hole included third instar larvae. The first collection from Peace Pipe Vista (9 July) included third instar and perhaps large second instar (5 mm) larvae, although third instar might range down to this length (Hilsenhoff, personal communication). Thus, the larvae at the shallower and warmer levels had progressed further in development than those in deeper sediments.

After 27 August there was a reappearance of a few larvae less than 14 mm long at 6, 7, and 8 m, and the modal length at those depths shifted downward. This suggests that a new generation might have appeared and that the larger, fourth-instar larvae from the earlier cohort had pupated and, perhaps, emerged. The eleventh week was characterized by a marked percentage increase in small larvae (those less than 18 mm long, for example) at all depths. This could have been brought about by the emergence of the largest 4th instar larvae and the arrival of the vanguard of a new generation in the samples. The latter may not have been sampled adequately with a No. 20 sieve (see Jónasson 1955).

#### Spatial Distribution of Larvae

Fisher's coefficient of dispersion had been used by several authors to determine the distribution patterns of aquatic organisms (Jones 1961; Comita and Comita 1957). This is the quotient of variance divided by the mean,  $s^2/\bar{X}$ . Although quadrat size may be important in determining the quotient which is calculated, in general,

a coefficient = 1.0 indicates Poisson dispersion; a coefficient significantly less than 1.0 shows regular spacing and a coefficient significantly greater than 1.0 implies high aggregation or contagious distribution.

Significance of deviation from unity (perfect randomness) was determined by the following equation chi-square =  $(N-1) s^2/\bar{X}$ , where N is the number of samples.

Figure 5 is a semi-log plot of  $s^2/\bar{X}$  and time, showing the analyses of the 55 collections during the 12-week span. This figure shows that larvae in few collections varied significantly from randomness, but usually the population in Siefert's Hole and Peace Pipe Vista depression had the highest coefficients of dispersion and in some instances were definitely clumped. The 6 m and 7 m populations usually were characterized by coefficients less than 1.0 but were regularly dispersed ( $p = 0.05$ ) on three occasions only. It is noteworthy that toward the end of the summer populations at all depths showed random dispersion (Fig. 5).

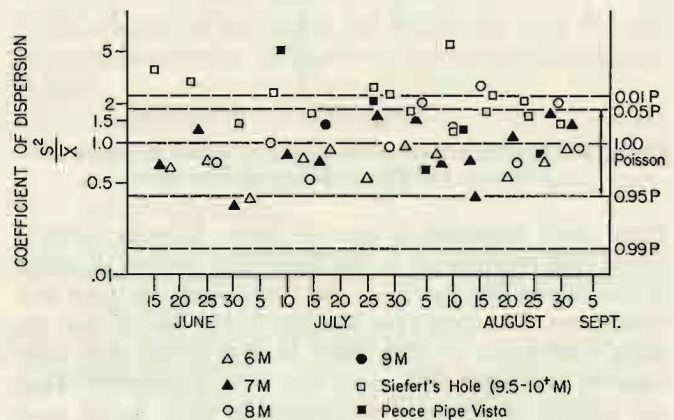


FIGURE 5. Distribution of *C. plumosus* larvae at six depths in Lake Itasca during the sampling period 15 June to 3 September 1965.

Data from the first six weeks showed that the mean number of larvae per dredge was significantly and negatively correlated with  $s^2/\bar{X}$ ;  $r$  was  $-0.847$ . This suggested that when the larvae were crowded they seemed to be randomly or, on rare occasions, regularly spaced. The data from the 35 collections of the second six weeks negated this, however. The correlation was  $-0.169$  ( $p > 0.1$ ). Also, the mean number of larvae per dredge for the entire summer, 55 collections, was not correlated with the coefficient;  $r$  was  $-0.121$  ( $p > 0.1$ ). However, when mean larval weight in each collection was correlated with  $s^2/\bar{X}$ , the  $r$  value was  $0.618$ , an extremely significant correlation (Fig. 6).

The strong negative correlation shown between population density and the coefficient of dispersion during the first half of the summer is explained by the occurrence of the smallest larvae in the deeper areas where the smallest populations were. Later, populations at all depths declined, but the larvae in deeper waters gained weight remarkably, becoming more nearly equal to those in shallower regions.

Factors other than size are involved in the above.

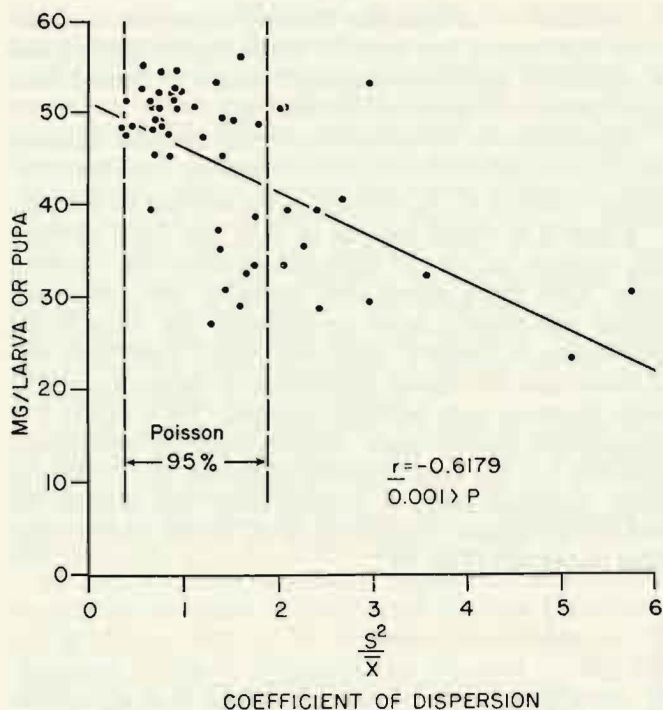


FIGURE 6. Correlation of mean weight of larvae or pupae of *C. plumosus* and the coefficient of dispersion.

Time since hatching is one of these. Mundie (1957) found high aggregation in the dispersion pattern of midge larvae during the summer, and particularly in June and September. His data (see his figs. 9-30) reveal that the main emergence periods were in the spring and early summer and, later, in August and early September. Thus the highest coefficients of dispersion were found soon after hatching. Our June collections were taken soon after the presumed May hatch and, as the summer progressed, our collections were temporally farther from that hatch. Probably the egg-mass stage of *C. plumosus* represents the most aggregated part of the life cycle after the adult mating swarms. The newly hatched larvae would be clumped in groups on the lake bottom and would gradually disperse, thus, toward randomness. This trend is shown in Fig. 5.

Colder water temperatures at Siefert's Hole and the Peach Pipe Vista depression may have delayed hatching so that these larvae were temporarily behind those in shallower waters when our sampling was initiated. The study of elaterid larvae by Salt and Hollick (1946) is instructive and suggests that time since hatching is important in spatial distribution. The smallest larvae are gathered together in groups but they gradually disperse and reach a random distribution when older and, therefore, larger. The adult females lay eggs together in more or less selected places and the wireworm larvae gradually disperse "—like the ripples from a stone dropped into water."

Mundie (1957) found randomness and regular spacing during late winter and early spring in chironomid larvae. This would be the time of year furthest in time from hatching.

Another factor to be considered is the difference in habits between instars of *C. plumosus*. Although most 4th-instar larvae were smaller in Siefert's Hole and the collections from Peace Pipe Vista than at stations farther up the basin slope, there were more third-instar larvae there also and especially during June. The fourth instar larvae live in deeper U-shaped tunnels than do the previous instar (see Hilsenhoff 1966). Perhaps there is a tendency toward the random spacing of burrows upon attaining the fourth instar. Furthermore, a natural pruning effect might lead toward regular dispersion; the mortality rate of larvae in adjacent burrows might be higher than well-spaced neighbors.

#### Pupal Productivity in Lake Itasca

The decline in larval mass at each depth during the 12 weeks represents about 222.67 kg/ha for the entire north arm from 6-10.5 m. This quantitative statement is invalidated somewhat by emergence, if we are to rely on it as an exact estimate of the production directly recycled by predation or decay. Again ignoring emergence there were 138.59 kg/ha available in the north arm for pupation on September 3. This figure represents the final net production of larvae. If the pupae weigh about 65% of the largest larvae, as determined by our few pupal weighings, and all the larvae present at the end of the sampling phase survived to pupate, the pupal crop was only 87.31 kg/ha. Possibly doubling this figure to account for the presumed spring emergence would approximate the annual pupal mass.

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