Seasonal Distribution of Midge Larvae in a Senescent Lake*

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The seasonal distribution of certain limnologically important species of midge larvae, which seems to vary from one lake to another, is incompletely understood. During the course of an ecological study on the food-cycle dynamics of Cedar Bog Lake, Minnesota, the author has been able to assemble quantitative seasonal data over a four-year period on seven important species of lacustrine larvae. It has been found that neither quantitative observations on larval populations nor the periodic collection of adults alone is adequate to determine the seasonal distribution of these species. Recognizing this, the author in 1939 and 1940 attempted to combine the above methods, and also to rear under controlled conditions the larvae of certain species captured at various intervals.

Cedar Bog Lake is a shallow senescent lake about 35 miles north of Minneapolis; its developmental status and ecological composition have been described in preceding papers of this series (Lindeman, 1941a, 1941b). During the period from March, 1937, to March, 1941, quantitative seasonal collections of the bottom fauna were made with a modified Birge-Ekman dredge (225 cm^2) from "open water," "pondweed" and "marginal" areas, respectively. The number of dredge samples taken on each date varied from 12 to 18 during the ice-free seasons, and 8 to 10 during the winter.

This paper summarizes the seasonal data for the seven most important midge species found in the lake: *Chironomus plumosus* Linnaeus, *Chironomus decorus* Johannsen, *Chironomus (Glyptotendipes) lobiferus* Say, *Chironomus (Endochironomus) nigricans* Johannsen, *Procladius culiciformis* (Linnaeus), *Palpomyia* sp. and *Chaoborus punctipennis* (Say). The many other species of midge larvae and adults which have been collected from Cedar Bog Lake during the course of this study have not been sufficiently abundant to give adequate indication of their general seasonal distribution.

Chironomus plumosus and Chironomus decorus

Chironomus plumosus, both Palearctic and Nearctic in its distribution, is perhaps the most important organism in the profundal regions of eutrophic lakes; it is also found in great numbers in ponds and sluggish ooze-bottomed streams. *Chironomus decorus,* apparently strictly Nearctic in distribution, is most abundant in shallow ooze-bottomed ponds and streams (Johannsen, 1937b). Both species are very tolerant of anaerobic conditions (Lindeman,

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1942). The larvae of these two species are extremely similar in appearance, in ecological status and even in their anaerobic capacities, and are here considered together.

Remarkable annual species-substitution between these two forms was noted in the lake. An abundant population of *plumosus* alone, present in the winter of 1936, was completely replaced by a sparse population of *decorus* during 1937. A small population of both species was present in 1938, while in 1939 both species increased tremendously in numbers and importance. During 1940 the population of *plumosus* greatly declined, while that of *decorus* seems to have disappeared completely. Richardson (1921) commented on the discrepancies between the presence of great numbers of both *plumosus* and *decorus* in the Illinois River and their apparent inability to traverse by wing the short distances across timbered ridges to oxbow lakes which presented the same degree of pollution. In another paper (1928) Richardson gave tables showing the same sort of tremendous annual fluctuations for *plumosus* as are here reported, but attributed this at least in part to the effect of floods at mating time. While it seems not unlikely that unfavorable weather at mating time may have disturbed the natural reproduction in Cedar Bog Lake, no explanation can be given for this remarkable alternation of species.

Several summer generations of *Chironomus decorus* seem to develop each year in shallow warm-water habitats. Ping (1917, p. 425) reported evidence that probably five generations per year may develop in the vicinity of Ithaca, New York. Cultures of larvae from Cedar Bog Lake maintained at a temperature of 20° C. were observed to pupate and emerge within a few weeks. The data for 1937 (Table 1) indicate that probably several sparse generations of *decorus* were developing and emerging throughout the summer months. In 1940 the emergence of adult midges in Cedar Bog Lake was carefully observed at biweekly intervals. *Chironomus decorus* was the first midge species to emerge; numerous pupae were collected on IV-28-40, and on V-11-40 multitudes of adults were seen emerging from the surface. By V-26-40 (see Table 1) almost all of this species had emerged, as had many of *plumosus*. For unknown reasons *decorus* did not reproduce itself in the lake; 2 pupae were collected on VI-24-40, and one adult was reared from larvae collected on VII-7-40, but the species was not found in subsequent summer collections. These meager data, however, suggest that three generations of adults had emerged in 1940 between April and the end of July.

The emergence of *Chironomus plumosus* adults in Cedar Bog Lake was also studied at biweekly intervals during the spring and summer of 1940. The first emergents appeared late in May. The majority of larvae and pupae had emerged by VI-24-40, and many larvae of the next generation occurred in the dredgings of this date. A month later (VII-27-40) all larvae collected (61 from 10 dredgings, 2250 cm.^{2}) were more than 18 mm. in length and averaged 25 mm. in length, indicating that all were members of a second generation of *plumosus*. Some of these larvae were cultured in the laboratory at 20° C., approximately the temperature of the lake ooze during this period, and emerged as second-generation adults on VIII-28-40. In late September (IX-29-40) 10 dredgings yielded only 12 very large larvae (ca. 30 mm.); these larvae, cultured in ooze collected at the same time and kept at 20° C., emerged between Oct. 15 and Oct. 22. An adult *plumosus* was collected over the lake on Oct. 20, presumably a member of this same generation. Benthic collections on this same date (X-20-40) yielded only 4 last-instar larvae in 10 samplings, suggesting that a third generation of adults was emerging during late October. These same collections (X-20-40) also yielded small larvae 2-9 mm. in length. Samplings on XII-8-40 and III-28-41 indicated that very few of these small larvae were able to survive the winter, in contrast to the relatively high survival of the preceding winter. These data strongly suggest that three generations of *plumosus* reached maturity in this shallow senescent lake during 1940.

TABLE 1.—Seasonal Populations of *Chironomus plumosus* and *Chironomus decorus* in Cedar Bog Lake.

Numbers and moist weights (in grams) per square meter for the "open water" area.

	Chironomus plumosus		*Chironomus decorus*	
Date	Numbers	Weights	Numbers*	Weights
III--8-37	128	4.16	....	....
IV-26-37	97	3.74	....	....
V-25-37	72	3.05	....	....
VI-26-37	40	2.29	3	.005
VII-16-37	13	0.52	6	.008
VIII-20-37	....	..	74	.052
IX-15-37	....	....	62	.072
X-17-37	...	....	170	.611
XI-13-37	....	....	150	.507
II-26-38	....	....	118	.447
IV—3-38	....	....	66	.370
VII-30-38	....	....	13	.005
X-16-38	22	0.50	359	.300
XII-22-38	12	0.28	188	.140
III—4-39	40	0.83	33	.053
V-23-39	....	....	929	.24
VI-15-39	....	....	335	.37
X-15-39	95	1.45	775	.30
I-13-40	264	9.95	2000	3.20
III—3-40	204	9.40	1810	6.80
IV-28-40	87	3.50	661	2.10
V-26-40	29	0.69	2	.01
VI-24-40	306	5.83	...	....
VII-27-40	246	16.75	....	....
IX-29-40	53	2.12	....	....
X-20-40	13	0.70	67	.20
XII—8-40	26	0.75	60	.10
III-28-41	....	....	15	.06

* These numbers represent larvae smaller than 18 mm in length, and thus may include some indistinguishable immature larvae of *Chironomus plumosus*.

The life span of *Chironomus plumosus* as found in Cedar Bog Lake is quite different from that of this species in other types of habitats. In Lake Pepin, a deep lake-like enlargement of the Mississippi River between Minnesota and Wisconsin, this same species has two generations per year (Johnson and Munger, 1930). In large eutrophic lakes *plumosus* has only one generation per year (Grosser Plöner See, cf. Lundbeck, 1926; Lake Minnetonka, cf. Wood, 1938; Lake Waskesiu, cf. Rempel, 1936). The summer bottom temperature of Lake Pepin is doubtless lower than that of Cedar Bog Lake, while the bottom temperatures of the large eutrophic lakes mentioned are still lower, seldom more than 10° C. Scott and Opdyke (1941) reported that the number of summer insects emerging from the waters of eutrophic Winona Lake is much greater over shallow water than over deep, with a corresponding general but inexact association between greater emergence and higher bottom temperature. In Costello Lake, Ontario (Miller, 1941), shallow water species also emerged first from the shallowest and last from the deepest parts of their range. In explanation of this, Miller suggested that a longer time is necessary in the deeper part of their range to accumulate the day-degrees of heat energy required by the species. It therefore seems probable that the number of generations produced each year is likewise more or less directly proportional to the temperature of the ooze in which the larvae live. Such a conclusion is quite in accord with the generalized temperature-sum rule (cf. Bodenheimer, 1938), which states that the product of time and effective temperature (= environmental temperature minus development threshold) is constant.

The seasonal weight and frequency distribution of *plumosus* and *decorus* in Cedar Bog Lake during the fall and winter of 1939-40 (Fig. 1) may profitably be compared with that given by Lundbeck (1926) for *plumosus* and *liebeli-bathophilus* (the latter seems analogous to *decorus* in America) for Plöner Becken, Germany (Fig. 2). The two diagrams are quite similar except for the late winter and spring periods.

The deleterious effects of extended winter conditions are shown in both figures. In Cedar Bog Lake, where the period of anaerobiosis was definitely known, subjection of the forms to 50 days of oxygen-free conditions took a rapid toll, and affected *plumosus* (43% survival) less seriously than *decorus* (38% survival, cf. Lindeman, 1942). While the late winter period in Cedar Bog Lake showed devastating reduction in numbers, the corresponding period in Grosser Plöner See is represented (Fig. 2) as conducive to rapid growth. An explanation for this great difference is suggested by facts recorded in an earlier portion (p. 95) of Lundbeck's paper. During February of 1924, very mild weather combined with high winds resulted in melting of the ice on Plöner See for a time. The water doubtless underwent premature warming and circulation; very probably this change accounted for the pre-vernal *Chironomus* growth he reported, assuming that his meager samplings were adequate. Lundbeck reported a similar pre-vernal growth effect the following year, but gave no data as to the lake conditions at that time. The larger lakes of that region, according to his data, appear to be normally ice-bound from mid-December until late March. That such a distinct individual weight increase should take place in the spring, simultaneously with complete circulation of the lake and a rise in temperature, is not unexpected, but that such an increase should occur before the usual time of ice-disappearance seems quite incredible. Lundbeck's curve would better conform to the expected type if the vernal increase in growth would follow rather than precede the spring break-up of ice. The corresponding vernal rise in the Cedar Bog Lake is masked by the emergence of *Chironomus decorus*.

Fig. 1.

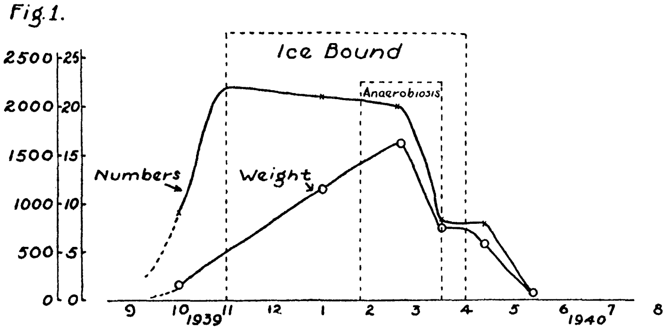


Fig. 2.

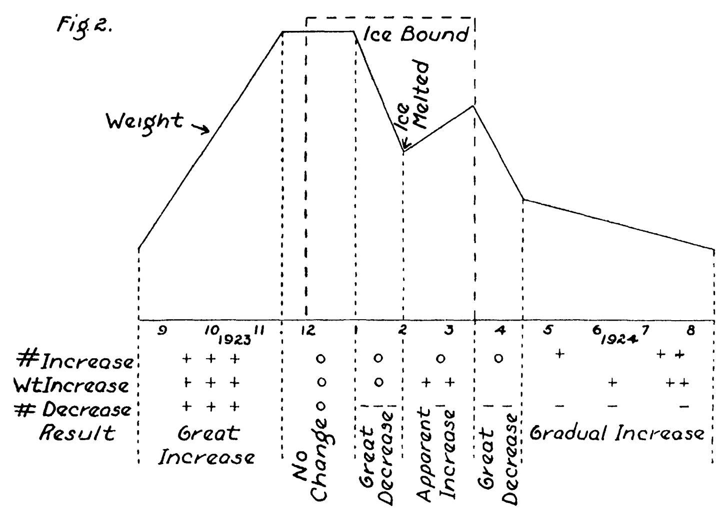


Fig. 1. Annual frequency and weight curves for *Chironomus plumosus* + *C. decorus* in Cedar Bog Lake, Minnesota. Numbers and moist weight (in grams) per square meter. (Cf. Table 1).

Fig. 2. Annual weight curve for *Chironomus plumosus* + *C. liebeli-bathophilus* in Grosser Plöner See, Germany (after Lundbeck, 1926).

The spring emergence of adults in Grosser Plöner See (Lundbeck, p. 213) showed that the smaller species, *Chironomus liebeli-bathophilus,* emerged earlier than *plumosus*. Lundbeck believed that emergence in the case of the former species was due to the ecological factor of rising temperature, and that in the case of *Chironomus plumosus* emergence was due to the onset of summer stagnation with lowering of the benthic oxygen tension. This same factor was suggested for *plumosus* by Rempel (1936) in Waskesiu Lake of Prince Albert Park, Saskatchewan. Lundbeck did admit certain exceptions to this rule in other lakes but explained these as due to differences of lake typology. Certainly the emergence of *plumosus* in Cedar Bog Lake and in Lake Pepin (Johnson and Munger, 1930) was not due to the onset of summer anaerobiosis; Lundbeck's and Rempel's explanation, therefore, is probably not the "determining factor" for the emergence of adults. It seems more probable that larval growth is largely a function of temperature, and that when growth is completed (the water being above some threshold temperature), pupation and emergence follow.

In summary, great fluctuations and species-substitutions occur in the Cedar Bog Lake populations of *Chironomus plumosus* and *Chironomus decorus*. The former species may have as many as three generations per year in this lake, and the latter may have even more. Both species occupy the same ecological niche in relation to the metabolism of the lake. The number of generations per year is believed to depend upon the temperature of the benthic ooze.

CHIRONOMUS (GLYPTOTENDIPES) LOBIFERUS

The important subgenus *Glyptotendipes* is represented in Cedar Bog Lake by *Chironomus lobiferus*. The larvae of at least some members of this group burrow in the submerged parts of aquatic plants. Three species of this subgenus, *lobiferus, barbaris* and *paripes,* are known for Minnesota, according to the Minnesota Entomology Museum specimens identified by Dr. H. K. Townes in 1938. Adults reared from Cedar Bog Lake larvae correspond most closely to *lobiferus,* although the adults are separated on what seem to the writer to be relatively minor characters. *Chironomus lobiferus* is Nearctic in its distribution. The larvae of this species have been reported from very antagonistic extremes of habitat types, ranging all the way from the sandy beaches of Lake Mendota (Muttkowski, 1918) and shallow prairie lakes of Minnesota (Wilson, 1938) to polluted backwaters of the Illinois River (Richardson, 1928) and the tenuous ooze of Cedar Bog Lake. One or two morphological features of the Cedar Bog Lake larvae are noteworthy: the size is greater than is usually indicated for the species, and the ventral gills on the eleventh segment are definitely vestigial, mere "lobes." These larvae were found to be most numerous in the pondweed and marginal areas, where the ooze is less tenuous than in the deeper areas.

The general seasonal distribution of *lobiferus* in Cedar Bog Lake is indicated in Table 2. In 1937 at least one summer brood developed in the marginal area, where large larvae and pupae were collected in July and August, with smaller larvae again in September. A period of emergence during October is also suggested, although no pupae were found. Relatively small populations were present in 1938, but by 1939 the species was again more abundant. In the early summer of 1940 observations on emergents were made at biweekly intervals. The overlapping larvae of 1940 grew rather rapidly following the spring thaw, so that by late May adults were emerging in great numbers. On May 26 thousands of exuviae were floating on the surface; 100 of these were collected and measured as an index of size variation. Johannsen (1937b) indicated the pupal length as 9 mm., but the Cedar Bog Lake forms were much larger, ranging from 9.5 to 13 mm. in length; and the mean length, based on 100 specimens, was 11.2±0.0085 mm. One month later (VI-24-40) myriads of tiny larvae (ca. 2 mm. long) were collected in the dredgings, particularly in the pondweed zone, atlhough some mature larvae and a few pupae were still present. By July 27 these tiny larvae had become a large population of mature and semi-mature larvae all over the lake bottom. From

TABLE 2.—Seasonal Populations of *Chironomus lobiferus* in Cedar Bog Lake. Numbers and moist weights (in grams) per square meter.

	Open Water Area		*"Pondweed" Area*		*Marginal Area*	
Date	No.	Wt.	No.	Wt.	No.	Wt.
III-28-37	3872	35.95	13398	54.82	*	*
IV-26-37	1254	16.46	3036	19.70	183	1.26
V-25-37	132	.57	726	4.31	4263	19.64
VI-26-37	....	....	....	....	1506	6.80
VII-16-37	44	.06	100	.10	6028	13.04
VIII-20-37	....	....	....	....	1422	3.01
IX-15-37	....	....	....	....	1000	.39
X-17-37	....	....	....	....	1906	4.27
XI-13-37	88	.04	....	....	783	2.06
II-26-38	33	....	100	.04	*	*
IV—3-38	....	....	....	....	1133	3.28
VII-30-38	....	....	....	....	511	.86
X-16-38	11	.01	286	.61	1578	4.40
XII-22-38	132	.04	66	.38	*	*
III—4-39	....	....	66	.04	*	*
V-23-39	11	.05	22	.01	183	.35
VI-15-39	....	....	902	.27	†	†
X-15-39	77	.26	396	.66	1510	1.78
I-13-40	....	....	736	1.76	*	*
III—3-40	11	.01	480	.69	*	*
IV-28-40	18	.07	409	1.61	2468	15.77
V-26-40	18	.15	204	1.25	3055	14.42
VI-24-40	1225	.41	12830	9.65	5010	4.11
VII-27-40	1291	4.26	2455	4.62	1145	.51
X-20-40	337	.11	169	.08	....	....
XII—8-40	....	....	....	....	*	*
III-28-41	....	....	....	....	*	*

* Marginal areas frozen solid in winter; no collections made.
† No quantitative collections made in marginal area on this date.

ooze samples of this date cultured at 20° C., numerous adults emerged during August. On September 1, several adult *lobiferus* of this second generation were captured over the lake. Although no regular sampling of the benthos was made in September, an extremely sparse population of tiny larvae was present on October 20; these apparently represented the offspring of a third generation. In marked contrast to the previous winter, the species was practically absent from samples collected in the winter of 1940-41.

Chironomus lobiferus is thus seen as a very irregular, but occasionally important, member of the ooze fauna of Cedar Bog Lake. It becomes most abundant in the pondweed and marginal areas, and apparently develops three generations per year.

CHIRONOMUS (ENDOCHIRONOMUS) NIGRICANS

The subgenus *Endochironomus,* represented in Cedar Bog Lake chiefly by *Chironomus nigricans* Johannsen, occurred in considerable numbers among

TABLE 3.—Seasonal Populations of *Chironomus nigricans* in Cedar Bog Lake. Numbers and moist weights (in grams) per square meter.

	Open Water Area		*"Pondweed" Area*		*Marginal Area*	
Date	No.	Wt.	No.	Wt.	No.	Wt.
III-29-37	....	....	....	....	*	*
IV-26-37	....	....	....	....	22	.01
V-25-37	....	....	....	....	....	....
VI-26-37	....	....	....	....	33	.07
VII-16-37	143	.19	165	.13	1367	.60
VIII-20-37	66	.02	374	.18	133	.09
IX-15-37	154	.04	308	.08	67	.06
X-17-37	....	....	11	.01	483	.19
XI-13-37	....	....	....	....	33	.02
II-26-38	....	....	....	....	*	*
IV—3-38	132	06	100	.12	350	.18
VII-30-38	33	.02	121	.17	1161	.59
X-16-38	11	.01	847	.48	4767	2.52
XII-22-38	....	....	....	....	*	*
III—4-39	....	....	....	....	*	*
V-23-39	11	.01	22	.01	6667	2.06
VI-15-39	....	....	....	....	†	†
X-15-39	....	....	11	.02	88	.22
I-13-40	....	....	9	.01	*	*
III—3-40	....	....	....	....	*	*
IV-28-40	89	.04	71	.08	4850	3.03
V-26-40	18	.06	9	.01	611	1.23
VI-24-40	9	.01	71	.08	389	.40
VII-27-40	....	....	18	.01	....	....
X-20-40	....	....	....	....	1511	1.06
XII—8-40	....	....	36	.02	*	*
III-28-41	....	....	....	....	*	*

* Marginal areas frozen solid in winter; no collections made.
† No quantitative collections made in marginal area on this date.

and beneath the pondweeds just off the marginal mat. Members of this subgenus are believed to have little resistance to anaerobic conditions; no larvae could be found in late winter collections (Table 3). It may be that the Cedar Bog Lake species overwinters in the egg stage. In the lakes of Japan, Miyadi (1932, p. 137) found that *Endochironomus* larvae occurred abundantly on deeper bottoms where dissolved oxygen was present, but were few or limited to shallow bottoms in those lakes in which the deep water contained little or no oxygen. Miller (1941) found this species in the non-anaerobic hypolimnion of Costello Lake, Ontario, where he suggested that it requires two years to reach maturity.

The seasonal distribution of *Endochironomus* larvae in Cedar Bog Lake is indicated in Table 3. Larvae first appeared in late April and persisted through the warm summer months until October. The data for 1937 suggest the presence of three generations of larvae. The 1938 and 1939 data are too infrequent to show seasonal generations. The summer samplings in 1940 appear to have missed a generation. Primarily on the strength of the 1937 data, this species is believed capable of developing three generations per year in Cedar Bog Lake.

PROCLADIUS CULICIFORMIS

Procladius culiciformis, an important ooze predator in eutrophic lakes, is "a cosmopolitan species widely distributed in the United States" (Johannsen, 1937a). In Lake Minnetonka, the species was found to be fairly evenly distributed from depths of 4 meters to 15 meters (Wood, 1938), but only a few individuals were found in the deepest profundal areas at 24 meters. Miller (1941) found this species at all depths (1-17 meters) in Costello Lake, Ontario, but more abundant in shallow water. In the senescent Cedar Bog Lake, a sparse *Procladius* population occurred over all parts of the bottom.

Concerning the seasonal distribution of *Procladius*, Johannsen (1937a) states that "the larvae hibernate when they are half grown," implying one generation per year. A similar distribution is reported for *Procladius culiciformis* in Costello Lake by Miller (1941), where emergence began late in June and lasted until early August. In explanation of a more or less simultaneous emergence from shallow and deep water, he suggested that individual larvae of this and a closely related species migrate back and forth through the thermocline, "each moving from one depth to another at random, and, consequently, each receiving the same amount of heat." The data from Third Sister Lake, Michigan (Eggleton, 1931) present a somewhat different picture: when the benthos population figures for depths from 7 to 15 meters are averaged together and plotted into a seasonal curve (Fig. 3), a definite suggestion of bimodality is attained. Although Eggleton records no values for March, it seems safe to assume that the population rise did not begin until after the spring thaw in late March, as indicated by the broken line. These seasonal figures are based upon a sufficient number of collections to minimize errors of sampling. Tables from a seasonal study of Lake Minnetonka by Miss Evelyn Wood (1938), whom the author assisted with field collections, indicate a *Procladius* population numerically comparable with that of Third

Seasonal Frequency Distributions of *Procladius calciformis.*

Fig. 3. Third Sister Lake, Mich. (data from Eggleton, 1931)

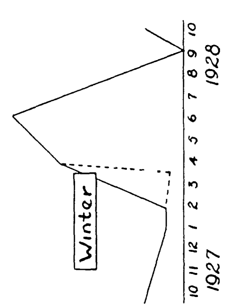


Fig. 4. Lake Minnetonka, Minn. (data from Wood, 1938)

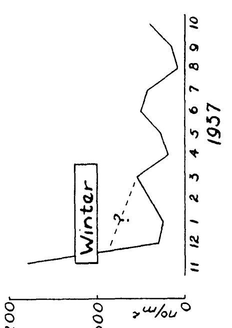
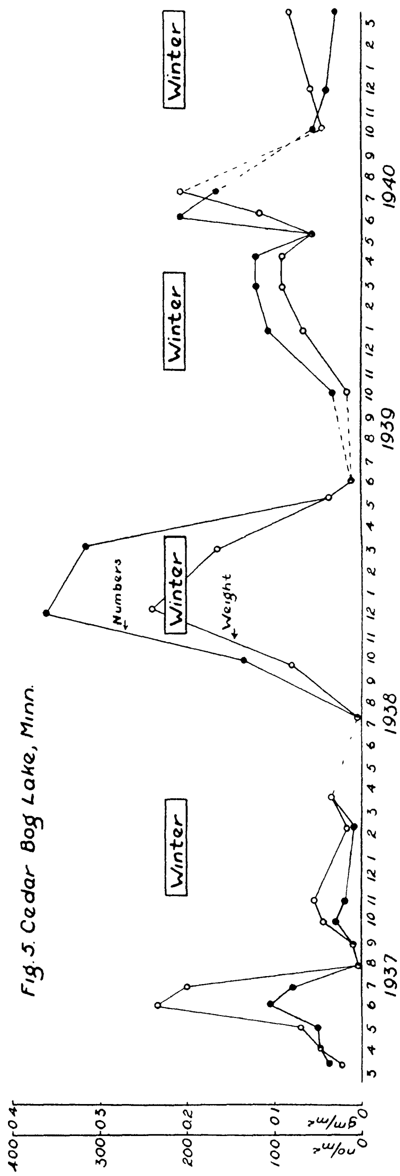


Fig. 5. Cedar Bog Lake, Minn.



Sister Lake. To obtain the data plotted in Fig. 4, Wood's figures for populations at depths of 4, 6, 10 and 15 meters were averaged; this represents sampling areas of at least 4 square feet (4 Peterson dredge samples) for each month of the winter, and somewhat more than this for summer samplings. The midwinter sag in the curve suggests a sampling defect probably correlated with extremely inimicable collecting conditions. Her summer data clearly suggest a second midsummer generation. It is interesting that the Minnetonka curve is almost the complement of that for Third Sister Lake, substituting winter for summer population peaks. Moffatt (1942) has recently reported that two generations of *Procladius culiciformis* develop per year in the littoral areas of Douglas Lake, Michigan.

The seasonal *Procladius* curves for Cedar Bog Lake are plotted in Fig. 5 as numbers and moist weights of the larvae. The collections during the winter of 1936/1937 show marked small-sampling effects, emphasized by the scant population; the curve has hence been arbitrarily drawn as the mean of all samples during that winter. The figures for the remainder of 1937, though still statistically objectionable, are very interesting: emergence of some large larvae just after the spring breakup is suggested, followed by an increase in numbers of small larvae, a rapid growth to maturity during June and July with emergence of the entire population before mid-August; small larvae were again found during late autumn, and these over-wintered beneath the ice. Incomplete data for the following year suggest a recurrence of this cycle, with larvae overwintering at a much smaller size; this seems to have disrupted the procedure for the 1939 season so that perhaps (serotinal data were unfortunately not collected) the summer brood did not develop during that year. The data for 1940 present a definitely bimodal curve, with the possible insertion of an additional midsummer generation in August and September. In general, these data suggest at least two generations per year of *Procladius culiciformis* in Cedar Bog Lake. The data from these various lakes indicate that *Procladius culiciformis* normally has two generations per year in the lakes of this region.

PALPOMYIA sp.

The vermiform larvae of the *Ceratopogonidae* are mostly littoral forms associated with beds of pondweeds and blanket algae. A very few forms may be found in profundal ooze of eutrophic lakes, but even these are wanderers from concentration zones of the same species in shallower water. Several species of the vermiform "*Palpomyia* group" of *Ceratopogonidae* occur in the Cedar Bog Lake. The most abundant member of this group is a species much resembling larval descriptions of *Palpomyia tibialis,* but which because of its size has been called here *Palpomyia* sp. This form seems well adapted to the tenuous ooze environment, and on the basis of winter survival experiments (Lindeman, 1942) it appears able to withstand anaerobic conditions as well as does *Chironomus plumosus*. Mayer (1934) indicates that such larvae are very resistant to freezing, and quotes other authors as having found them in frozen ponds.

The literature seems to contain very little data on the life histories of this group, although many forms have been reared to adulthood in captivity. The best paper encountered which included life history data was by Rieth (1915), but even this limited itself to a mention of dates when the various stages were found in different localities. His data suggested that *Palpomyia* adults emerge in May, and that *Bezzia* adults occur from the beginning of June to the middle of August. Thomsen (1937), who studied the metamorphosis of many species near Cornell University, reported finding pupae of *Palpomyia* at the edge of a pond "in mid-summer." She also reported for *Bezzia varicolor* (p. 78) that "the developmental period from egg to adult averages two months." Speaking of these forms in general, Muttkowski (1918, p. 408) reported that "they pupate in July." Such information does not shed much light on the problem at hand.

The population data for Cedar Bog Lake from 1937 to 1940 are shown in Table 4. It seems evident that during those years when summer collections were frequent (1937 and 1940) this species developed at least two genera-

TABLE 4.—Seasonal Populations of Palpomyia species in Cedar Bog Lake. Numbers and moist weights (in grams) per square meter.

	Open Water Area		*"Pondweed" Area*		*Marginal Area*	
Date	No.	Wt.	No.	Wt.	No.	Wt.
III–29–37	396	1.80	550	2.20	*	*
IV–26–37	176	1.19	231	1.52	56	.01
V–25–37	88	.44	66	.37	167	.98
VI–26–37	44	.13	44	.11	50	.21
VII–16–37	44	.26	33	.13	22	.09
VIII–20–37	....	...	11	.03	72	.16
IX–15–37	11	.03	55	.18	33	.07
X–17–37	11	.04	....	....	39	.17
XI–13–37	....	...	22	.08	83	.26
II–26–38	11	.04	11	.04	*	*
IV—3–38	55	.19	22	.06	44	.10
VII–30–38	....	....	....	....	6	.01
X–16–38	583	.93	814	1.65	39	.08
XII–22–38	528	.88	1540	2.36	*	*
III—3–39	517	1.10	275	.44	*	*
V–23–39	550	.44	143	.12	367	1.21
VI–15–39	143	.15	297	.31	†	†
X–15–39	110	.37	187	.69	356	.27
I–13–40	213	.55	115	.29	*	*
III—3–40	278	.94	160	.56	*	*
IV–28–40	124	.21	187	.83	94	.35
V–26–40	71	.51	116	.27	494	2.86
VI–24–40	53	.11	532	.94	22	.04
VII–27–40	198	.84	303	.95	155	.39
X–20–40	231	1.29	472	1.68	155	.33
XII—8–40	312	1.53	1040	4.45	*	*
III–28–40	244	.80	177	.53	*	*

* Marginal areas frozen solid in winter; no collections made.

† No quantitative collections made in marginal area on this date.

tions; collections during 1938 and 1939 were too infrequent to be of value. The adults emerge in early June. On VI-9-40 great numbers of pupae were floating at the surface near the margin. Large larvae of the second generation were collected in considerable numbers on VII-27-40. Large larvae were also collected on IX-1-40 and emerged in about two weeks when cultured in ooze from the lake maintained at 20° C. Great numbers of various-sized larvae were found on X-20-40, at least some of which were probably offspring of the September (third) generation. These data indicate that the species of *Palpomyia* develops two, and perhaps three, generations per year.

CHAOBORUS PUNCTIPENNIS

The species of *Chaoborus* found in Cedar Bog Lake, *Chaoborus punctipennis,* is widely distributed over the lake-states of North America, and is the species most commonly reported from lacustrine benthos. The genus is still widely known by the former name of *Corethra.*

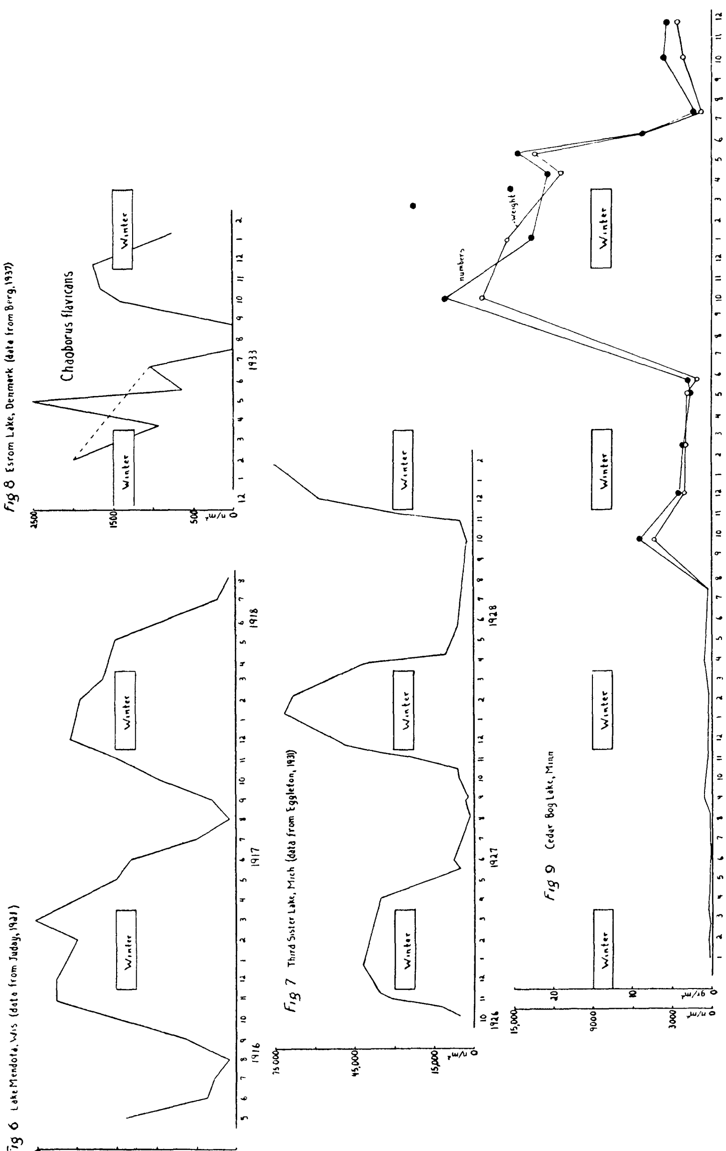
Fortunately for our purpose, considerable data have been collected on the seasonal distribution of this species for two eutrophic lakes in nearby regions: Lake Mendota, Wisconsin (Juday, 1922), and Third Sister Lake, Michigan (Eggleton, 1931). Seasonal data on *Chaoborus flavicans* from Esrom Lake, Denmark, are also available (Berg, 1937). Seasonal curves of *Chaoborus* in the profundal benthos of these lakes, together with the curve for Cedar Bog Lake, are plotted comparatively in Figs. 6 to 9.

The normal seasonal distribution of stabilized *Chaoborus* populations in the profundal zones of Third Sister Lake and Lake Mendota, two quite different types of eutrophic lakes, is shown in Figs 6 and 7. The generalized seasonal curves for *Chaoborus* in these two lakes are similar: very high larval populations built up in late autumn are slightly decreased during the winter and very rapidly decreased in the spring as a result of pupation and emergence of adults; following this initial spring decline, the population declines gradually to an August minimum, after which the autumnal rise again becomes apparent. Muttkowski (1918) suggested the existence, in Lake Mendota, of two rapid summer generations in addition to the over-wintering one. The different curve gradients for the two lakes are perhaps due to a more rapid response to seasonal temperature changes in the smaller lake.

The periodicity of *Chaoborus* was discussed in some detail by Berg (1937). He maintained that in the large Esrom Lake but one generation of *Chaoborus flavicans* (Fig. 8) is produced each year, with the adults emerging in "swarms" during mid-July. In shallower Frederiksborg Castle Lake two generations seemed apparent. Meinert (1886) believed that two generations could be produced per year, as did also Frankenberg (1915). Lundbeck (1926) reported a one-year cycle for *Chaoborus plumicornis* in Pluss-See, as did also Miyadi (1932, p. 130) for the Japanese "*Corethra*-lakes."

The Cedar Bog Lake curve, as indicated by the data for 1939-1940 (Fig. 9), shows a different seasonal pattern from that of the other lakes. An October maximal population of 43,726 individuals per square meter for the open water area (20,108 for the lake as a whole) gradually declined during the late fall and

Seasonal Frequency Distributions of *Chaoborus punctipennis.*



winter, affecting numbers more strikingly than size; this suggests the possibility that the population decline was caused primarily by starvation and that the larger larvae may have cannibalistically devoured the smaller individuals (cf. Meinert, 1886, p. 409).

The possibilities of faulty winter sampling were studied, primarily for the purpose of determining any phototropic effects which might follow the cutting of a "window" through the curtain of ice and snow over the lake. For this reason the collections of I-13-40 were taken by two techniques, seven collections taken immediately upon cutting holes through the ice, and three collections taken more than an hour after cutting the holes. The data showed no evidence of either positive or negative phototropism. No further regard for this factor was believed necessary for the two following winter series (March 3 and 30), and on these dates the holes were opened some time before dredging so that plankton and chemical samples could be taken. Upon analysis of the benthic counts, however, the author was astonished to find a great increase over the expected numbers, consisting mostly of *large* larvae, as indicated by their weight values. In searching for an explanation of such obvious sampling errors, it was noticed that at the time "controlled samplings" were made on Jan. 13, dissolved oxygen was abundant beneath the ice (12.0 ppm.), while on the subsequent winter sampling dates anaerobic conditions prevailed. This strongly suggests that on the latter dates large individuals were responding to the slight amount of oxygen entering the water during the interval between cutting of the holes and the taking of benthos samples. Just why more of the larger larvae should respond in this fashion is still unknown. Because of this phenomenon, the values for III-3-40 and III-30-40 in Fig. 9 are not considered to be valid.

The population changes in Cedar Bog Lake during the spring of 1940 suggest a small emergence of adults shortly after the spring break-up, as a few tiny larvae occurred in the IV-28-40 samples; these small larvae were joined by others during May, while the main mass of older larvae were accompanied by numerous pupae, causing a secondary rise in the seasonal curve for V-26-40. It is not inconceivable, however, that the early spring brood of young larvae might have hatched from over-wintering eggs laid the preceding fall; no adults were collected in marginal sweeps on IV-28-40 and no pupae occurred in the bottom samples. During June a great emergence of adults occurred, coincident with marked growth of the young larvae. By late July the benthic population had become minimal, consisting of a general mixture of small and large larvae, as well as pupae which may well have developed from eggs laid during the same summer. It should be emphasized that collections taken from May through September contained mixed sizes of larvae as well as pupae. No quantitative samplings were analyzed during August or September, but by October the population, particularly of smaller forms, had considerably increased; on the basis of larval development in experimental aquaria, it is believed that at least some of these small larvae were offspring of a third generation of adults which had emerged during September (cf. Berg, 1937, p. 25). These data indicate that *Chaoborus punctipennis* may develop several over-lapping generations per year.

Annual changes in the Cedar Bog Lake *Chaoborus* population (Fig. 9), unexplained at the present time, are rather startling, and seem to follow great fluctuations in the food-cycle dynamics of the lake. During 1936 and 1937 the *Chaoborus* fauna was very small, perhaps correlated with low water level. Beginning in the autumn of 1938 the popualtion increased continually until the summer of 1940; by autumn (1940) the water level was again low, as was also the population of *Chaoborus*.

Summary

1. A four-year study of Cedar Bog Lake, a senescent eutrophic lake in Minnesota, revealed striking annual and seasonal changes in the populations of midge larvae.

2. *Chironomus plumosus, Chironomus decorus, Chironomus lobiferus* and *Chironomus nigricans* were found to develop three generations per year.

3. *Procladius culiciformis* and an undetermined species of *Palpomyia* were found to develop at least two, and probably sometimes three, generations per year.

4. *Chaoborus punctipennis* was found to develop several over-lapping generations per year.

5. Temperature seems to play a primary rôle in determining the seasonal distribution of midge larvae and the number of generations developed per year. Midge larvae living in the cold profundal ooze of deep eutrophic lakes usually have but one generation per year, while in the warm ooze of the shallow senescent lake here studied, these species have additional generations produced during the summer months. These conclusions are in agreement with the temperature-sum rule of insect development.

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