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A CONTRIBUTION TO THE ECOLOGY OF THE CHIRONOMIDAE OF COSTELLO LAKE, ALGONQUIN PARK, ONTARIO

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A CONTRIBUTION TO THE ECOLOGY OF THE CHIRONOMIDAE OF COSTELLO LAKE, ALGONQUIN PARK, ONTARIO

ABSTRACT

In Costello lake fifty species of chironomids were found in sufficient numbers to determine their distribution. Thirty-three of these were found confined to the epilimnion, seven to the hypolimnion, and ten both in shallow and deep water. This distribution was correlated with temperature, the greatest number of species being found in the warmest water and the least number in the coldest water. The greatest number of species emerged during the warmest week of the summer.

The shallow water species are of two kinds: those having one, and those having two generations per summer. The former group require about twice as many day-degrees to grow from larva to adult as the latter. Some of the species having one generation per summer are known to have two generations in warmer water of more southern latitude.

The growth rate in the deep, cold water is very slow, and some of the species there require two years to complete their life cycle.

When the same species lives both in warm shallow, and cold deep, water, emergence occurs at the same time from all depths. The carnivorous diet of some of these larvae leads them to roam over the bottom in search of food. This movement perhaps occurs from shallow to deep water and *vice versa* at random, thus explaining their simultaneous emergence from all depths.

Differences in times of emergence and maturing were observed between males and females of a species. Males tend to emerge before females, and females are more abundant in water colder than the normal for the species.

The large number of closely related species in the shallow water, as opposed to the small number of less closely related species in the deep water, suggests that evolution is more rapid in the former habitat. This more rapid evolution is probably associated with the wide summer temperature range in the shallow water.

Calculations show that the average standing crop of larvae on the bottom is renewed per summer about eight or nine times in the shallow, and two, or at most three, times in the deep water.

INTRODUCTION

During the summer of 1936 a general survey of the bottom fauna of five Algonquin Park lakes was made by the author (Miller, M.A. thesis, University of Toronto), as a part of the programme of the Ontario Fisheries Research Laboratory. This study revealed not only that the lakes had a large chironomid fauna but that the fauna changed markedly in both the number of individuals and in species from spring to autumn. Since the data obtained in the 1936 survey were not sufficient to show what factors were involved in these seasonal changes, it was decided to make an intensive quantitative study of the larvae and adults in one lake throughout an entire season, from a series of stations so selected that they would represent a gradient of varying depths from shallow to deep water. This study, which forms the basis for the present paper, was begun on Costello lake in the spring of 1937. The general plan was to collect insects emerging from the surface of the lake by floating tent-traps and to estimate the larval population by the Ekman dredge.

The field work covered the periods from May 24 until September 19, 1937, and from May 3 until November 20, 1938. In the latter year field work began nine days after the ice had left the lake and before the surface water had warmed to 10°C., and lasted until the winter freeze-up. Costello lake was selected for the investigation for the following reasons: (1) it was known from the 1936 survey to possess a rich chironomid fauna; (2) it is twenty metres deep and shows a well-developed hypolimnion during the summer; (3) it is a small lake well suited for the type of intensive study that had been planned.

PREVIOUS WORK

The tent-trap method of collecting adults was first described by Needham in 1908. He pointed out the value of this method of collecting in quantitative ecological work. In 1923 Adamstone and Harkness set out floating tent-traps in lake Nipigon with the view of obtaining quantitative data. Their experiment lasted over a period of nine days, during which time the trap was moved from place to place and emergence of chironomids from different depths recorded. This experiment was not continued long enough to obtain data on seasonal variation, but did show the practicability of tent-trap methods for lake studies. Recently, Ide (1940) has used a modification of the tent-trap method to obtain quantitative determination of insects emerging from streams.

The seasonal variation of chironomid larvae has been observed by many workers on bottom fauna. Lundbeck (1926) working on north German lakes was the first to present a detailed account. His discussion, while relating to bottom fauna as a whole, applies particularly to the chironomid population. He followed the monthly variation in numbers of larvae over a period of two years and found a minimum in July and a maximum in January. He states that depopulation is due to consumption by bottom feeders, and, eventually, by emergence of adults.

Eggleton (1931) investigated the seasonal variation of the profundal fauna of certain Michigan lakes. His findings agree well with those of Lundbeck. Other North American authors have mentioned that seasonal variation occurs in the bottom fauna; Rawson (1930) states that samples taken at random throughout the season, and at different depths of the lake, should give a picture of the average condition and thus eliminate error due to seasonal fluctuations.

While such investigations have demonstrated the existence of seasonal variation, it is believed that information as to the daily, or at least weekly, emergence of adults is needed to give an accurate picture of changes occurring throughout the summer: information that is necessary for a thorough understanding of the fauna.

ACKNOWLEDGEMENTS

I wish to express my thanks to members of the Ontario Fisheries Research Laboratory who have co-operated in the work, and especially to Mr. V. E. F. Solman, from whose records much of the physical and chemical data presented here have been taken. To Professor W. J. K. Harkness, Director of the Laboratory, I owe my thanks for making this work possible.

It is with pleasure that I acknowledge the counsel and guidance of Dr. F. P. Ide, who has assisted in the field during both summers of the investigation and made many useful suggestions. I am also indebted to Dr. H. K. Townes of Cornell University, who has identified the adults of the subfamily Chironominae (exclusive of *Tanytarsus*).

DESCRIPTION OF COSTELLO LAKE

Costello is a typical dystrophic lake of the mesohumus type as set forth in Lundbeck's scheme in 1926. It lies in the Precambrian shield 45°35′ north latitude, 78°20′ west longitude, at an elevation of 1,370 feet. It has an area of ninety-four acres, and a maximum depth of twenty metres; however, over a third of the area of the lake is five metres or less in depth (figure 1 and table 1). A good proportion of this shallow water is concentrated in a bay at the north-west angle of the lake. From the middle of June until the freeze-up this bay is choked with aquatic vegetation and has a heavy growth of sponges.

TABLE 1.—Percentage of the area of Costello lake between certain contours.

Depth zone (metres)	Area (acres)	Per cent total area
0–5	33	35
5–10	22	23
10–15	15	16
15–20	24	26
0–20	94	100

The waters of Costello lake come from Brewer lake to the south-east, two small bog lakes to the south-west, and a marsh to the north-east. This last source dries up in July. The lake empties by one outlet to the north-west into lake Opeongo. Opeongo drains by the Opeongo river through numerous lakes to the Petawawa, and thence to the Ottawa river.

The lake has its long axis running east and west and hence presents little surface to the action of the prevailing northwest wind. For this reason, and because of the fact that there are high hills on all sides, there is little development of beaches. The lake is surrounded by poplar-birch-coniferous woods which give way a few yards from the lake to dense thickets of low shrubs.

The bottom is a sandy, glacial drift, covered with ooze that varies in thickness from little or none at one metre to six inches or more at twenty metres. Undecayed twigs and other allochthonous materials are commonly found in the deeper water.

The water is brown, ranging from 39 to 200 on the platinum cobalt standard of the United States Geological Survey. Thermal stratification begins about the middle of May, the thermocline first being formed between one and two metres. Owing to the slight wind action, it is never driven deeper than seven or eight metres before autumnal cooling occurs (table 2).

TABLE 2.—Physical and chemical data from Costello lake.

1937

Date	Levels of thermocline in metres	pH		Oxygen in c.c./1	
		0 M.	18 M.	0 M.	18 M.
May 28	1–3				
June 20	3–4				
July 3	3–4			5.7	3.2
July 17	3–4			5.0	4.1
July 23	3–4				
July 31	3–6			5.3	4.0
Aug. 14	3–6			5.3	3.2
Aug. 28	3–6	6.7	5.7	5.0	3.0
Sept. 11	4–6	6.5	5.7	5.4	3.3
Sept. 21	6–7			6.2	1.9

1938

Date	Levels of thermocline in metres	pH		Oxygen in c.c./1		CO_2 in p.p.m.		Colour	
		0 M.	18 M.	0 M.	18 M.	0 M.	18 M.	0 M.	18 M.
May 21	1–2								
May 31	2–3			6.9	6.2	3.1	7.6		
June 15	5–6	6.5	5.9	6.4	5.7	5.9	7.1	68	150
June 28	4–6	6.5	5.7	5.7	3.6?	2.9	9.1	56	83
July 14	3–4	6.3	5.5	5.9	5.1	4.7	16.3	58	80
July 28	4–5	6.5	5.7	6.2	4.4	2.9	12.8	48	71
Aug. 10	4–5	6.6	5.6	6.1	2.8	2.7	17.5	39	149
Aug. 25	4–5	6.4	4.6	6.4	2.5	3.8	18.0	48	176
Sept. 7	6–7	6.3	6.1	6.7	2.0	5.1	22.5	48	202
Sept. 16	5–7	6.3	5.7	7.0	2.2	4.2	21.2	48	200
Oct. 9	no thermocline								

The reaction of the water is acid, having a pH range of 4.6 to 6.6 throughout the summer. The deep water is slightly more acid than the surface water. The oxygen content at eighteen metres dropped from 6.2 c.c./litre on May 31 to 2.2 c.c./litre before the fall turnover in 1938. Carbon dioxide in the hypolimnion increased from 7.6 p.p.m. on May 31 to 21.2 p.p.m. on September 16, 1938. The water is poor in calcium and rich in dissolved and suspended humic materials.

Description of Stations

All stations were located about the same distance from the shore. Their positions are shown on the map (figure 1). They were chosen at different depths so that data, both biotic and physico-chemical, obtained from them would show a shallow to deep water gradient.

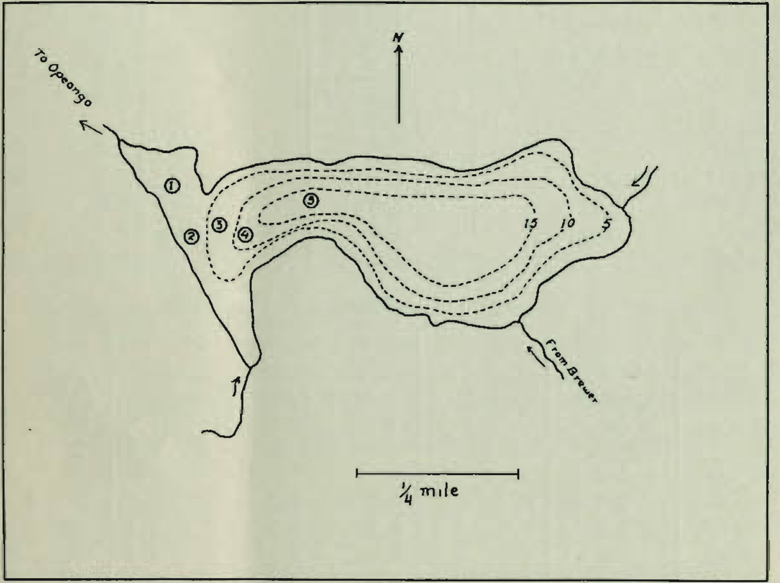

FIGURE 1.—Costello lake, contour interval five metres. Numbers in circles indicate stations.

Station 1 was located in the north-west corner of the lake where the water was one metre deep. The bottom here was sandy with a film of ooze one-quarter inch or less in thickness. There were several large boulders, some of which projected through the water surface, but few small stones or gravel. During May and early June the bottom was clear, but by July there was a luxuriant growth of the sponge, *Spongilla lacustris*, and of rooted aquatic vegetation, the chief components of which were *Brasenia peltata*, *Castalia odorata*, *Nymphaea advena*, *Eriocaulon articulatum*, and *Lobelia Dortmanna*. By the end of July the bottom was almost obscured by great masses of algae, mostly *Spirogyra* and later, *Nitella*.

Station 2 was located where the water was three metres deep. The bottom here was very similar to that at station 1, but the sand was coarser, the ooze thicker, and there were numerous small stones. Only a few *Brasenia* grew in water as deep as this and none occurred within the area chosen.

At station 3 the water was seven metres deep. The bottom here was almost the same as that at three metres, except that there was a small amount of mud on top of, and mixed with, the sand.

The bottom at station 4, where the water was twelve metres deep, had a thick layer of mud over the sand. On the top of the mud, and mixed with it to some extent, were numerous coarse allochthonous fragments, mostly the result of lumbering operations on the lake shore.

At station 5, where the water was seventeen metres deep, the mud was a little finer and deeper than at station 4 and the allochthonous fragments were not so coarse.

Apparatus and Methods

Collection of Adults

In the summer of 1937 four tent-traps (figure 2) were used for the collection of adults. These were made of cotton stretched on a wood and wire frame covering four square feet. They were provided each with two one-gallon tins to float them, and were anchored at stations 1, 2, 3, and 5. In 1938 a fifth trap was placed at station 4.

The traps were lifted daily between the hours of 9 A.M. and 11 A.M. and the insects in them collected. It was assumed that the adults in each trap comprised the emergence from four square feet of bottom during the preceding twenty-four hours. The insects were taken from each cage by means of an entomological aspirator and transferred to an appropriately numbered cyanide bottle. The catch of each station for each day was then sorted beneath a binocular microscope, determined, and recorded. Specimens of each species were pinned for taxonomic verification by specialists as well as for permanent record. The remainder were discarded.[1]

FIGURE 2.—Tent-trap used in collection of adults.

Collection of Larvae

A six-inch Ekman dredge was used in the collection of larvae. Every two weeks during the summer of 1937 five dredgings were taken at each station. In 1938 this was modified to two dredgings at each station once every week. The dredgings were washed in a galvanized iron pail, the bottom of which had been replaced by screening of forty meshes per linear inch. Washing was accomplished by swirling the pail in the lake until the mud, silt, and fine detritus had been eliminated. The residue was then placed in a shallow white-enamelled dish, water was added, and the larvae were picked out with fine forceps. All of the larvae collected in 1937 were preserved in vials of alcohol, and permanent balsam mounts were made of most of them. In 1938, determination of the larvae was done from fresh specimens; diagnostic parts were temporarily mounted in glycerine or in water, identified, and then discarded.

Physical and Chemical Data

During 1937 bottom temperatures were taken for each station every two weeks or oftener with a maximum and minimum thermometer. Oxygen determinations (Miller method) were made every two weeks at the surface and at a depth of eighteen metres. In 1938 a Negretti and Zambra distance recording thermometer was installed at station 1, which gave a continuous record of bottom temperatures from May 3 to November 7. Oxygen and temperatures at other stations were determined as in the previous summer and, in addition, carbon dioxide, pH, and colour were measured every two weeks at the surface and at eighteen metres. Carbon dioxide was determined by methods of standard water analysis, pH by the Lamotte comparator, and colour by the platinum cobalt standard of the United States Geological Survey.

TEMPERATURE RELATIONS OF THE STATIONS

The bottom temperatures recorded for stations 1 to 5 inclusive in 1937 and 1938 are shown in table 3.

TABLE 3.—Temperature records for stations one to five, in degrees centigrade.

1937

	Stations				
	1	2	3	4	5
May 8	0				
15	10				
21	15				
June 9	16.5	16.5		5.5	4.4
11	16.5	16.1		5.5	4.4
14	17.8	15.5		5.5	4.4
18	17.2	15.5			
21	19.4			5.5	4.4
23	22.8	16.5		5.5	4.4
25	25.0	17.8		5.5	4.4
28	23.3	16.5		5.5	4.4
30	20.0	18.9		5.8	4.4
July 2	20.5	19.4		5.5	4.4
4	20.5	17.2		5.5	4.4
10	25.5	16.5		5.5	4.4
18	23.3	19.4		5.5	4.4
21	22.2	19.4		5.5	4.4
23	23.5	20.8			
31	21.7	20.4	8.9	5.8	4.8

---

[1] In 1937 the "remainder" were preserved in alcohol but such specimens proved to be unsatisfactory for taxonomic study.

1937—*cont.*

	Stations 1	2	3	4	5
Aug. 5	20.0	17.8		5.5	3.9
8	24.4	18.3		5.5	3.9
13	20.5	18.3		5.4	3.9
21	22.2				
26	22.4	20.8	8.0	5.8	4.9
Sept. 4	20.3				
11	19.1	18.9	8.0	5.5	4.8
21	13.0	12.0	8.5	5.6	4.8

1938

	Stations 1*	2	3	4	5
April 29	0				
May 3- 9	10.1				
10-16	10.8				
17-23	12.1				
21		11.6	7.8	4.4	4.4
24-30	14.1				
31		12.5	8.2	4.8	3.8
31-June 6	16.7				
June 7-13	15.6				
15		15.7	7.3	4.9	3.9
14-20	19.9				
21-27	22.4				
28		17.7	6.6	4.9	3.9
28-July 4	19.9				
July 5-11	21.3				
14		20.6	7.2	4.8	3.9
12-18	20.3				
19-25	22.4				
28		22.4	7.9	5.0	4.2
26-Aug. 1	23.4				

*Weekly average of daily maxima and minima.

1938—*cont.*

	Stations 1*	2	3	4	5
Aug. 2- 8	24.1				
10		22.3	7.3	5.0	3.8
9-15	22.1				
16-22	23.5				
25		20.6	7.8	4.5	3.8
23-29	20.1				
30-Sept. 5	17.6				
Sept. 6-12	15.7				
2		16.6			
7			7.0	5.0	4.0
11		15.0			
16		13.3	8.4	5.0	4.0
13-19	14.8				
20-26	12.8				
27-Oct. 3	11.8				
Oct. 4-10	10.0				
9	9.5	9.5	8.8	4.8	4.4
11-17	11.0				
18-24	9.6				
25-31	6.7				
Nov. 1- 5	7.5				
20	2.2				

*Weekly average of daily maxima and minima.

The data in table 3 have been plotted against time to give two graphs, one for each year (figure 3). Each graph shows five time-temperature curves, one for each station. Throughout each summer the greatest variations in temperature occurred at station 1, the next at station 2, then at station 3, and finally the least variation occurred at stations 4 and 5, where the time-temperature curves are nearly straight lines.

These temperature characteristics of the five stations can best be expressed by comparing the totals of day-degrees for the season at each station. The number of day-degrees is computed by calculating the area under the time-temperature curves and amounts to

2800, 2350, 1300, 940, and 770 in 1937 and 3000, 2650, 1380, 970, and 790 in 1938, for stations 1 to 5 respectively. These figures have been converted into a more workable form by taking the number of day-degrees at station 5 as unity. The resulting temperature gradients are 3.6 : 3.3 : 1.7 : 1.2 : 1 in 1937 and 3.8 : 3.4 : 1.7 : 1.2 : 1 in 1938 for stations 1 to 5 respectively.

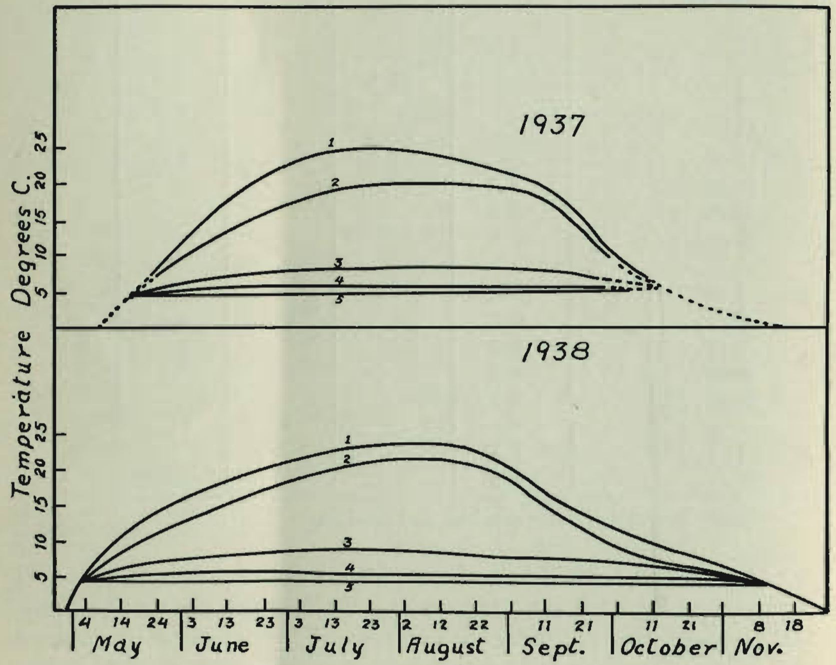

FIGURE 3.—Time-temperature curves for bottom water at stations 1 to 5.

A LIST OF CHIRONOMIDAE FOUND IN COSTELLO LAKE[2, 3]

Subfamily Tanypodinae
Pentaneura carnea Fabricius
" *illinoensis* Malloch
" spp.
** *Procladius (Procladius) culiciformis* Linne
** " " *fasciger* Curran
** " *(Psilotanypus)* sp.

Subfamily Diamesinae
* *Protanypus* sp.
Diamesa sp.

Subfamily Orthocladiinae
Metriocnemus sp.
* *Cricotopus bicinctus* Meigen
** " *trifasciatus* Panzer
Spaniotoma (Psectrocladius) sordidella Zetterstedt (?)
" " spp.
" *(Orthocladius) curtistylus* Goetghebuer (?)
" " spp.
" *(Eukiefferiella)* sp.
" *(Smittia)* sp.
Corynoneura celeripes Winnertz

Subfamily Chironominae
Pentapedilum (Sergentia) coracinum Zetterstedt
" *(Phaenopsectra) obediens* Johannsen
" " *flavicauda* Malloch
" sp.
Pseudochironomus fulviventris (Johannsen)
" spp.
Chironomus (Chironomus) spp.:—
Chironomus Meigen, s. str. Edwards
* *staegeri* Lund (?)
** *decorus* Johannsen

---

[2] Classification according to Edwards (1929).

[3] Species in the list that are marked with two asterisks have been reared; species marked with a single asterisk have been associated with their larvae but not their pupae.

Xenochironomus Kieffer
xenolabis Kieffer
Limnochironomus Kieffer
modestus Say
** *lucifer* Johannsen
sp. c
sp. d
Cladopelma Kieffer
claripennis Malloch
laminatus Kieffer
Cryptochironomus Kieffer, s. str. Edwards
** sp. a
sp. ?
Parachironomus Lenz
abortivus Malloch (?)
tenuicaudatus Malloch
sp. b
sp. f
Harnischia Goetghebuer
curtilamellatus Malloch
edwardsi Kruseman
Chironomus (*Glyptotendipes*) *lobiferus* Say
* " (*Endochironomus*) *nigricans* Johannsen
" " n. sp. (close to *tendens* Fabricius)
" (*Kribioxenus*) *babiyi* Rempel
" (*Microtendipes*) *pedellus pedellus* Degeer
" " *pedellus* n. ssp.
** *Chironomus* (*Stictochironomus*) *devinctus* Say
* " (*Polypedilum*) *halteralis* Coquillet
" " *illinoensis* Malloch
" " *scalaenus* Schrank
" " *fallax* Johannsen
" " sp. e
" (*Lauterborniella*) spp.:—
Zavreliella Kieffer
varipennis Coquillet
Lauterborniella Bause, s. str. Edwards
agrayloides Kieffer
nigrohalteralis Malloch

* *Tanytarsus* (*Micropsectra*) sp.
* " (*Tanytarsus*) *signatus* van der Wulp
* " " *dubius* Malloch (?)
" " *confusus* Malloch (?)
" " *viridiventris* Malloch
" " *pusio* Meigen (?)
" (*Phaenopelma*) *simulatus* Malloch (?)

and in addition some eight species of *Tanytarsus* (*Tanytarsus*) which require more material and further study for determination.

Fifty of these species (table 11, appendix) occurred in sufficient numbers to give adequate information as to distribution and times of maximum emergence. The remainder have not been used in the discussion to follow. *Chironomus* species a, b, c, d, e, and f have been determined as new by H. K. Townes of Cornell University.

Tables containing the emergence data for each species and record of larval abundance are on file in the library of the Ontario Fisheries Research Laboratory, University of Toronto.

THE CHIRONOMID POPULATION

In this section the daily emergence of chironomids is discussed with reference to the population as a whole rather than to individual species. The numbers of individuals emerging each day at the different stations have been compared to show the relative contributions of the different depths in the lake. The seasonal change in number of species emerging has also been considered.

Emergence

Adult chironomids began appearing in the shallow water tent-traps as soon as the ice left the lake in the spring. A large number of individuals emerged during the first few days in May (1938) shortly after the break-up. Following this few individuals were found in the tent-traps until the end of May. From this time to the middle of August large numbers of chironomids emerged at stations 1 and 2. In late August shallow water emergence dwindled and by the middle of September few chironomids were caught (figures 4 and 5).

Emergence from below the thermocline was small and sporadic throughout both summers. During September, however, the large numbers of one species make the deep water emergence the major part of the final peak of the season (figures 4 and 5). This emergence has been observed only to September 19, when routine collections were discontinued. Collections from tent-traps on October 9 and 10 and November 20, 1938, failed to show evidence of any new emergence. The relative numbers of larvae of each species living on the bottom at station 1 were found to be the same on November 20, 1938, as on May 5, 1938; i.e., the fauna had returned to the spring condition.

A comparison of the emergence curves for 1937 with those of 1938 reveals a striking similarity between the two years. During June, July, and August the various peaks coincide almost to a day. Since collection in 1937 did not begin until late in May the early peak of this month was not obtained. The late May peak of 1937 was a week later in appearing than in 1938. This is possibly the result of the earlier spring in 1938 (time-temperature curves, figure 2).

Although having no direct bearing on the total emergence, an analysis of the emergence over a period of twenty-four hours is believed to be worthy of note, and has been included here. Most of the emergence from the bottom above the thermocline occurred between the hours of four and seven A.M., a time of low light intensity and minimum temperature (table 4).

TABLE 4.—Emergence of Chironomidae at station 1 over a period of twenty-four hours.

Time	Number of adults
12.00 noon (July 13) to 7.00 A.M. (July 14)	17
7.00 A.M.– 2.00 P.M.	2
2.00 P.M.– 3.00 P.M.	3
3.00 P.M.– 4.00 P.M.	3
4.00 P.M.– 7.00 P.M.	1
7.00 P.M.– 8.00 P.M.	1
8.00 P.M.– 9.00 P.M.	1
9.00 P.M.–10.00 P.M.	1
10.00 P.M.– 4.00 A.M. (July 15)	0
4.00 A.M.– 5.00 A.M.	15
5.00 A.M.– 7.00 A.M.	6

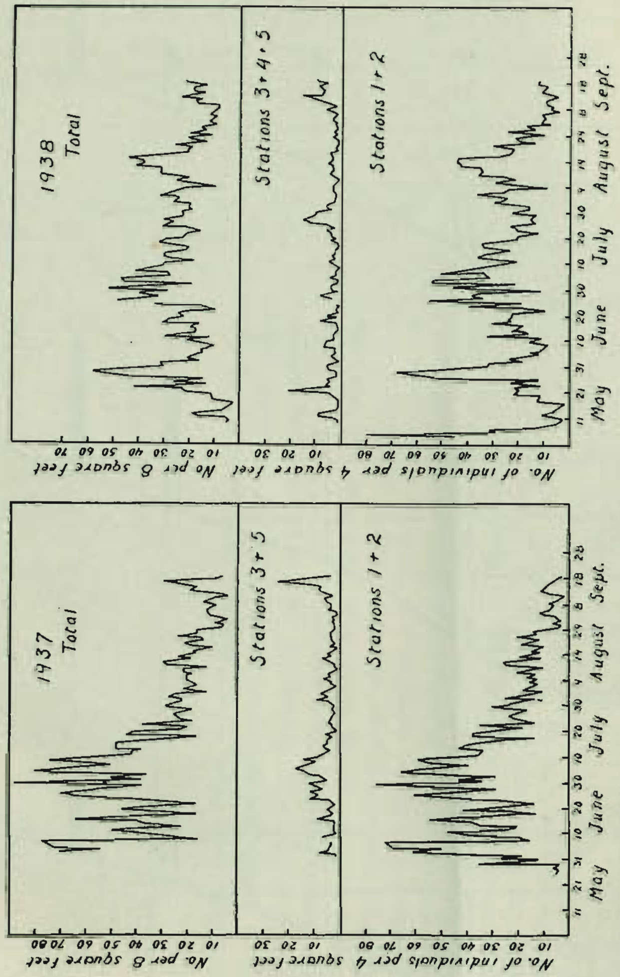

FIGURE 4.—Total daily emergence curves, 1937 and 1938.

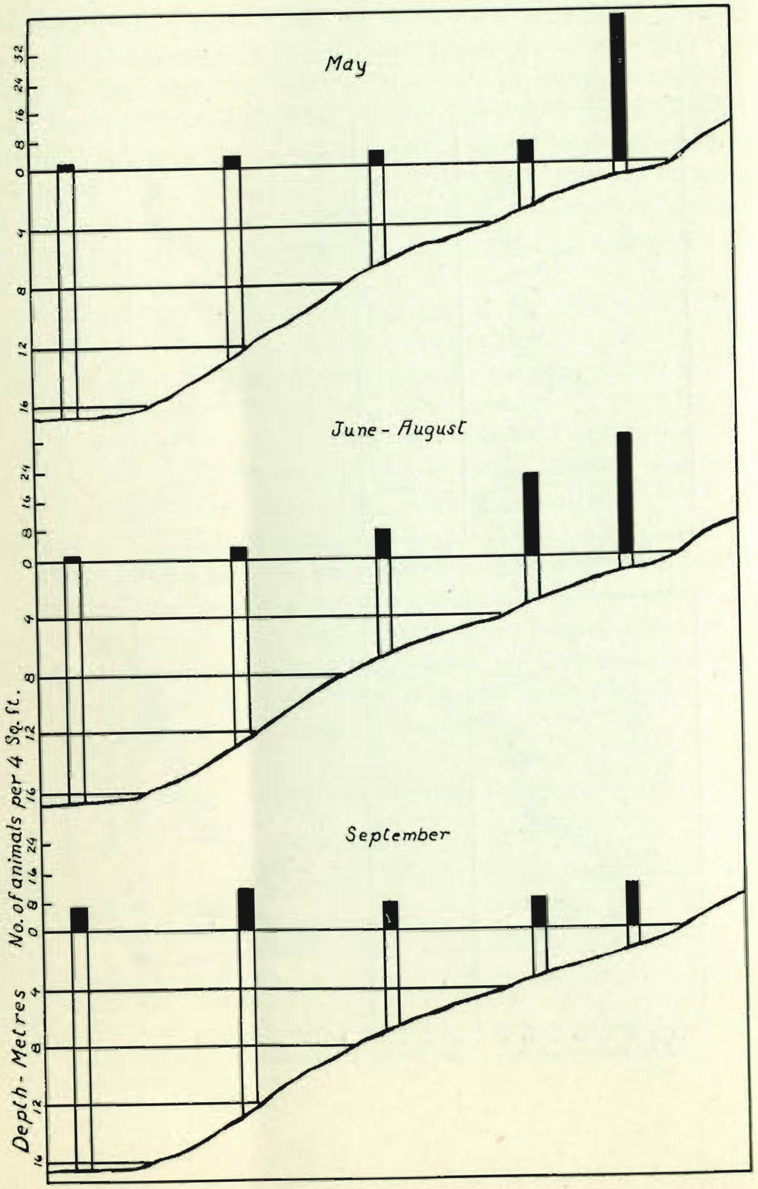

FIGURE 5.—Average daily emergence per four square feet at each station for the summer months of 1938.

From the bottom below the thermocline emergence occurs at random throughout the day. During the late summer peak (September 12) insects were seen leaving the surface above the deep water at any time of the day or night. This lack of diurnal peaks is possibly the result of the constant temperature and reduced light intensity below the thermocline.

Seasonal Variation

The emergence curves (figure 4) deal with the daily totals of individuals of all species of chironomids which were taken in the tent-traps. They show little evidence of a seasonal effect on the *number* of individuals emerging. On the contrary, large and practically equal numbers of chironomids emerged during June (average

TABLE 5.—The number of species appearing at all stations each week of the summers of 1937 and 1938.

Week of	Number of species 1937	Number of species 1938
May 4-10	*	7
11-17	*	9
18-24	*	14
25-31	13	17
June 1- 7	17	19
8-14	15	19
15-21	18	20
22-28	28	27
29-July 5	35	30
July 6-12	35	31
13-19	33	29
20-26	32	26
27-Aug. 2	26	29
Aug. 3- 9	33	30
10-16	28	25
17-23	18	26
24-30	16	13
31-Sept. 6	10	12
Sept. 7-13	7	11
14-19	4	6

*No observation.

of eleven per four square feet per day), July (average of thirteen per four square feet per day), and August (average of twelve per four square feet per day), a period when seasonal change of temperature was in progress. It is, therefore, safe to conclude that summer temperature changes have little effect on the *numbers* of individuals emerging. If, however, the numbers of *species* emerging are considered, a different situation is found.

The number of species appearing each week was small in the spring, increased rapidly to a maximum in mid-July (thirty to thirty-five per week), and from this point declined until freeze-up in November (figure 6 and table 5). Summer temperatures followed the same general course. The week of highest average temperatures (July 6-12) produced the greatest number of species in both summers. It would appear from this that seasonal variation in the emergence of species of chironomids is directly correlated with temperature changes.

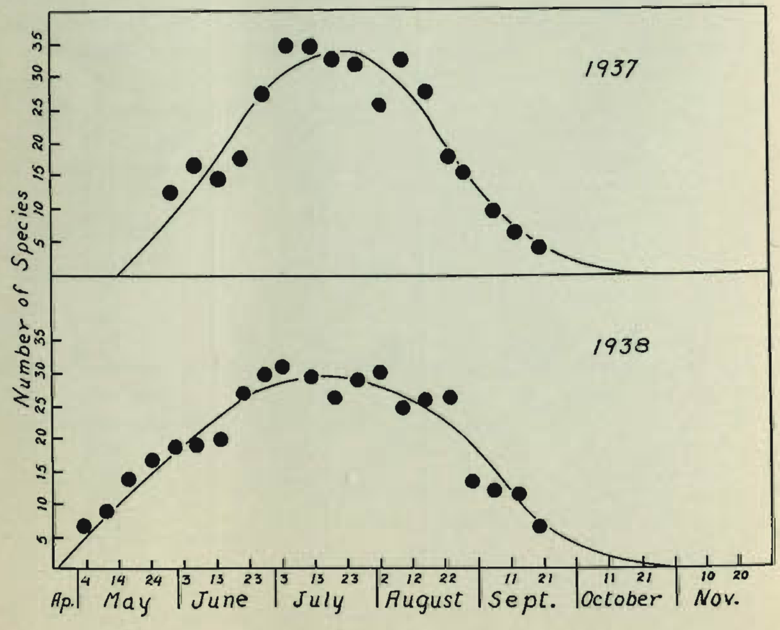

FIGURE 6.—The number of species appearing each week.

Vertical Distribution

Early in the investigation it became apparent that collections from the bottom in deep water yielded fewer species than similar collections from shallow water. This variation in vertical distribution has been calculated by totalling the number of species occurring at each station throughout the summer. There were 36, 32, 14, and 10 at stations 1, 2, 3, and 5 respectively in 1937, and 41, 39, 15, 17, and 10 species at stations 1 to 5 respectively in 1938. The larger number of species found in 1938 is due partly to the use of an additional tent-trap and partly to the earlier beginning of collecting in this year. The names of the species and the station or stations at which each occurs during both summers are given in table 11, in the appendix. It will be noted that more species are listed on pages 19-21 than are used in the vertical distribution calculations. This is because either only those species which occurred in sufficient numbers to indicate their true habitat, or species whose larvae are known, could be definitely assigned to a given vertical distribution.

If the number of species occurring at station 5 is taken as unity the vertical distribution can be expressed as a ratio, viz., 3.6 : 3.2 : 1.4 : 1 in 1937, and 4 : 1 : 3.9 : 1.5 : 1.7 : 1 in 1938. In table 6 these ratios are compared with the temperature gradients.

TABLE 6.—A comparison of the temperature gradient and the vertical distribution ratio of the fauna.

	Station	1	2	3	4	5
	Temperature gradient	3.6	3.3	1.7	1.2	1
1937	Vertical distribution ratio	3.6	3.2	1.4	...	1
	Temperature gradient	3.8	3.4	1.7	1.2	1
1938	Vertical distribution ratio	4.1	3.9	1.5	1.7	1

From table 6 it is clear that the vertical distribution ratio and the temperature gradient ratio correspond very closely; i.e., the number of species at each depth is approximately in direct proportion to the summer temperature at the same depth. Station 3 in 1938 offers an exception to this statement. This is believed to be due to its position in the thermocline, and will be discussed under the effects of the thermocline (page 50).

Of the fifty species whose distribution is known for 1938, thirty-three are confined to the epilimnion and seven to the hypolimnion. The remaining ten species are found in both shallow and deep water. They may be placed in three groups on this basis, species living above the thermocline, species living below the thermocline, and species living both above and below the thermocline. In this discussion the summer position of the thermocline has been considered to be from four to seven metres.

SPECIES LIVING ABOVE THE THERMOCLINE

The species whose larvae are confined to the bottom above the thermocline form the largest group in the lake, both in numbers of individuals and numbers of species. Thirty-three of a total of fifty species whose depth ranges are known (1938) are found only in the shallow water. Emergence of this fauna as a whole is continuous, beginning when the ice leaves the lake in the spring and continuing until shortly before freeze-up. Two types of shallow water species have been recognized: those which have one and those which have two generations per summer. There were twenty species in the former group and thirteen in the latter in 1938.

Species with One Generation

Of the twenty shallow water species with one generation per summer, only a few occurred in sufficient numbers to give reliable information as to abundance and time of maximum emergence. Three of these are discussed here; and others are listed in table 12 (page 62).

Spaniotoma (*Eukiefferiella*) sp. In 1937 the emergence of this species began at station 1 on June 27 and lasted until late July. Most of the individuals emerged near the beginning of this period, the major peaks occurring on June 30 and July 10. At station 2 emergence began on June 30, a little later than at station 1, but lasted into August; peaks occurred on July 10 and 15. Emergence in 1938 began at station 1 on June 19 and lasted until late in July. As in the preceding summer, the greatest emergence occurred early in this period, peaks occurring on June 30 and July 4 and 7. At station 2, emergence was again later, beginning on June 24 and lasting into August, with major peaks on July 10 and 15.

The greater part of the emergence occurred over the same short period in both summers (June 27 to July 12 at station 1 and July 5 to 20 at station 2) (figure 7).

Tanytarsus dubius (?) is another shallow water species having one generation each summer. This is an early form emerging in May and early June, and hence the exact dates of its appearance depend on the time when the ice leaves the lake in the spring. Thus in 1937 the lake broke up on May 12 and *T. dubius* (?) appeared on May 31 and had its peak from June 2 to 6; in 1938 the ice had left the lake by April 23 and *T. dubius* (?) began emerging on May 25 and had its peak May 29. Thus more than half the total emergence from station 1 had taken place in 1938 before the date at which emergence began in 1937. Emergence at station 2 was more nearly similar for the two summers (figure 7).

The behaviour of these two species is similar in one respect, i.e., emergence begins and comes to a peak earlier in the shallow water. Such a behaviour is typical of all species living above the thermocline. The more rapid warming and sustained higher temperatures of the shallower station cause earlier maturing and emergence.

In the case of *Chironomus* (*Polypedilum*) *halteralis*, a shallow-water species of the one generation group, it has been possible to correlate decrease in larval abundance with the emergence of adults. The larvae of this species are readily recognizable in dredgings, because of their bright red colour and relatively large size (8 mm.), and accurate data on larval abundance have been obtained, particularly in 1938. Large numbers of larvae were found on the bottom at station 1 early in the spring (over thirty per 0.5 square feet). Throughout May the number became gradually less and in early June emergence began and the number of larvae fell off rapidly to one or two per 0.5 square feet. This condition of minimum persisted until the first of August when first instar larvae were found in the dredgings. These larvae gradually increased in size and numbers until freeze-up. Specimens taken at the time of freeze-up on November 20, 1938, were still quite small. These larvae represented the individuals destined to emerge during June of 1939 (figure 8).

This account of the larva of *C. halteralis* is believed to apply to the larvae of all species of the one generation type.

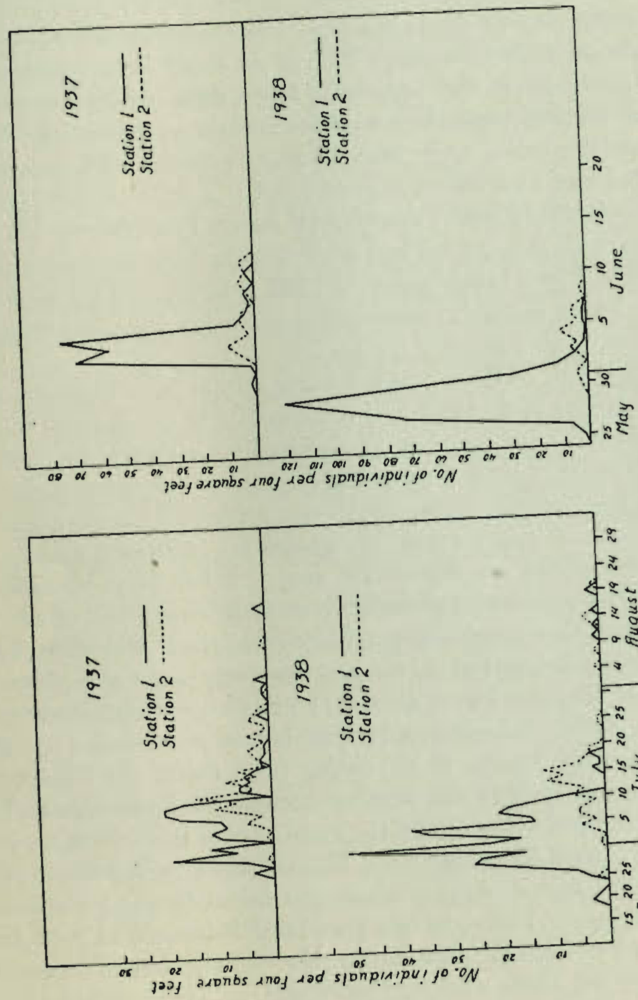

FIGURE 7.—The emergence of *Spaniotoma* (*Eukiefferiella*) sp. (left) and of *Tanytarsus dubius* (?) (right) at stations 1 and 2 in 1937 and 1938.

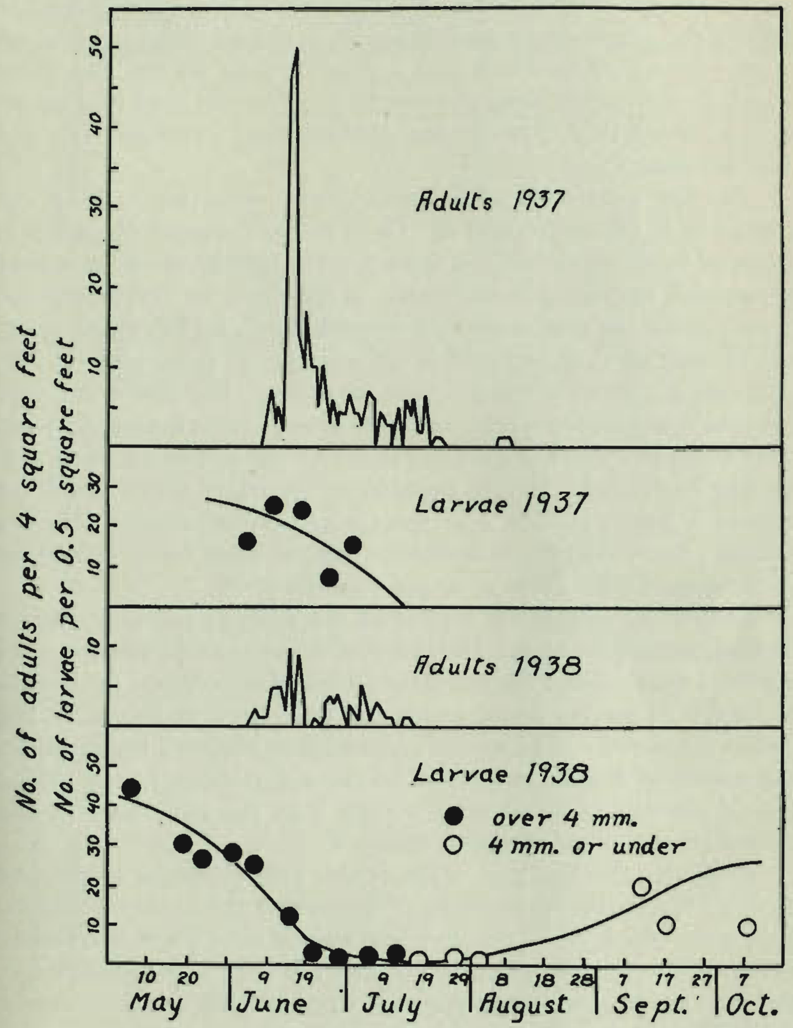

FIGURE 8.—The variations in larval abundance and the emergence of *Chironomus* (*Polypedilum*) *halteralis* at station 1 in 1937 and 1938.

Species with Two Generations

Two of the species which have two generations are discussed in detail; the others are listed in table 13, in the appendix. They are of two types: those which first appear in early spring, and those which do not appear until June or July. There are but two species of the former type, *Spaniotoma* (*Orthocladius*) *curtistylus* (?), and *Metriocnemus* sp.

The first generation of *S. curtistylus* (?) occurring in May was similar to *S.* (*Eukiefferiella*) sp.; i.e., a large emergence at station 1, followed by a smaller one at station 2. The emergence of the second generation, appearing in September, is different; the first emergence occurs at station 2 followed by a somewhat smaller one at station 1, the reverse of what occurred in the spring. *S. curtistylus* (?) has, perhaps, a restricted temperature tolerance. The limits are such that the temperature is suitable for its growth twice during the year, once when the water is warming in the spring, and again when it is cooling in the fall. Hence, suitable temperatures would obtain at station 1 before station 2 in the spring, and at station 2 before station 1 in the fall; this is thought to explain the different behaviour of the second generation of this species (figure 9).

Tanytarsus signatus is typical of the summer group of species having two generations. In both summers the main emergence at station 1 began about the middle of June and lasted until the middle of July. At station 2 emergence was from early in July until the end of the month. The second generation at station 1 began before the middle of August and lasted to the end of August. In 1938 a second generation occurred at station 2 at the same time as the second generation at station 1 (figure 9).

Evidently the first generation of this type is similar to the one generation group in that emergence occurs first at station 1 and then, after a few days, at station 2. The second generation is different as it appears simultaneously at stations 1 and 2. It is significant in this connection that temperatures at these stations are more nearly similar in late than in early summer.

SPECIES LIVING BELOW THE THERMOCLINE

A group of seven species was found whose larvae were confined to the bottom below the thermocline (table 14, appendix). The

temperature in this region ranges from a maximum of 8.8°C. just below the thermocline to a minimum of 3.9°C. in the deepest water. The slow growth rate of the species living in this region appears to

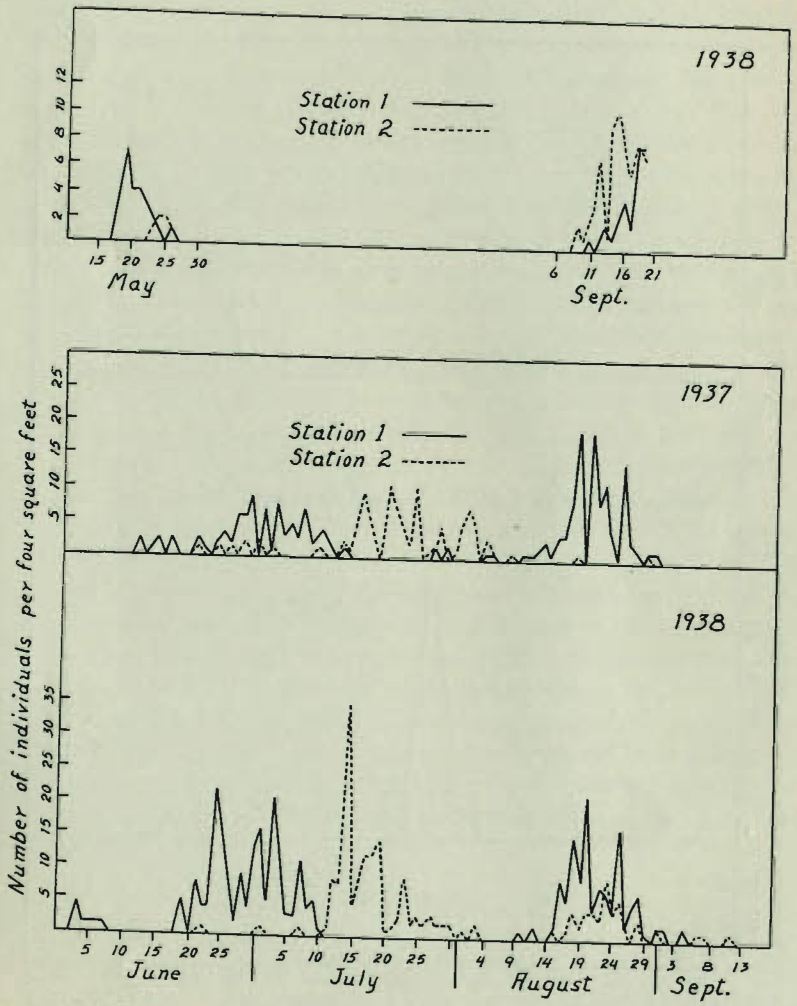

FIGURE 9.—The emergence of *Spaniotoma* (*Orthocladius*) *curtistylus* (?) (upper panel) at station 1 and of *Tanytarsus signatus* at stations 1 and 2 in 1937 and 1938.

be correlated with this low and relatively constant temperature. Two of these species require two years to complete their life cycles. Emergence of deep water species tends to extend over a long period of time and to show no marked peaks.

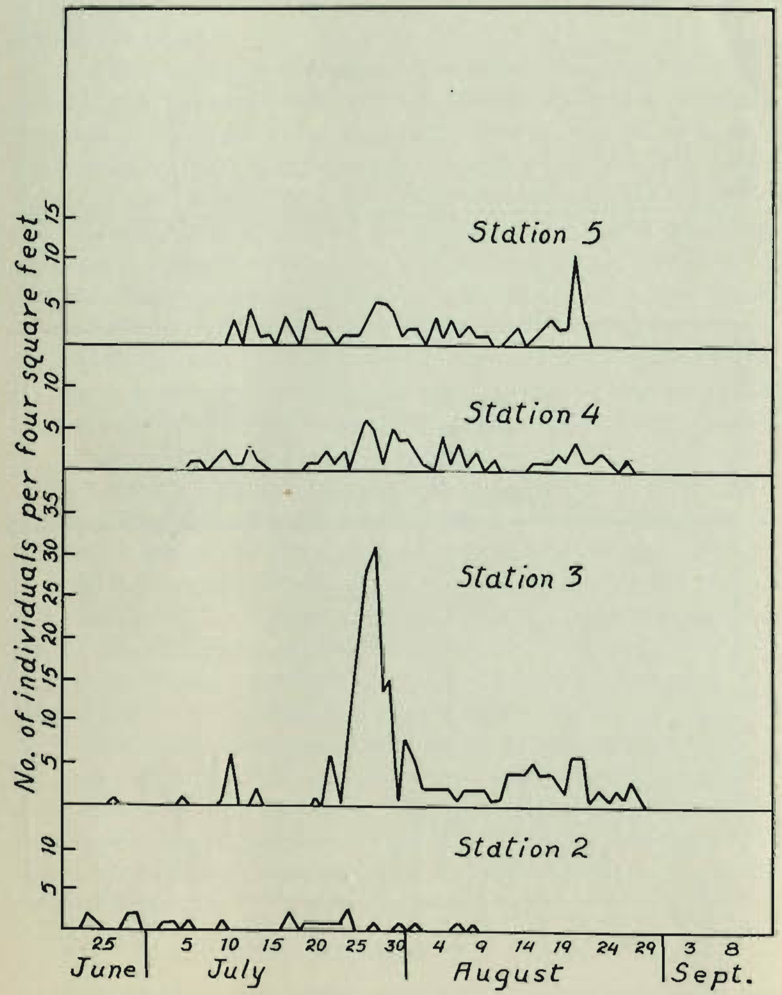

FIGURE 10.—The emergence of *Cricotopus bicinctus* in 1938.

Species with a One-Year Life Cycle

Cricotopus bicinctus is a typical deep water species which has one generation each year. It emerged during the summer of 1938 at stations 2, 3, 4, and 5, the greatest numbers occurring at station 3, just within the thermocline. The emergence at station 2 (above the thermocline) began on June 22, earlier than at the other stations, but was small, no more than two individuals appearing on any one day. At the other stations emergence began early in July and lasted until late in August; peaks occurred at all depths from July 26 to 29, and again around August 20 (figure 10). The behaviour of this species is different in several respects from that of a shallow water species. The period of emergence is longer, resulting in a flatter curve, with the greatest numbers appearing, not near the beginning as in shallow water species, but at about half way through the period of emergence. Also the peaks at different depths, instead of being later in deeper water, are more or less coincident; the temperature gradient between the deep water stations is apparently not great enough to cause marked differences in times of emergence.

Cricotopus bicinctus evidently is most successful at station 3, where the temperature is about 12°C. throughout the summer. *Tanytarsus* (*Micropsectra*) sp., however, is found chiefly at stations 4 and 5 where the summer temperature ranges from 4° to 6°C. This species began emerging on September 5 in 1937 and on September 3 the following year, and continued until September 19 in both summers when routine collecting was discontinued. The greatest numbers occurred both years in the week of September 10 to 17, and the general shapes of the emergence curves were similar (figure 11). This species is peculiar in that its larva, after a period of rapid growth following hatching, spends the summer in the last instar in a state of apparent inactivity. This will be further discussed under effects of dissolved gases.

Species with a Two-Year Life Cycle

Chironomus (*Endochironomus*) *nigricans* and *Chironomus staegeri* (?) are the only species in Costello lake which seem to require two years to attain maturity. They are restricted to the deepest water, and hence the lowest temperature, in the lake. The slow growth rate responsible for the two-year life cycle may be a result of this condition. Conclusions on their distribution have been based chiefly on larval evidence as emergence takes place over a long period of time and in small numbers.

Effect of Dissolved Gases

It has already been mentioned that the larvae of *T.* (*Micropsectra*) sp. spend the summer in the last instar and that no visible growth takes place during this time. The emergence of large numbers of this species during a relatively short period in September contrasted with the long, sporadic emergence periods of other deep water species suggests that *T.* (*Micropsectra*) sp. emerges as a response to some stimulus. As the temperature of their environment remains constant from spring to fall, this stimulus must be sought in other environmental factors. The carbon dioxide content of the hypolimnion has increased from 7.6 p.p.m. in the spring to 20.0 p.p.m. when this species begins pupating in September. The oxygen content has decreased to 2.0 c.c. per litre. Larvae transferred to water of this gas content in August died, but not before they had developed prominent thoracic swellings such as appear prior to pupation. This suggests that the lowered oxygen and increased carbon dioxide stimulate the larvae to begin pupation.

SPECIES LIVING BOTH ABOVE AND BELOW THE THERMOCLINE

Ten species, which have been found in Costello lake (table 15, page 63), have larvae that are able to live and mature at all depths. Not only do these species complete their life cycles at different depths, but within a given species individuals in the deep water emerge at nearly the same time as do those in shallower and much warmer water.

Four of these species belong in the genera *Procladius* and *Pentaneura* of the subfamily Tanypodinae. Johannsen (1937) has pointed out that "The larvae of the members of the subfamily Tanypodinae . . . are predaceous, feeding largely upon other Chironomidae. . . ." It is interesting that the carnivorous larvae are those which have the widest distribution in the lake. In some terrestrial animal communities a similar condition exists; a small herbivorous animal is confined to a relatively small area while a carnivore, of necessity, ranges over a much wider territory.

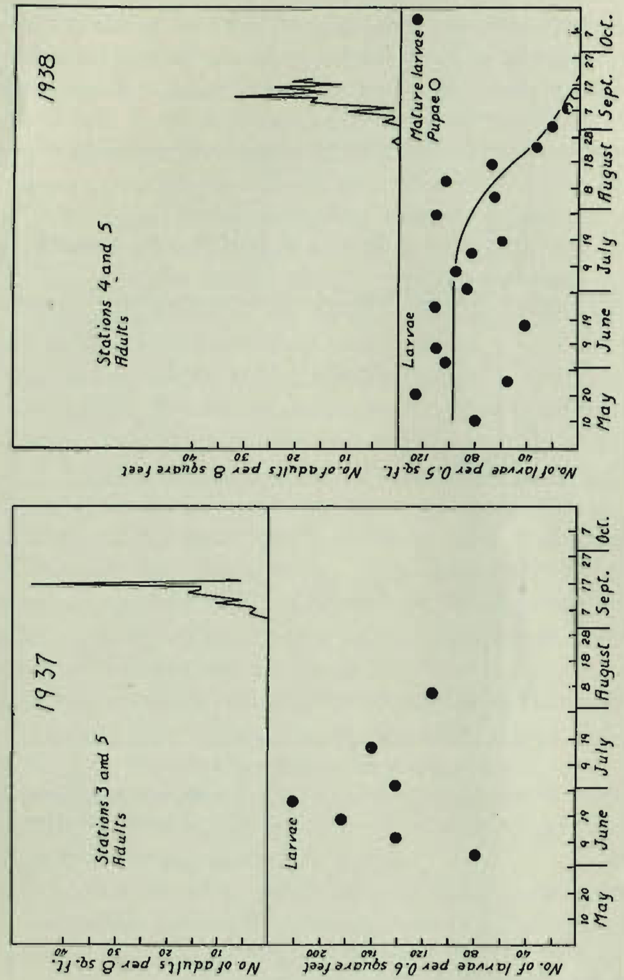

FIGURE 11.—The variation in larval abundance and the emergence of *Tanytarsus* (*Micropsectra*) sp. in 1937 and 1938.

Procladius (*Psilotanypus*) sp. emerged from all depths in Costello lake beginning on June 17, 1938, at all stations. Emergence lasts into early August, but the majority of the individuals appear in June. The most interesting feature of the emergence is the coincidence of the peaks at each station. In the period from June 17 to 28 two major peaks occurred at each station. Apparently the temperature difference between deep and shallow water has no effect on this species, except possibly to cause greater emergence in the shallow water (figure 12).

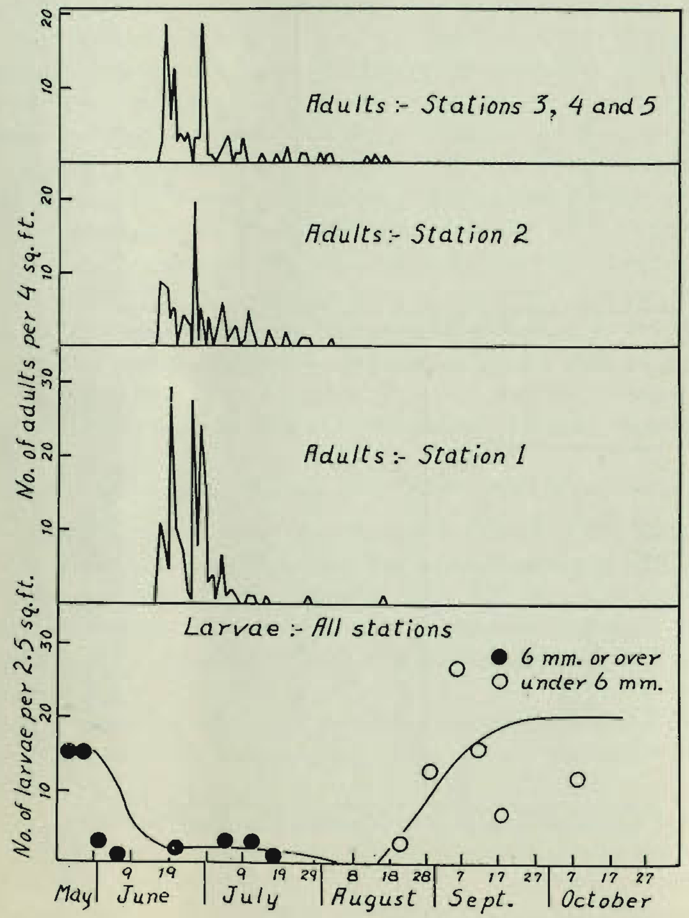

Figure 12.—The variation in larval abundance and the emergence of *Procladius* (*Psilotanypus*) sp. in 1938.

The larvae of *Procladius* (*Psilotanypus*) sp., being bright green in colour, was readily recognizable in the dredgings, and reliable distribution data have been obtained. These show that the larvae are abundant at all depths, maximum numbers being found in the spring. Through May and early June there was a gradual decrease in numbers (due perhaps to consumption by bottom feeding fishes) which culminated in the emergence and larval minimum throughout July and August. In late August and September the young larvae began appearing in the dredgings. Dredgings taken on November 20, 1938, revealed that the larvae were approaching the spring condition in size and numbers (figure 12).

The larvae of *Procladius* (*Psilotanypus*) sp. and those of the related species, *Procladius culiciformis*, differ from other larvae in the lake in their habit of roaming over the bottom and not building tubes. This activity is associated with their carnivorous diet and may be the reason for their wide distribution in the lake. It is even possible that individual larvae of these 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. This, if true, would explain their simultaneous emergence from shallow and deep water.

Procladius culiciformis is another species which tolerates a wide temperature range. Emergence began late in June and lasted until early August; the peaks occurred within a short time of one another at the different stations. *P. culiciformis* is not as cold-tolerant as *Procladius* (*Psilotanypus*) sp., a much greater proportion of the total emergence occurring in shallow water.

In addition to the carnivorous forms there is also a group of four non-carnivorous species which occur early in the spring and which emerge simultaneously from the deep and shallow water. The members of the subfamily Diamesinae are typical early spring forms. *Protanypus* sp., belonging to this group, emerged early in May, 1938, from deep and shallow water. *Tanytarsus* (*Phaenopelma*) *simulatus* (?) emerged from May 4 to 15, 1938, in large numbers. The most of the emergence occurred at station 1, but an appreciable number of individuals appeared at the other stations over the same time (figure 13). *Pentapedilum* (*Sergentia*) *coracinum* also behaves in this way.

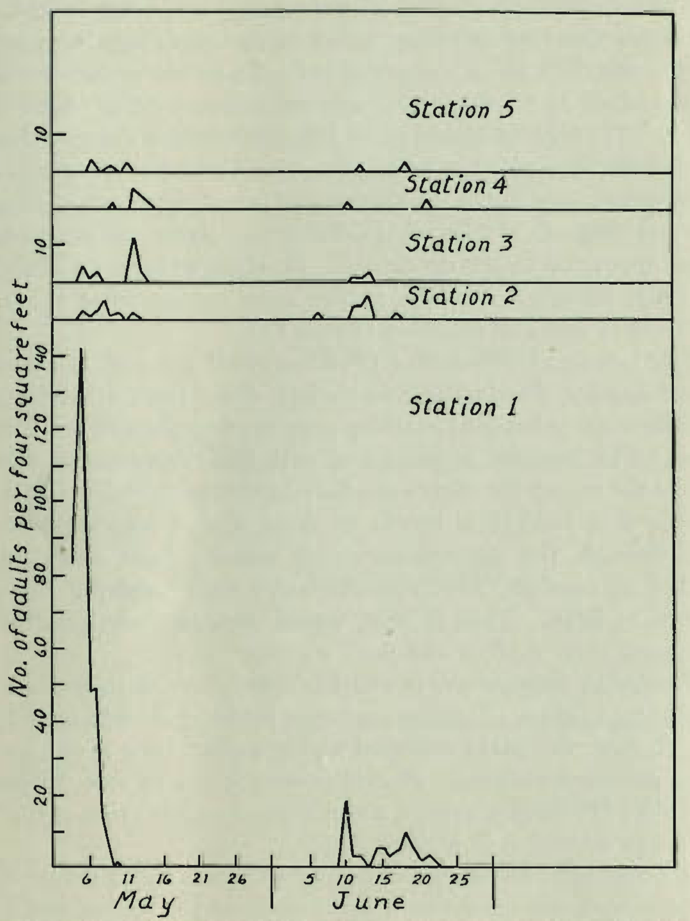

FIGURE 13.—The emergence of *Tanytarsus* (*Phaenopelma*) sp. in 1938.

Although these spring forms are similar in vertical distribution to the carnivorous species, they are not subjected to the same temperature conditions. In early May, the time of their emergence, the temperature gradient from shallow to deep water is small, and the shallow water is almost as cold as the deep. Hence, in temperature requirements at least, this group is more like the deep water species.

SEXUAL DIFFERENCES

During the summer of 1938 a record was kept of the number of males and females of each species which emerged into the tent-traps. Slight differences in the time of emergence and distribution of the sexes were observed; males have a tendency to reach their peak of emergence a short time before females, and females are more abundant in deeper water.

Maturation

The difference in the time required for maturation of the sexes seems to be correlated in some way with temperature. In the case of *Cricotopus bicinctus*, a deep, and hence, cold water species, males and females emerge at nearly the same time. *Tanytarsus dubius* (?) and *Tanytarsus viridiventris* are shallow water species which emerge early in the year when the water is still cool. The males of these species have their emergence peaks from one to two days before the females. *Procladius culiciformis* occurs in June at station 1; the emergence peak of the males of this species is one week earlier than that of the females. The males of *Chironomus* (*Lauterborniella*) *nigrohalteralis*, a shallow water species emerging in June, emerge for ten days before any females appear (figure 14). Pelseneer (1926) reports that males appear before females in many species of insects.

It seems plausible in the case of these species that the degree of separation of emergence of males and females is a function of temperature. In the cold water no separation occurs; in moderately cold water, a small separation occurs and in warm water males emerge well in advance of females. Possibly increases in temperature accelerate the growth rate of males more than they do that of females. This conclusion is only in partial agreement with the results of Rau and Rau (1914) who found that in four species of saturnid moths, males emerged from 0.23 to 4.98 days in advance of females, but were unable to observe any difference in male priority at lower or higher temperatures.

Vertical Distribution

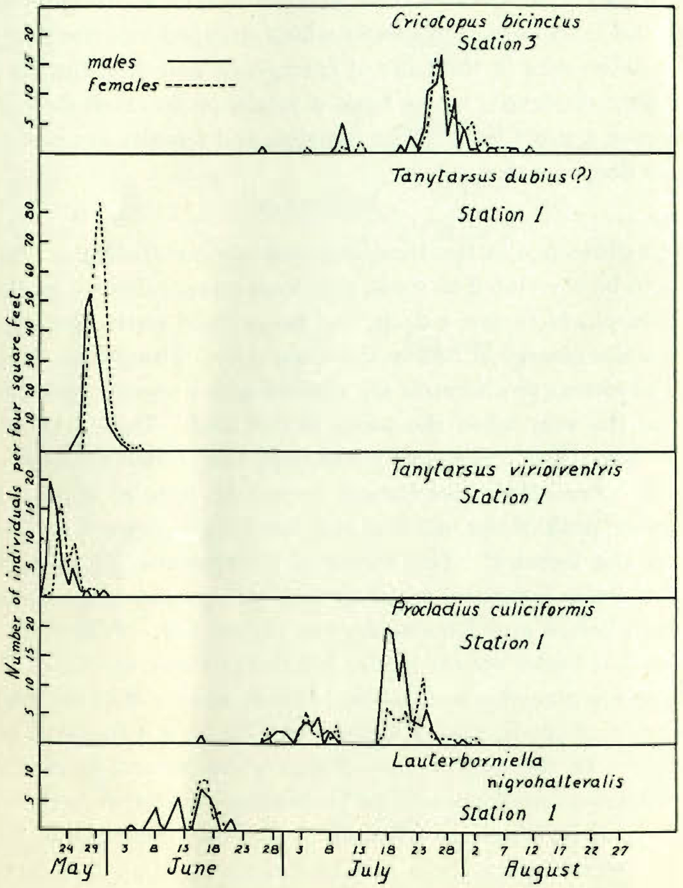

FIGURE 14.—Male, female emergence curves, 1938.

Of the thirty-three shallow water species, eleven have occasional occurrences below the thermocline (table 7). Above the thermocline these species emerge in the proportion of 100 males to 121 females, whereas below the thermocline the proportion is 100 males to 149 females. It is evident that in the colder water fewer males survive. These facts are in agreement with the findings of MacArthur and

Baillie (1932), who conclude, "it is not unreasonable to suppose that a male, with more intense physiological activity, more rapid expenditure of energy and a stronger and more sensitive response to stimuli, would probably prove less stable and less resistant as a mechanism, be more easily disturbed and upset, and more frequently eliminated by unfavourable environments, both external and internal."

TABLE 7.—The number of males and females of certain shallow water species emerging from depth above and below the thermocline.

	ABOVE		BELOW	
	Males	Females	Males	Females
C. tenuicaudatus	8	1	8	3
P. illinoensis	4	0	5	8
C. lucifer	30	21	0	4
Pentapedilum sp.	6	6	3	5
R. coracinum	3	1	3	6
C. nigrohalteralis	53	61	1	1
Tanytarsus sp.	133	154	7	8
T. signatus	201	296	2	6
T. dubius (?)	195	262	5	7
Corynoneura celeripes	108	88	1	2
Metriocnemus sp.	19	31	2	5
TOTAL	760	921	37	55

THE ROLE OF TEMPERATURE IN THE ECOLOGY OF THE CHIRONOMIDAE

The evidence throughout the investigation has pointed toward temperature as the most influential factor of the environment. Differences in the number of species and times of emergence at different depths have been shown to be correlated with differences in temperature. No other environmental factor varies either from spring to fall or from shallow to deep water in a way that corresponds to changes in the fauna. The oxygen and carbon dioxide content of the epilimnion remain constant throughout the summer, and hence cannot be influential in the seasonal changes of the shallow water fauna. In 1937 and 1938 the hypolimnion was saturated with oxygen until the end of July; for half the summer the whole lake was saturated with oxygen. Hence differences in vertical distribution of the fauna could not be attributed to differences in oxygen at different depths. During the latter half of the summer the decline of oxygen content of the deep water to 2.0 c.c. per litre in September was not accompanied by any changes in the fauna. The increasing carbon dioxide content of the hypolimnion from July to October may account for the emergence of one species (page 36), but no general changes occurred which could be attributed to carbon dioxide effects.

In the following sections the warmth-tolerance and the day-degree requirements of the different species of chironomids are discussed. The warmth-tolerance of a species refers to the upper and lower limits of the temperature range within which it can complete its life cycle; the day-degree requirement of a species is the number of day-degrees which it needs for the same purpose. The ecological terminology employed by Hesse, Allee, and Schmidt, and as defined by them in *Ecological Animal Geography*, has been used in these sections.

Warmth-Tolerance

In the presentation of the data the chironomid fauna has been discussed in three groups according to the depth of habitat relative to the thermocline. This division, made primarily for convenience in handling the data, is partially a natural one. It places the fauna in three classes according to temperature tolerances. Those species living on the bottom above the thermocline are subject to a temperature range of 0°-25°C. They have been considered, however, as a warmth-tolerant group, as growth and maturation take place only in the season of open water. During the winter, eggs, and in some species larvae (*Chironomus halteralis*, *C. devinctus*, *C. lucifer*), lie dormant. The species below the thermocline are stenothermal cold-tolerant (range 4°-8°C.), and species living both above and below the thermocline are eurythermal. These terms must, however, be applied with caution.

In the shallow water forms different degrees of warmth-tolerance are found. *Tanytarsus dubius* (?) occurs early in May during periods of moderate temperature (12°C.); *C. halteralis*, *Spaniotoma* (*Eukiefferiella*) sp. and *Tanytarsus signatus* emerge in July during periods of maximum temperature (20°-25°C.); *Corynoneura celeripes* occurs throughout the whole summer and is therefore not affected adversely by summer temperature changes. Very early spring forms such as *Protanypus* sp. and *Pentapedilum coracinum* are evidently restricted to a season of low temperature, but are quite distinct from species living in still colder water below the thermocline. *Spaniotoma curtistylus* (?) (figure 9) emerges in May and again in late August and early September, times when temperatures are considerably lower than in midsummer. From these examples it is evident that the shallow water fauna, although predominantly warmth-tolerant, exhibits a gradation to cold-tolerant forms on the one hand, and eurythermal forms on the other.

The group designated as eurythermal also shows specific variations of temperature tolerance. Thus *Procladius* (*Psilotanypus*) sp. and *P. culiciformis*, while living successfully at all depths, are most successful in warmer water on bottom above the thermocline, while *Pentaneura* spp. have equal or even greater numbers in the deeper water.

Similarly, among the stenothermal cold-tolerant species it has been pointed out that different degrees of cold-tolerance occur. *Cricotopus bicinctus* finds optimum conditions at seven metres; *Chironomus nigricans* and *C. staegeri* have maximum numbers at seventeen metres, where the water is 4° to 6° cooler.

These data indicate that although specific differences in temperature tolerance are well marked, no boundaries of warmth-tolerance can be erected; the whole fauna grades smoothly between two extremes, stenothermal cold-tolerant forms in the deep water and warmth-tolerant forms (adapted to resist winter cold) in the shallow water.

The evidence indicates that the summer temperature range taken in conjunction with the day-degree requirements are controlling factors in determining the depth of habitat of a species.

Day-Degree Requirements

Blunck (1923) and others have shown that for all practical purposes the effective temperature multiplied by the time required to reach maturity is a constant. Blunck obtained this relation by observing the time required by *Dytiscus marginalis* L. to pass a certain stage of its life-history at different constant temperatures. The relation holds over only a portion of the temperature range, known as the medial range. There is a considerable discrepancy in the curve at both the upper and lower ends.

Shelford (1927) has pointed out that humidity, rainfall, air movement, and quality and intensity of light as well as temperature affect the rate of development in the codling moth. These factors, with the exception of light, are of small significance for aquatic stages. It is probable, therefore, that for aquatic larvae a simple summing up of mean temperatures will give a usable estimate of development velocities.

Shelford has further shown that fluctuating daily temperatures, if not of too great an amplitude, give a faster rate of development than a constant temperature equal to the mean of the fluctuating temperatures. For this reason the rate of growth of the same

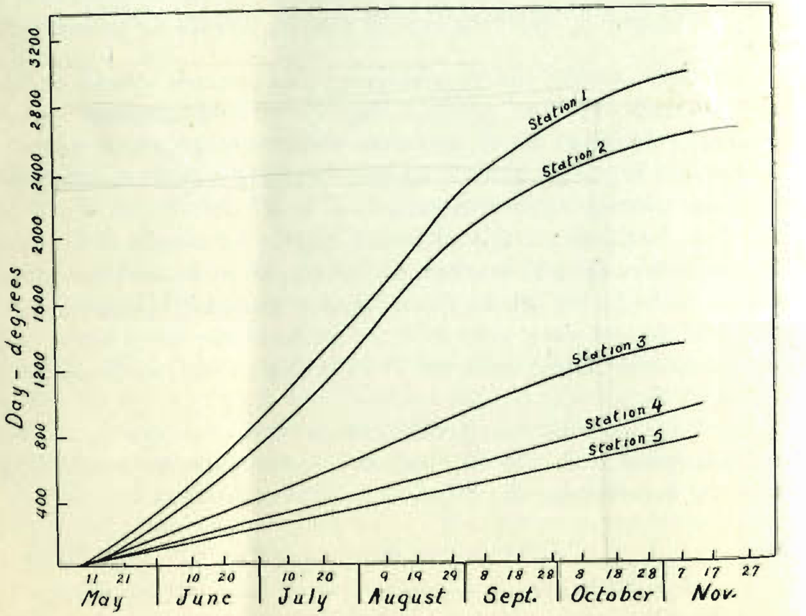

FIGURE 15.—The accumulation of day-degrees at stations 1 to 5 in 1938. The graph shows the total of day-degrees to which the fauna at each station has been exposed at any particular date.

species in different depths of water cannot be said to be directly proportional to the temperature conditions at these depths. A species of larva in deep water is subjected to more nearly constant temperature than the same species in shallower water. In the epilimnion of a lake, however, the temperature differences at different depths are small, and for practical purposes the number of day-degrees required by a species of larva at one depth is the same as that required by the same species at other depths.

As shown on page 7, the total of day-degrees has been calculated from temperatures above 0°C. This total, therefore, is greater than the effective total since the threshold of development is probably above 0°C. Uvarov (1931) has discussed the temperatures at which development begins: they range from 0°C. to around 10°C. for most insects. The threshold of development is probably around 4°C. for many chironomid larvae, but in the absence of definite knowledge, 0°C. has been taken.

The accumulation of day-degrees is shown plotted against time in figure 15. The number of day-degrees to which a larva has been exposed over any period of time at any station can be determined from these curves. Half the population of *Tanytarsus dubius* (?) at station 1 (1938) had emerged by May 28. From the appropriate curve of figure 15 the thermal sum from spring to this date is seen to be 280 day-degrees. On the assumption that the same thermal sum will be required at station 2, one may read from figure 15 the date at which 280 day-degrees had accumulated there. This date is June 2; actually half the population had emerged at station 2 by June 3. These curves, therefore, can be used to predict the dates of appearance of a given species at different depths.

The day-degree requirements of three species having one generation per summer are shown in table 8.

The larvae of certain species are found on the bottom as early as August of the summer before the year of their emergence. They are thus exposed to at least 600 day-degrees before freeze-up. This amount should be added to that required by the species from the time of spring break-up to emergence. Thus *C. halteralis* and *T. dubius* (?) which are of this type require a total of 800-900 and 1000-1100 day-degrees respectively. *Chironomus devinctus* also belongs to this group.

It is indicated by table 8 that for species having one generation per summer one can assume that the same number of day-degrees will be required at station 2 as at station 1. The curves of figure 15 can thus be used to predict the dates of appearance of such species with reasonable accuracy.

TABLE 8.—The day-degree requirements of certain species living at stations 1 and 2.

	Station	"a" Date by which half the population had emerged	Total of day-degrees from spring break-up to "a"	Amount of heat larva received in preceding summer	Total
Tanytarsus dubius (?) 1937	1	June 8	190	600	790
	2	June 6	200	600	800
Tanytarsus dubius (?) 1938	1	May 26	280	600	880
	2	June 3	300	600	900
Chironomus halteralis 1937	1	June 18	430	600	1030
	2	June 26	490	600	1090
Spaniotoma (*Eukiefferiella*) sp. 1937	1	July 8	870	none	870
	2	July 14	790	"	790
Spaniotoma (*Eukiefferiella*) sp. 1938	1	July 2	910	"	910
	2	July 13	1000	"	1000

The day-degree figures for *Tanytarsus signatus* serve as an example of the requirements of species having two generations per summer. Each generation of *T. signatus* at station 1 required 550 day-degrees from the time of the appearance of the larvae until half the adults had emerged. At station 2 the first generation required 670 day-degrees, 120 more than at station 1. From this it would appear that in the spring and early summer (when the first generation of *T. signatus* is maturing) the temperatures at station 2 fall below the medial range (the temperature range in which the growth-temperature curve is a straight line). The curves of figure 15 could not be used, therefore, for a strictly accurate prediction of the appearance of spring generations of two generation species.

From the foregoing considerations of day-degree requirements certain temperature relationships are suggested. In general, species requiring around 1000 day-degrees to grow from larva to adult are not able to complete more than one generation in a year. Species having two generations per summer require only about half as many day-degrees as one generation species, e.g., *Tanytarsus signatus* requires 550 day-degrees. Deep water species having one generation every two years require about three times as many day-degrees as the one generation shallow group.

The shallow water species which appear only once during each summer are probably near the northern limit of their range. The same species further south could conceivably have two generations per summer. Several actual examples are known. *Chironomus halteralis*, *C. decorus*, *C. devinctus*, and *C. scalaenus* all occur at Costello lake once only each summer, during June and July. Malloch's report on Illinois species (1915) records all these occurring in early May and June and again in September and October in the vicinity of Urbana. There the summer is long enough to permit these species to have two generations. Records of other species having one generation at Costello, e.g., *Chironomus babiyi*, *C. varipennis*, and *C. tenuicaudatus* are for early May at Urbana (Malloch, 1915; Rempel, 1937). It seems probable that these have a second generation at Urbana which has not been reported.

The total number of day-degrees required, while determining the length of time a species takes to mature in any one locality, does not determine the depth of the habitat of a species. The most influential factor in depth determination is probably the summer temperature range. This range (in shallow water) includes suitable temperature ranges for many species. If the temperature suitable for the growth and maturing of any one species is maintained at any one locality long enough to fulfil the total day-degree requirements of that species, then, other factors being suitable, it can live at that locality. The thirty-three species living above the thermocline are found there because temperatures suitable for their growth occur sometime during the summer, and are maintained long enough to fulfil their day-degree requirements (since no migrations of larvae occur). A sudden rise in temperature may exceed the maximum which a species can tolerate and thus wholly or partially eliminate it from that locality. This is believed to have occurred in the case of *C. halteralis*.

In 1937, *C. halteralis* emerged at station 1 from June 8 to July 24. The peak, fifty-two individuals per four square feet, was on June 16. Also sixty-one individuals emerged from station 2 during the same summer. In 1938 this species began emerging at station 1 on June 5 and continued to July 15. The peak occurred on June 15, but consisted of only ten individuals per four square feet. None emerged at station 2. The larval population previous to June 15 was the same for both summers. The surface temperature on June 15 and 16, 1937, was 17.8°C., while in 1938 it was 22.2°C. This difference of 4.4°C. may have been sufficient to kill eighty per cent of the pupae at station 1 and perhaps all the pupae at station 2.

The fact that each species has its maximum emergence at a time when other species have either not yet emerged or are past their peak suggests that each has a slightly different optimum temperature range. This condition helps to eliminate competition for food among some of the species living in the same habitat, as they are not all present at the same time. This condition is similar to that which has been shown to exist in the mayfly fauna of a stream (Ide, 1935).

THE EFFECTS OF THE THERMOCLINE

Throughout most of the summer the thermocline is present in Costello lake from four to seven metres. This means that temperatures in depths of four metres or less will be suitable for warmth-tolerant animals, and below seven metres will be suitable for cold-tolerant animals. The thermocline is thus seen to act as a barrier marking the upper limit for cold-tolerant forms and the lower limit for warmth-tolerant forms. The area of bottom included in the four to seven metre contours lies wholly within the thermocline; it is a region of intermediate and unstable temperature conditions which are believed to be suitable for neither warmth- nor cold-tolerant forms. This hypothesis is based on evidence from the collections. On page 27 the number of species found at each depth was given. Fewer species were found at station 3 than at station 4. Although station 3 is shallower, and hence warmer, than station 4, it is situated within the thermocline, and is subject to the conditions described for this region.

The two years of larval life required by certain of the cold-tolerant species is probably because of the constant low temperatures of the deeper water. These low temperatures are a result of the resistance to mixing by wind action set up by the thermocline.

TEMPERATURE AND THE ORIGIN OF SPECIES

The chironomids confined to the deep, cold water of Costello lake are remarkable in that only two of them are at all closely related (*Cricotopus bicinctus* and *C. trifasciatus*). The members of the group show no close morphological inter-relationships; indeed, excepting the two mentioned, each deep water species possesses its nearest relative in the shallow water fauna. These facts have been interpreted as indicating that species formation in the deep water is either not occurring at all or going on very slowly. In their discussion of polar freshwater communities, Hesse, Allee, and Schmidt (1937) conclude that polar lakes are very poor in species; the same conclusion applies to lakes of high mountains which are free from ice for only a short period of the year.

In the shallow water of Costello lake, a picture strikingly different from the deep water is presented. Here the genera are represented by many, often closely related species. There are ten species of *Tanytarsus*, eleven species of the subgenus *Chironomus*, and four species of the subgenus *Polypedilum* as opposed to one of each in the deep water. The range of temperature variation in the shallow water is from 4°C. to 25°C.; in the deep water the maximum variation is from 3.9°C. to 8.8°C.

The environments where few and distinct species are found, as polar and mountain lakes and the deep water of Costello lake, share one feature, uniformity of temperature. But where there are many species, often indistinctly separated, as in the shallow water of Costello lake, there is a large temperature change both from spring to midsummer and from day to night. The stimulus to the formation of species is provided probably not by any one optimum temperature, but by temperature variation.

There is some evidence that in the shallow water still more species are being formed. Forms which have been identified as *Chironomus* (*Lauterborniella*) *agrayloides* show two distinct periods of emergence, one about the middle of June and the other about the middle of July (figure 16). The time between the two peaks is believed not to be long enough to allow the development of a second generation, yet the peaks are too far apart to be considered part of one generation of one species. This phenomenon has been interpreted as indicating that there are two races of *C. agrayloides* present which have not been distinguished morphologically.

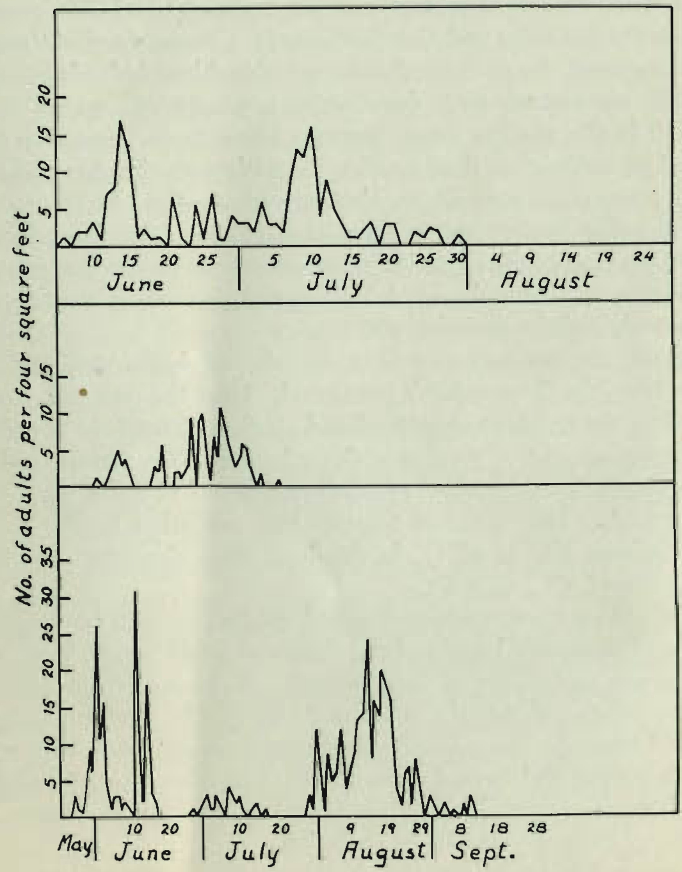

FIGURE 16.—The occurrence of bi- and trimodal emergence curves, station 1, 1938. Upper panel *Chironomus* (*Lauterborniella*) *agrayloides*, second panel *Tanytarsus pusio* (?), lowest panel *Tanytarsus confusus* (?).

The emergence of *Tanytarsus pusio* (?) (figure 16) shows an irregular series of peaks lasting from late May to mid-July. It is unlikely that a single species would emerge irregularly for this length of time; probably at least two incipient species have been considered together. *Tanytarsus confusus* (?) (figure 16) has three separate emergences from late May to early September. Of these the first and the third are probably two generations of the same species; the second emergence in July is probably that of a different group in which no morphological differences which would distinguish them were observed.

The emergence of these three species, *C. agrayloides*, *T. pusio*(?), and *T. confusus* (?) is believed to illustrate the early stages in the formation of new species. Slight physiological differences, perhaps in the nature of altered temperature requirements, may have determined that certain individuals of these species emerge at a different time from the rest. As these differences become more marked the divergent individuals might become morphologically distinct from the parent group, and give rise to new and recognizable species.

PRODUCTIVITY

A fitting introduction to the problem of productivity is provided by the following quotation from Rawson (1930). "The average amount of bottom fauna present throughout the summer season is not representative of the productivity of the bottom. A true estimate of the bottom productivity must take into account the rate of production as well as the amount of fauna present at a given time. . . ."

Lundbeck (1926) recognized the importance of this in his bottom studies of the Plöner See. Using data on rate of growth, numbers present and depletion by emergence and mortality, he estimated that the annual crop or production was three or four times the average summer fauna. For chironomid larvae his factor is three.

If we accept productivity as being the rate of production of adults, then the tent-trap returns give the productivity of the Chironomidae. Such an estimate of productivity would, however, be inadequate in a limnological investigation because it gives no information about the number of larvae which failed to emerge. In this investigation, therefore, productivity is interpreted as meaning the number of larvae which reach maturity during the summer plus the number of larvae which are eaten by fish or fail to mature for some other reason.

The estimate of the average percentage of the larval population which emerges during each week of the summer has been calculated as follows:

From figures for the daily emergence of chironomids at different depths the average daily emergence for each week of the summer of 1938 has been calculated. The numbers of chironomid larvae found at different depths each week of the same summer are given in table 9.

TABLE 9.—Total number of chironomid larvae at each depth zone.

1938

(*Number per 0.5 square feet*)

Station	1	2	3	4	5
May 6-13	208	38	30	54	46
19-23	74	23	22	57	53
24-9	143	54	10	17	31
31-June 4	103	54	4	69	50
June 6-10	109	23	31	44	67
15-18	52	11	16	10	27
21-5	51	14	18	46	64
28-July 2	37	21	16	71	12
July 5- 9	22	19	7	67	37
12-16	18	34	5	73	25
18-20	14	9	7	50	16
27-30	20	9	19	71	61
Aug. 2- 6	16	14	4	68	14
9-13	19	26	9	101	34
15-18	25	29	13	74	25
21-6	28	22	12	24	25
30-Sept. 2	13	15	22	34	23
Sept. 6-10	17	18	23	22	32
12-16	98	19	10	19	16
18	32				

Using the figures in table 9 and the average daily emergence of adults per week, the average daily percentage of the larval population lost through emergence each week of the summer has been calculated (table 10).

TABLE 10.—The average daily percentage of the larval population lost through emergence each week of the summer of 1938.

Station	1	2	3	4	5
May 6-13	1.2	1.6	2.1	1.2	0.3
19-23	4.9	2.7	1.1	0.7	3.3
24-9	6.1	1.4	2.5	2.9	1.6
31-June 4	4.4	3.0	6.25	1.1	0.25
June 6-10	2.1	3.8	1.2	2.3	0.2
15-18	10.8	5.7	3.1	2.5	1.4
21-5	8.3	9.9	0.7	0.8	0.2
28-July 2	22.0	9.5	4.1	0.4	1.0
July 5- 9	35.0	9.9	3.6	0.6	0.3
12-16	16.6	13.2	5.0	0.2	1.0
18-20	27.0	36.2	5.4	1.0	2.3
27-30	5.0	34.8	11.8	1.2	0.9
Aug. 2- 6	10.9	37.4	6.25	0.4	1.6
9-13	15.6	10.6	5.6	0.2	0.4
15-18	17.5	18.1	5.8	0.3	1.5
22-6	8.0	15.3	2.1	1.0	0.0
30-Sept. 2	19.2	9.2	1.7	0.7	0.0
Sept. 6-10	8.1	3.5	2.7	3.4	0.8
12-16	0.89	6.6	10.0	9.2	4.7

The data in table 10 have been plotted to give five smooth curves (figure 17) showing the daily depletion of the larval population through emergence at each of the five stations. The area under each of these curves has been calculated and then divided by the number of days in the summer. This yields figures which represent roughly the average daily depletion of the larval population by emergence for the whole summer at each station. The figures are as follows:

Station 1, 11.7 per cent; station 2, 12.4 per cent; station 3, 4.2 per cent; station 4, 1.3 per cent; station 5, 0.96 per cent.

The washing technique employed in working over the dredgings is only adequate for large larvae. It is estimated that about half the larvae at stations 1 and 2 are not counted. The percentage of the larval population lost through emergence as calculated above is, therefore, twice too large and should be 5.8 per cent and 6.2 per cent at stations 1 and 2 respectively.

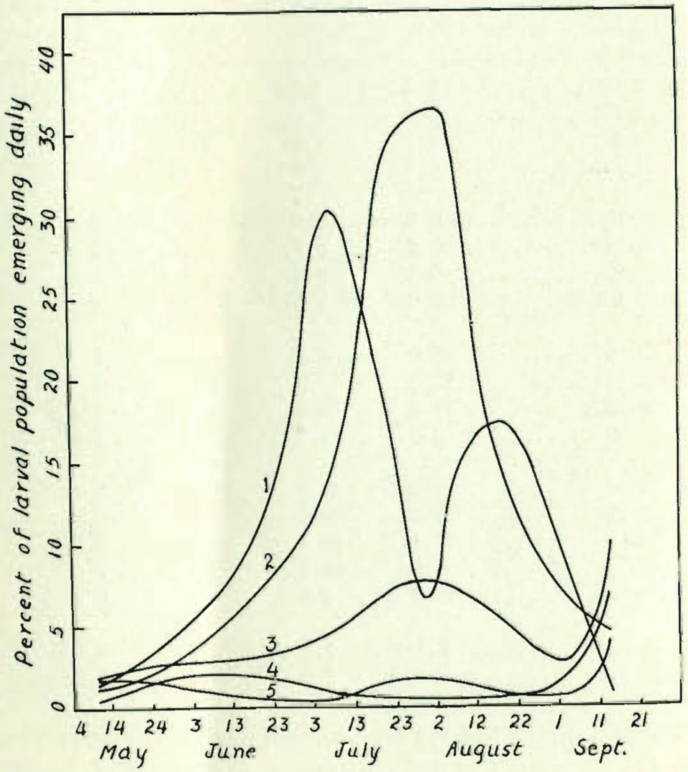

FIGURE 17.—The percentage of the larval population emerging each day of the summer of 1938 at stations 1 to 5.

The correction for larval mortality has been calculated as follows: In 1938 the maximum number of larvae of *Tanytarsus dubius*(?) at station 1 was 767 per four square feet; 424 adults emerged from the same area.

For the first generation of *Tanytarsus signatus* in 1938, 160 larvae per four square feet were found at station 1 at the time of maximum numbers; 179 adults were collected from the same area.

The data for these two species indicate a small mortality in the shallow water. Possibly thick rooted vegetation at this depth provides considerable protection for the larvae living there. Therefore at station 1, and probably also at station 2, the number of adults emerging represents the total productivity fairly closely.

The larvae of *Tanytarsus* (*Micropsectra*) sp. at the time of their maximum abundance occurred in numbers of 400 and 168 per four square feet at stations 4 and 5 respectively. The total emergence for the same area and stations was 120 and 72. The mortality here is from 57 to 70 per cent. As the collection of adults was discontinued before the emergence of this species was completely over, a mortality of fifty per cent has been assumed for use in the calculations. Data for other deep water species indicate a much higher mortality than this, but owing to the sporadic nature of their emergences they have been disregarded in this calculation. The emergence data for stations 4 and 5 hence measure only half the total loss of larvae at these depths; therefore the average daily production of larvae at stations 4 and 5 amounts to 2.5 to 3.5 per cent of the larval population.

If one now assumes that the rate of larval production is equal to the rate of renewal of the population (discounting the fact that many more eggs must be laid than larvae produced) the following turnover figures may be estimated:

Stations 1 and 2	Complete turnover every			16-17 days
" 3	"	"	"	24 "
" 4 and 5	"	"	"	40-50 "

In a summer of 130 to 140 days the standing population of chironomid larvae in Costello lake would be renewed completely eight or nine times in the epilimnion and two, or at most three, times below the thermocline.

SUMMARY

1. Costello lake lies in the Precambrian shield at 45°35′ north latitude, 78°20′ west longitude, and at an elevation of 1,370 feet. It has an area of 94 acres, over one-third of which is five metres or

less in depth; the maximum depth is 20 metres. The water is brown and has a pH range of 4.4 to 6.6 throughout the summer. Thermal stratification begins in May and lasts until October.

2. The emergence of chironomids begins in May as soon as the ice has left the lake, and lasts until freeze-up in November. The shallow water produces more individuals than the deep water except in late summer (September). Emergence in the shallow water occurs mostly between the hours of four and seven A.M.; in the deep water it is equal throughout the day.

3. The number of individuals emerging appears to have no relation to temperature; the number of species emerging is definitely correlated with temperature, the most species appearing during the warmest week of the summer (23°C.-25°C.).

4. Thirty-three of a total of fifty species in 1938 were found above the thermocline in the shallow water. Of these, twenty species have one, and thirteen species have two generations per summer.

5. Seven of the fifty species were confined to depths below the thermocline. Two of these require two years to complete their life cyles.

6. Ten of the fifty species were found both above and below the thermocline. Of these, six are summer and four spring species.

7. Males of the shallow water species emerge slightly in advance of females. Over the deeper part of their range, females of the shallow water species emerge in greater numbers than the males.

8. It has been proposed that these differences among the species can be explained by assigning to each a definite reaction to temperature. Shallow water species have been considered as warmth-tolerant; deep water species as cold-tolerant; and species living both above and below the thermocline as eurythermal.

9. Shallow water species emerge first from the shallowest and last from the deepest parts of their range. The number of day-degrees required to develop from larva to adult has been calculated for certain of these species. It is proposed that the longer time necessary for a given number of day-degrees to accumulate in the deeper parts of their range explains their later emergence there.

10. The ten species living above and below the thermocline offer an exception to this. A given species of this group emerges at the same time both above and below the thermocline. Four of these

species emerge in May when the temperature difference between deep and shallow water is small; the other six emerge in the summer when there is a steep shallow to deep water temperature gradient.

11. *Chironomus* (*Polypedilum*) *halteralis*, *Tanytarsus dubius* (?), and *Spaniotoma* (*Eukiefferiella*) sp. have been shown to require around a thousand day-degrees, which allows them but one generation per summer. Certain species with smaller day-degree requirements have two generations per summer. Some of the shallow water one generation species have been found by other workers to have two generations in Illinois where the summer is longer.

12. Evidence has been put forward in support of the theory that environments with wide temperature ranges support more species than environments with constant temperatures.

13. It has been calculated from emergence and larval data that the standing population of chironomid larvae is replaced during the summer eight or nine times in the epilimnion and two or three times in the hypolimnion. Mortality of larvae, due perhaps to consumption by fish, is small in the shallow water and great in the deep water where it amounts to fifty per cent of the total population of larvae.

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APPENDIX

TABLE 11.—Vertical Distribution

	1937				1938				
Station	1	2	3	5	1	2	3	4	5
Pentaneura carnea	x				x	x			
" *illinoensis*	x				x	x	x	x	
" sp. 1	x	x			x	x	x	x	x
" sp. 2	x	x	x		x	x	x	x	
" spp.	x				x	x			
Procladius (*Procladius*) *culiciformis*	x	x	x	x	x	x	x	x	x
" " *fasciger*	x	x			x	x			
" (*Psilotanypus*) sp.	x	x	x	x	x	x	x	x	x
Protanypus sp.							x	x	
Diamesa sp.					x	x			
Metriocnemus sp.					x	x	x		
Cricotopus bicinctus		x	x	x			x	x	x
" *trifasciatus*			x	x			x	x	
Spaniotoma (*Psectrocladius*) *sordidella* (?)					x				
" " sp. 1	x	x	x	x					
" " sp. 2					x	x			
" (*Orthocladius*) *curtistylus* (?)					x	x			
" " sp. 2	x	x	x	x					
" (*Eukiefferiella*) sp.	x	x	x		x	x			
Corynoneura celeripes	x	x	x		x	x			
Pentapedilum (*Sergentia*) *coracinum*						x	x	x	
" sp.					x	x	x	x	
Pseudochironomus spp.	x								
Chironomus (Chironomus) *staegeri* (?)				x				x	x
" " *decorus*		x							
" " *xenolabis*	x	x							
" " *lucifer*	x	x			x	x			
" " sp. *c*	x	x			x				
" " sp. *d*	x				x	x			
" " *claripennis*	x	x			x	x			
" " sp. *a*	x	x			x	x			
" " sp. ?	x				x				
" " *tenuicaudatus*	x	x	x		x	x	x		
" " sp. *b*	x	x			x	x			
" " *curtilamellatus*	x	x			x	x			
" (*Endochironomus*) *nigricans*				x				x	x
" (*Kribioxenus*) *babiyi*	x				x				
" (*Stictochironomus*) *devinctus*	x	x			x	x			
" (*Polypedilum*) *halteralis*	x	x			x	x			
" " *illinoensis*		x	x	x		x	x	x	x

TABLE 11.—*Cont.*

	1937				1938				
Chironomus (*Polypedilum*) *scalaenus*........	x	x			x	x			
" (*Lauterborniella*) *varipennis*.....	x	x			x	x			
" " *agrayloides*.....	x	x			x	x			
" " *nigrohalteralis*..					x	x			
Tanytarsus (*Micropsectra*) sp..............			x	x				x	x
" (*Tanytarsus*) *signatus*..........	x	x			x	x			
" " *dubius* (?)........	x	x	x		x	x			
" " *confusus* (?).......	x	x	x		x	x			
" " *viridiventris*.......	x	x			x	x			
" " *pusio* (?).........	x	x			x	x			
" " sp. *2*.............	x	x			x	x			
" " sp. *3*.............					x	x	x	x	
" " sp. *4*.............								x	x
" " sp. *5*.............					x	x			
" (*Phaenopelma*) *simulatus* (?).....	x	x			x	x	x	x	x

TABLE 12.—List of species living above the thermocline and having one generation per summer (1937 and 1938).

Pentaneura carnea
Pantaneura sp.
Procladius (*Procladius*) *fasciger*
Diamesa sp.
Spaniotoma (*Psectrocladius*) *sordidella*
" (*Eukiefferiella*) sp.
Pseudochironomus spp.
Chironomus (*Chironomus*) *decorus*

" " *xenolabis*
" " sp. *c*
" " sp. *d*

Chironomus (*Chironomus*) *claripennis*
" " sp. *a*
" " sp. ?
" " *tenuicaudatus*
" " *curtilamellatus*
" (*Kribioxenus*) *babiyi*
" (*Stictochironomus*) *devinctus*
" (*Polypedilum*) *halteralis*
" " *scalaenus*
" (*Lauterborniella*) *varipennis*
Tanytarsus (*Tanytarsus*) *dubius* (?)
" " sp. *2*

TABLE 13.—List of species living above the thermocline and having two generations per summer (1937 and 1938).

Metriocnemus sp.
Spaniotoma (*Psectrocladius*) sp.
" (*Orthocladius*) *curtistylus* (?)
Corynoneura celeripes
Chironomus (*Chironomus*) *lucifer*
" " sp. *b*
" (*Lauterborniella*) *agrayloides*
" " *nigrohalteralis*
Tanytarsus (*Tanytarsus*) *signatus*
" " *confusus* (?)
" " *viridiventris*
" " *pusio* (?)
" " sp. *5*

TABLE 14.—List of species living below the thermocline (1937 and 1938).

Cricotopus bicinctus
" *trifasciatus*
Chironomus (*Chironomus*) *staegeri* (?)
" (*Endochironomus*) *nigricans*
Chironomus (*Polypedilum*) *illinoensis*
Tanytarsus (*Micropsectra*) sp.
" (*Tanytarsus*) sp. *4*

TABLE 15.—List of species living both above and below the thermocline (1937 and 1938).

Pentaneura illinoensis
" sp.
Procladius (*Procladius*) *culiciformis*
" (*Psilotanypus*) sp. *2*
Spaniotoma (*Psectrocladius*) sp. *1*
Spaniotoma (*Orthocladius*) sp. *2*
Pentapedilum (*Sergentia*) *coracinum*
" sp.
Tanytarsus (*Tanytarsus*) sp. *3*
" (*Phaenopelma*) *simulatus*(?)