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A STUDY OF THE PROFUNDAL BOTTOM FAUNA OF LAKE WASHINGTON[1]

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INTRODUCTION

Lake Washington has been the object of intensive study in recent years (Comita, 1953; Anderson, 1954; Edmondson, *et al.*, 1956; Comita & Anderson, 1959; Shapiro, 1960; Edmondson, 1961, 1962, 1964, and 1965; and others). These studies have been primarily concerned with the chemistry and plankton of the lake; the bottom fauna has remained almost entirely unknown. Thus the opportunity was presented to approach a relatively unexplored community with the benefit of a considerable background of basic limnological data and knowledge.

There is no scarcity of studies on the bottom fauna of lakes, although knowledge of this group does lag behind that of the plankton and fish. However, most studies either consider the bottom fauna en masse, often as part of a survey of the fish food of a lake, or consider in detail only a few species or a single taxon.

With a single exception, this paper treats individually each and all of the species which make up the macrofauna of Lake Washington. This makes it possible to assess the role of interactions between species particularly as regards the effect on spatial distribution. The paper stresses the contributions made by the individual species to the spatial and temporal patterns of the bottom fauna as a whole. Basic life history data, such as time of reproduction or emergence and the sequence of the various life stages, are considered in detail.

DESCRIPTION OF LAKE

Lake Washington has an area of 8762 ha and a maximum depth of 65.2 m with a mean of 32.9 m (Fig. 1). It is a long (30.8 km north to south), narrow lake (average width, 2.5 km) bordering the city of Seattle on the east. There are 2 main inlets, the Sammamish River at the north end and the Cedar River at the south. The only outlet is the Lake Washington Ship Canal, emptying into Puget Sound to the west.

The lake basin is a glacial trough sculptured by the Vashon ice-sheet, the last continental glacier to invade the Seattle area. Excepting the areas around inlets and bays, the basin rises steeply from the lake floor to precipitous bluffs 90 m or more in altitude. The bottom topography consists of 3 principal elements: a wave-cut bench generally does not extend farther than 200 m from shore and reaches a depth of about 12m; the steep marginal slope descends to the lake floor with a declivity ranging from 6 to 24 degrees and averaging approximately 14; the deep floor constitutes the major part of the projected area of the lake, averaging about 2 km in width. An east-west cross-section of the lake basin outlines the shape of a "W" with a broad ridge rising to more than 10 m above narrow valleys at the bases of the marginal slopes. According to Gould & Budinger (1958), this is effected by water cooling in the shallow bays and flowing down the steep slopes, thereby scouring the sediment at their bases. (For further details on morphometry, see Gould & Budinger, 1958; Brown & Caldwell, 1958.)

The bottom deposits are chiefly gyttja 2 to 15 m in thickness underlain by an unknown depth of glacial blue clay. The gyttja is thickest on the deep floor and quite shallow on the steep slopes; often the blue clay is exposed. At the north and south ends, silt, sand, and gravel have been deposited by the incoming rivers.

Any discussion of the physical, chemical, and biological properties of Lake Washington should include

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a consideration of its recent history. During the period 1941 to 1952, 10 sewage treatment plants were erected in the communities surrounding Lake Washington. Concomitantly, the amount of treated effluent released into the lake increased. Up until 1943, only 0.3 million gal of effluent entered the lake per day. With the construction of the largest of the plants at Lake City in 1952, the figure rose to 2.5 million and, with the subsequent addition of a number of smaller plants, rose to as high as 13.2 million in 1962 and 1963. The treated sewage has a high concentration of nitrogen and phosphorus compounds. In 1957, over one-half of the phosphate phosphorus income for Lake Washington was derived from treatment plants.

This nutrient increase has effected changes both in the species composition and standing crop of the plankton community. In 1955, Lake Washington had a bloom of *Oscillatoria rubescens* for the first time, a species which appeared in Zürichsee in the latter part of the 19th century when similar cultural influences were visited upon this lake. The standing crop of phytoplankton has shown striking increases. The mean standing crop in the summer of 1963 was about 15 times the summer mean of 1950.

Although some members of the zooplankton have grown more numerous in the period following 1950, the increase has not been as great as that of the phytoplankton. This relative lack of success appears to be due to a striking qualitative shift in the phytoplankton. In 1950, diatoms and dinoflagellates were the dominant phytoplankton forms; filamentous algae never contributed more than 35% to the total algal standing crop. By 1963, filamentous blue-green algae contributed as much as 98% to the total and the unicellular forms had actually decreased from a maximum of 3.0×10^6 μ^3/ml in 1950 to 1.1×10^6 in 1963. It has been suggested (Edmondson, 1965) that these large filamentous forms are less readily available as a food source to the small filter-feeding zooplankters than are the solitary algae. Consequently, there could not have been a corresponding increase in zooplankton numbers. Most of the benthic animals in Lake Washington feed in such a manner that their numbers may have been similarly limited.

The increase in algal production has accounted for a decrease in the concentration of dissolved oxygen in the hypolimnion, particularly in the summer. In 1950, the oxygen concentration at 60 m never fell below 5.7 mg/l; in 1963, it fell to as low as 1.1 mg/l.

Due to the often disagreeable side-effects of an increase in productivity and some peculiar unpleasant properties of *Oscillatoria rubescens* and other Cyanophyta, the sewage discharges were gradually diverted to nearby Puget Sound. By 1968 this diversion was complete. The absence of this source of nutrients halved the total phosphorus income as compared to the time when all treatment plants were discharging into the lake.

Thus Lake Washington affords a unique opportunity to study the relationship between nutrient income and the production of the various communities, including the benthic. The sewage diversions were begun in 1963; the study here reported took place from 1963 to 1964. The phosphate and oxygen values for this period indicate that the lake was still in the eutrophic phase of its recent development during the course of this study (Table 1). Unfortunately, this "off-on-off again" situation cannot be utilized to best effect with the bottom fauna as no complete benthic survey was made before the influx of treated sewage. The only reference to the Lake Washington benthos prior to this study is found in the paper of Scheffer and Robinson (1939), from page 139:

TABLE 1. The summer concentrations of phosphate phosphorus and dissolved oxygen at 60 m from 1933 to 1964 for Lake Washington.

Year	Maximum Phosphate Phosphorus Concentrations (µ/l)	Range of Dissolved Oxygen Concentrations (mg/l)
1933........	25	5.8–8.2
1950........	23	5.7–9.0
1957........	89	0.0–5.0
1960........	86	
1961........	87	2.0–6.0
1962........	78	3.9–7.0
1963........	80+	1.1–6.6
1964........	87	2.0–6.9

> "Brief mention is made of the occurrences of certain organisms in samples of bottom mud brought up with an Ekman dredge. The lake bottom is composed of smooth, very fine, gray to olive-brown silt, mixed with a slight amount of plant detritus, blackened fragments of leaves, fir needles and twigs. Organisms screened from the mud include midge larvae, oligochaetes, a single specimen of leech, a small mollusc of the *Sphaerium* type, the ostracod *Candona*, and the amphipod *Pontoporeia*. All were taken at depths of from 30 to 60 meters. Midge larvae from 60 meters at Madison Park in all months of the year were identified by Professor O. A. Johannsen as members of the genus *Procladius*, probably *culiciformis*, a common, widespread species. A few additional midge larvae from 30 meters at South Point were reported as *Chironomus*, group *decorus*. Ostracods taken at 30 meters off South Point in May were identified by Dobbin (1933) as *Candona caudata* Kaufmann. Miss Dobbin states that this is the first recorded occurrence in the United States."

MATERIALS AND METHODS

A transect was sampled which runs from Cozy Cove due north to a point off the city of Kirkland (Fig. 1). Ten stations were spotted along the transect at 5-m depth intervals from 10 to 55 m. The range of 10 to 55 m includes about 78 % of the total surface area of the lake.

The stations were located using a fathometer and reading landmarks on shore with a sextant. Four samples were taken at each station, using a 15-cm² Ekman dredge with a hexagonal frame for stabilization. This is a modification adapted from that described by Rawson (1947) for use in deep water.

The transect was sampled over a year's time—September, 1963 to September, 1964—at approximately

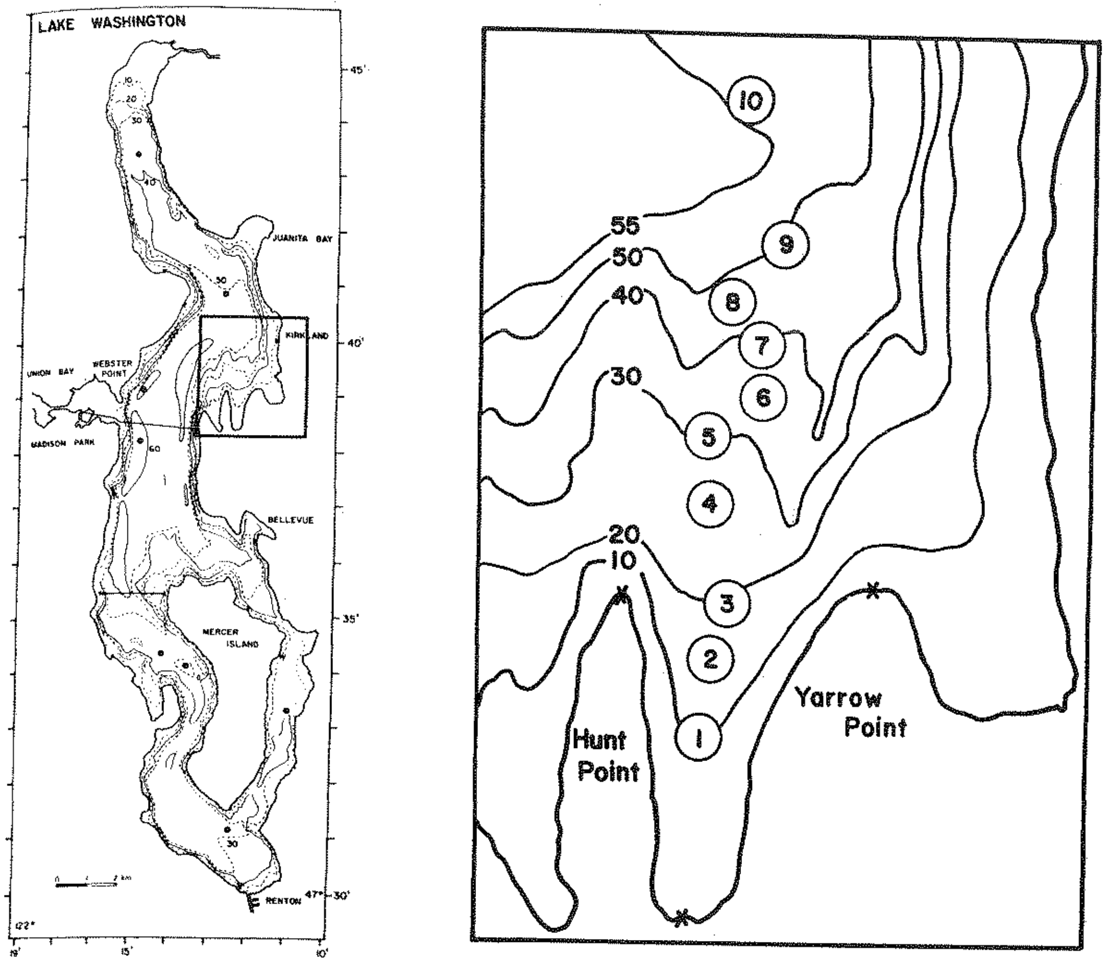


FIG. 1. Contour map of Lake Washington (intervals, 10 m). Outlined area enlarged at right with location of sampling stations.

monthly intervals. Open-water samples, taken at monthly intervals in the period July of 1963 to July of 1964, were made available by the University of Washington College of Fisheries. These were taken with an Isaacs-Kidd midwater trawl of cross-section 30.3 ft^2 and aperture size 1.5 stretch mesh to 00 plankton netting. The trawl was towed for a distance of a mile at depths ranging from 6 to 54 m. With it, the pelagic phases of certain bottom organisms were recovered.

The bottom samples were brought back to the laboratory and washed through a sieve of mesh gauge 0.4 mm. The sieve was fine enough to detect the presence of the earliest instars of almost all the insect larvae encountered as well as the small early stages of the other bottom organisms. This made it possible to evaluate the temporal sequence of the various life stages. However, the densities of the smallest organisms were certainly much greater than indicated in the counts.

The samples, after washing, were stored in 10% formalin. To facilitate the sorting process, a few drops of a 10% aqueous solution of Rose Bengal were added to each sample. The stain is picked up by exposed animal tissues, and a few plant tissues such as *Oscillatoria,* and thus makes it easier to differentiate the organisms from the debris.

A number of samples, such as those from the shallow cove, contained a large volume of coarse peaty material which would not wash through the sieve. Handsorting of such samples is long and arduous. Thus the sucrose-flotation technique (Anderson, 1959) was utilized which exploits the density difference between animals and most of the debris found at the bottom of a lake. A few samples from a depth of 45 to 50 m contained a considerable amount of sand. For these, a sluice-like apparatus was employed whereby the lighter plant and animal material was washed free from the sand.

In addition to counting the animals in the sample, a variety of biometrical techniques were employed by which the populations were characterized. Each species presents different properties by which this can be accomplished. The methods used will be discussed in detail when each of the organisms is considered. Lengths were obtained with an ocular micrometer or a millimeter rule. Representative animals were dried to a constant weight at 60° C and weighed on an analytical balance sensitive to a tenth of a milligram.

In the following pages, each species will be treated separately, with the exception of the species of the Oligochaeta. Two basic kinds of data will be presented for each: distribution with depth and population dynamics through the year. For the purpose of graphical representation, the points for the former will be determined by deriving an annual mean at each depth considering all the dates together; for the latter by deriving a mean for each sampling date considering all the depths together. Thus each point will ideally represent 40 separate samples, that is, 4 replicates times the 10 dates or 4 replicates times the 10 depths.

SELECTED PHYSICAL AND CHEMICAL DATA

Lake Washington is a warm monomictic lake whose mixing period generally extends from December to April (Fig. 2). It is tightly stratified from June through September. As a rule of thumb, during periods of stratification, the epilimnion includes the upper 10 m and the metalimnion 10 to 20 m. Thus temperatures at depths 0 to 20 m vary considerably throughout the year; temperatures at 30 m and deeper are conservative and low, 8 to 9° C. The temperature readings were invariably higher at 30 and 60 m in 1963 than in 1964; at 15 and 20 m, the 1964 readings were higher after the lake stratified—reflecting the presence of a deeper metalimnion—but otherwise were lower.

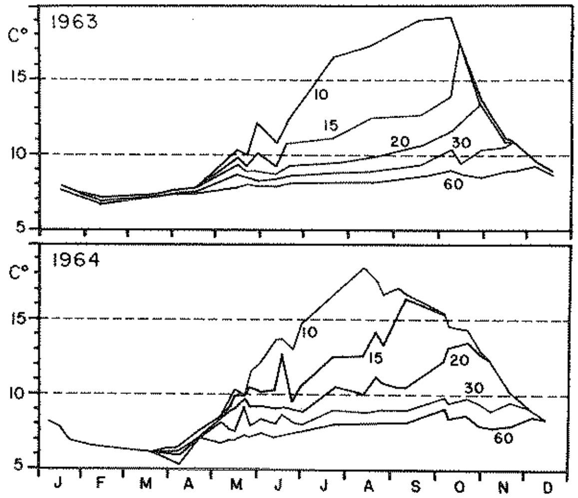


FIG. 2. Temperature at 10, 15, 20, 30, and 60 m for 1963 and 1964.

To test the relevance of temperatures taken from the open water with a bathythermograph to the temperatures encountered by the bottom organisms, measurements were made directly by thermometer on dredge samples for 2 dates and compared to bathythermograph readings at the same depth. The mud temperatures were consistently higher by about 1° C with the exception of the values from the epi- and metalimnion where there was no consistent relationship.

TABLE 2. Total seston at 10 through 60 m in 1963 and 1964 for Lake Washington (mean dry weight in mg/1)

Depth	10	20	30	40	50	60
Date						
14 Jan 63-30 Apr 63 (homothermal)	1.27	1.17	1.11	1.07	1.17	1.26
11 Jun 63-8 Oct 63 (stratified)	4.01	0.74	0.69	0.76	0.57	1.23
7 Jan 64-22 Apr 64 (homothermal)	1.78	1.72	1.75	1.68	1.78	1.97
17 Jun 64-6 Oct 64 (stratified)	3.82	1.06	0.69	0.65	0.72	1.16

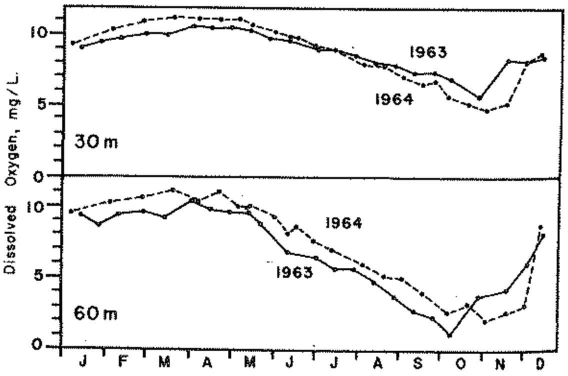


FIG. 3. Oxygen concentration at 30 and 60 m for 1963 and 1964.

When the lake was homothermal, the seston values were essentially the same throughout the water column—the readings were slightly higher at 60 m, probably reflecting the proximity of the flocculent bottom (Table 2). When stratified, the values were very high at 10 m and very low at the other depths. Comparing the 2 years, the values for 1964 were higher early in the year but nearly the same once the lake stratified.

Early in the year, the oxygen concentration at 30 m was slightly higher in 1964 than in 1963; the reverse was the case in the latter half of the year (Fig. 3). At 60 m, the 1964 values were consistently and substantially above those of 1963. These are open-water values and, since there is a microzone above the mud surface where oxygen is utilized at a high rate, the values relevant to the bottom organisms will be somewhat lower than those presented. However, they should serve for comparative purposes.

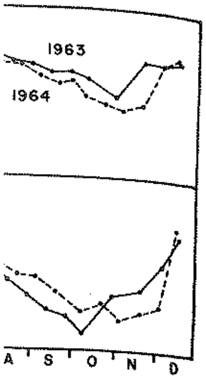
GENERAL SYSTEMATIC SURVEY

Following is the list of organisms recovered during the study period along the transect:

- Arthropoda
  - Insecta
    - Diptera
      - Chironomidae
        - *Procladius culiciformis*
        - *Chironomus plumosus*

ugh 60 m in 1963 and
dry weight in mg/l)

20	30	40	50	60
.17	1.11	1.07	1.17	1.26
74	0.69	0.76	0.57	1.23
72	1.75	1.68	1.78	1.97
06	0.69	0.65	0.72	1.16



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SURVEY

recovered during

Chironomus sp. (nr. *ferrugineovittatus*)
Polypedilum sp. (nr. *fallax*)
Polypedilum sp.
Paratendipes sp.
Glyptotendipes sp. (nr. *lobiferus*)
Cryptochironomus sp. (*Harnischia* group)
Cryptochironomus sp. (*defectus* group)
Calopsectra atridoreum
Calopsectra bausei
Hydrobaenus (*Eukiefferiella*) sp.
Hydrobaenus sp.
Ceratopogonidae
Trichoptera
Oecetis sp.
Crustacea
Mysidacea
Neomysis awatchensis
Amphipoda
Pontoporeia affinis
Annelida
Oligochaeta
Tubifex tubifex
Limnodrilus hoffmeisteri
Peloscolex variegatus
Ilyodrilus frantzi
Hirudinea
Helobdella stagnalis (and others)
Mollusca
Pelecypoda
Pisidium casertanum
Gastropoda
Gyraulus sp.

A number of other organisms were found which were too small to recover quantitatively. These include species of the Hydrozoa, Nematoda, Ostracoda, Turbellaria, and Acari.

This species list is probably nearly complete for the 10- to 65-meter zone for the whole of Lake Washington. A number of survey trips to other parts of the lake discovered no new organisms. However, the list might very well have doubled in size if the littoral had been extensively surveyed. The list of organisms found in 1963 and 1964 may very well include all of the organisms mentioned by Scheffer & Robinson in 1933 even after the process of artificial eutrophication. The fact that many more species were found in 1963 than in 1933 probably only indicates that many more samples were taken.

Of the organisms found, 2 groups were by far the most common, the Chironomidae and the Oligochaeta. The Amphipoda and the Sphaeriidae, the other 2 of the "four groups which represent the basic profundal fauna of most lakes" (Welsh, 1935), were present but in much smaller numbers.

CHIRONOMIDAE

About 45% of the total biomass of the study area was contributed by the Chironomidae. Thirteen species were found during the study. They included predators, deposit-feeders, and filter-feeders; they ranged in size from the 10 mg of a fully-grown *Chironomus plumosus* larva to the 0.06 mg of a fully-grown *Calopsectra bausei* larva.

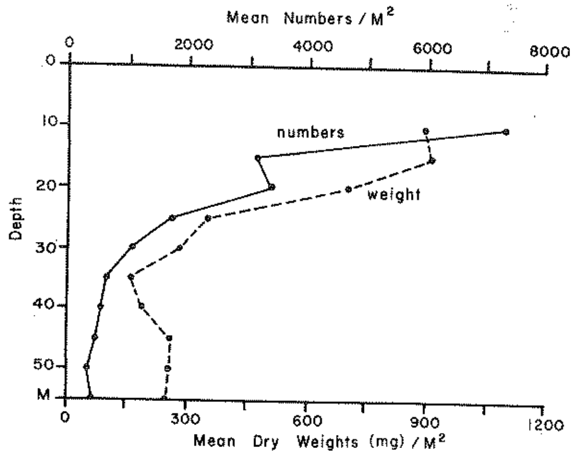


FIG. 4. Distribution with depth of mean numbers and of mean dry weights of Chironomidae.

The plot of the depth distribution of Chironomidae described a hyperbolic curve with the greatest numbers occurring at the shallowest depths (Fig. 4). The inverse correlation between numbers of Chironomidae and depth may be due to a number of factors, including competitive interaction with the Oligochaeta, whose greatest numbers were found at the deepest stations. However, one very important set of factors is derived from the limitations imposed by a life cycle which includes a terrestrial phase. Since mating occurs near the shoreline, a female must fly some distance if she wishes to deposit her eggs over deep water. Even if the eggs were deposited over deep water, their chances of being preyed upon should be greater the farther and the longer they must sink. A lifetime later, the same will hold true for the pupae the farther and the longer they must rise. Pupae constitute part of the diet of the pelagic *Spirinchus thaleichthys*, the long-fin smelt, which is very common in Lake Washington, and of the bottom-feeding *Cottus asper*.

The plot of the depth distribution of the biomass of the Chironomidae differed somewhat from the plot of numbers (Fig. 4). The occurrence of considerable numbers of the very large *Chironomus* sp. (nr. *ferrugineovittatus*) at depths of 40 to 55 m and *C. plumosus* at depths of 10 to 20 m accounted for the deflection of the curve to the right at these depths. As will be seen, the early instars were most often found in shallow water thus accounting for the small mean size at 10 m.

Each of the 13 species was tabulated separately. The numbers of each of the 4 larval instars typical of the Chironomidae and the number of pupae were determined. For some species, last instar larvae which are nearing pupation can be readily differentiated by their swollen thoracic segments and these were noted. The instars can be recognized by measuring the hard sclerotized head capsules. Whereas the soft body of the larva gradually increases in size as the animal grows, the hard parts can increase only at times of moulting when the exoskeleton is relatively soft. Thus each instar has a head capsule of characteristic size which does not grow through the duration of that instar. Further, the ratio of the size of the head capsule of one instar to the size of that of the succeeding instar is nearly constant. This conforms with the so-called Dyar's rule which is widely applicable in the Arthropoda. Practically any dimension or part of the head capsule can be measured for this purpose—head length and width and labium width have been most often used. In this study, the head length was measured. The range of head lengths of one instar is quite distinct from that of the succeeding instar. The ratios from one instar to the next are generally between 1.5 and 2.0 and thus the instar can be identified at a glance once a little experience is gained.

Procladius culiciformis

Procladius culiciformis is primarily predaceous; the larvae of this species have been reported to prey upon cladocerans, copepods, ostracods, tubificids, and other chironomid larvae. The digestive tracts of *P. culiciformis* were very often empty or nearly so in contrast to the tracts of the deposit-feeders which were invariably full. Much of the material found was of an amorphous character but many ostracods, cladocerans, a mite, and three chironomid larvae (third instars of both species of *Hydrobaenus* and of *Procladius* itself were found in fourth instar individuals) were also noted. They were also discovered in the process of feeding on large pieces of plant debris and on the cast skins of chironomid larvae.

Unlike most of the other Chironomidae, the larvae of *Procladius* do not construct mud-tubes but actively move about on the substrate searching for food. This was reflected for *P. culiciformis* in a number of ways. All of their food items are found on the surface of the substrate; they were the only chironomids frequently encountered in the stomachs of *Cottus asper* which feeds just over the bottom; lastly, they were one of only two chironomid species whose larvae were found in the open water. Fourth instars were found at a depth of 6 m in water 55 m deep.

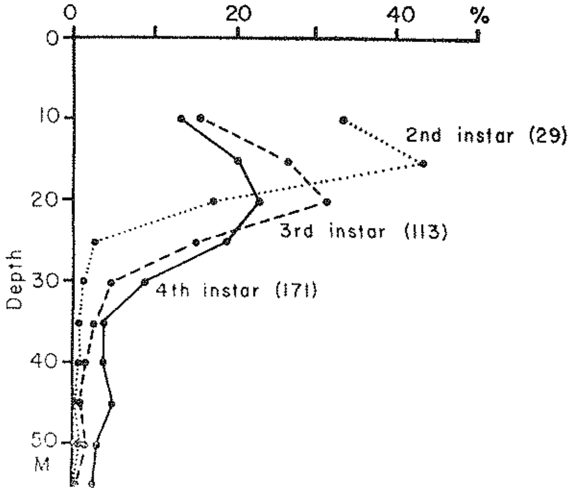
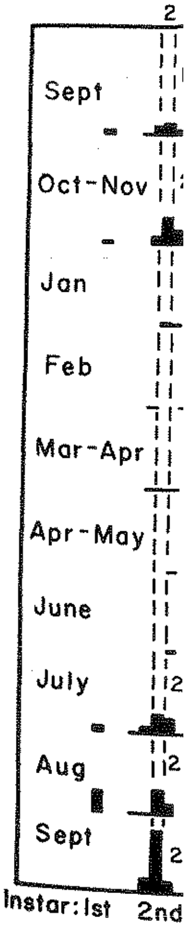


FIG. 5. Distribution with depth of the percentages of second, third, and fourth instars of *Procladius culiciformis*. To determine mean numbers per square meter, multiply the percentages by the numbers on the right-hand side of the figure.

The depth distribution of each of the instars of *Procladius culiciformis,* except the 1st which was recovered in very small numbers, is presented as the per cent of the total number found at each depth sampled (Fig. 5). *P. culiciformis* is seen to have been most abundant at 15 and 20 m but fairly common from 10 through 25 m and present at all depths. A larger percentage of the earlier instars was to be found in the 10- to 20-m zone than the later instars. All of the 1st instars were found between 10 and 20 m with a peak at 15 m. There appears to have been a progressive shift, albeit a subtle shift, to deeper water by this population. This shift can be demonstrated within a given instar as well. For example, the mean length of 4th instars on any given date was less at the shallower stations than at the deeper.

There are 2 possible ways in which this progressive shift could take place: either there is a net movement of larvae into deeper water or those at the greater depths have a lower mortality rate. As already mentioned, this species was taken from the open water with an Isaacs-Kidd midwater trawl indicating its mobility. However, only very large last instars nearing pupation or pupae were found. It is conceivable that the mesh size of the trawl was too large to capture anything smaller but this is unlikely as 3rd instars are only slightly smaller than the pupae. Rather, it would seem that these large-scale movements are associated with the emergence period. Further, other species showed this same shift and were not found in the open water. Small-scale movements in or just above the bottom could be responsible if there were some factors favoring those which moved into the deeper water. Otherwise one could assume that there was little significant movement but that those deposited in deeper water by the adult females fared better. Intraspecific competition could have been responsible in either case. Those animals deposited in shallow water would be surrounded by more members of the same species than those deposited in deeper water and hence at a disadvantage.

The time during which *Procladius culiciformis* emerged can be estimated by noting the numbers of pupae and of fourth instars nearing pupation (Fig. 6). Pupae were generally difficult to find owing to their short duration. A few were found from late March through early May on the bottom, and in April and June in the open water. Larvae nearing pupation were more often encountered and the pattern of emergence can best be derived by considering them. They accounted for 14% of the total number of 4th instars on the April-May sampling date; 20% in June; and 11% in July and August. A very few were found from January to April. Allowing 2 to 4 weeks for such larvae to reach the adult stage, the peak of emergence will be seen to have been from May through June and have continued to a lesser



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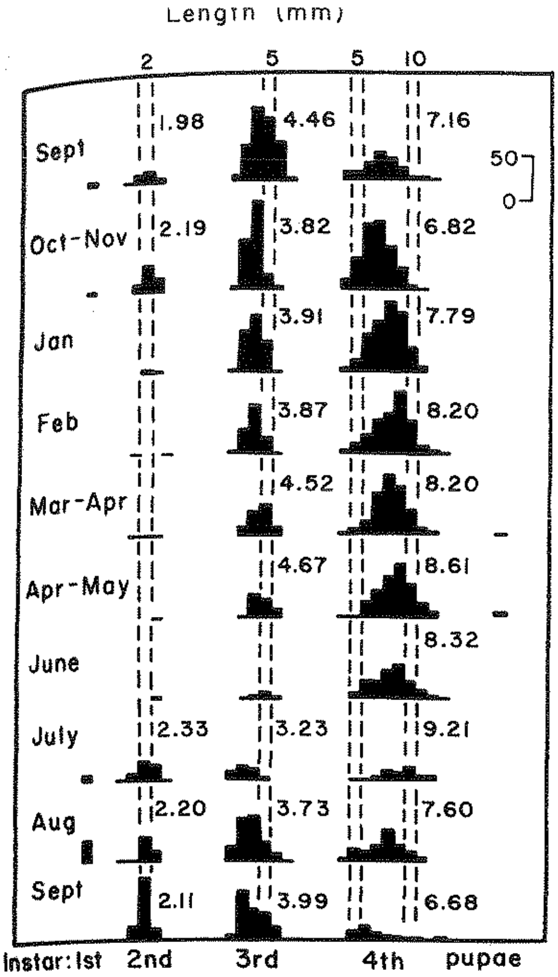

FIG. 6. Seasonal changes in instar and length frequency of *Procladius culiciformis*. Numbers to the right of instar histograms are the mean lengths for a given instar at a given sampling date. The numbers at the top of the figure and the vertical dashed lines designate the size of a length class, e.g., 5 means 5.0 to 5.9 mm.

degree into September. The number of last instars gradually decreased during this period. In July, there were a few very large last instars; in August, their numbers were supplemented by animals, hatched early in the breeding season, having recently left the 3rd instar stage (note the striking drop in mean length). 1st and 2nd instars appeared in fair numbers in July. 3rd instars were abundant in August and September and, generalizing from 1963, were gradually replaced by 4th instars which dominated the picture from November through June. In conclusion, it appears that *P. culiciformis* had one generation per year with an extended breeding season, March to September with a peak in May and June.

Those *P. culiciformis* taken from the open water were either pupae or very late 4th instars nearing pupation. The mean length of these larvae was considerably larger than the mean length of those on the bottom of any given date (Table 3). Although as

TABLE 3. Number of *Procladius culiciformis* and *Polypedilum* sp. (nr. *fallax*) recovered from the open water.[a]

Date	*P. culiciformis*			*P.* sp. (nr. *fallax*)		
	Time	No.	Mean Length	Time	No.	Mean Length
July, 1963	night-PM	1	12mm	aftern.	1	13mm
				night-PM	9	12.6
Aug.		0		aftern.	2	13.0
				night-PM	4	13.2
Sept.		0		aftern.	9	12.6
				night-PM	11	12.6
Oct.		0			0	
Nov.		0		night-AM	1	14.0
Dec.		0		night-PM	2	13.0
Jan., 1964		0			0	
Feb.		0			0	
Mar.		0			0	
Apr.	night-AM	0(+1)		night-AM	2	11.0
				morning	2	13.5
May	night-PM	6	10.3	morning	1	11.0
				night-PM	3	12.0
June	night-PM	1(+3)	11.0		0	
July	night-PM	1	9.0		0	

[a] Numbers in parentheses indicate pupae recovered. All larvae recovered were last instars.

many trawls were taken during the day as during the night, almost all the animals were recovered at night. It has been generally reported that emergence of chironomids is highest in the hours of darkness.

Chironomus spp.

The largest animals and the largest contributors to the total biomass of the bottom fauna were the 2 species of *Chironomus*. *C. plumosus* and *Chironomus* sp. (nr. *ferrugineovittatus*) are closely related; the only obvious difference is the presence of ventral blood gills in *C. plumosus* and their lack in *Chironomus* sp. *C. plumosus* attains a larger size (to 32 mm in Lake Washington) than *Chironomus* sp. (to 23 mm). Both species can function as filter-feeders, constructing a salivary net across the lumen of their

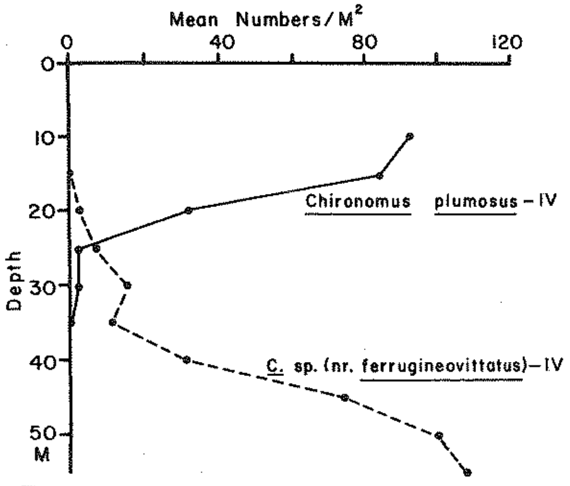

FIG. 7. Depth distribution of the fourth instars of *Chironomus* sp. (nr. *ferrugineovittatus*) and *C. plumosus*.

mud-tubes and undulating their bodies to create a current through the tubes. The net picks up suspended material from the overlying water and the net and its contents are eaten. At night, however, they may leave the tubes and feed on particulate matter lying on the bottom (personal communication, W. E. Cooper, Michigan State University). Only 2 specimens were recovered in the open water with the Isaacs-Kidd trawl.

Almost all of the last instars of *C. plumosus* were found between 10 and 20 m; it is quite likely that greater numbers were to be found at depths shallower than 10 m (Fig. 7). *Chironomus* sp. extended from the deepest station to about 20 m. These distributions suggest that competitive interactions may have been involved. *C. plumosus* has often been reported from deep water (Lake Simcoe, Plöner See) and, indeed, has been found at 60 m, with no trace of *Chironomous* sp., in Lake Washington (in 1962 and 1963 off Madison Park). Along the study transect, only 2 samples were taken in which both species occurred. The presence of the species without ventral blood gills in deep water to the exclusion of a species with them speaks poorly for the theory that maintains that these gills function in multiplying the surface area of the animal in order to facilitate gas exchange in oxygen-poor water.

Only the depth distributions of the last instars of these two species are presented. The earlier instars were to be found in small numbers and in a very clumped dispersion pattern. This was particularly true of *Chironomus* sp.; 115 of the 235 third instars recovered were found in just 2 samples and 74 of the 117 2nd instars in 2 others.

The small number recovered of early instars of *C. plumosus* makes the estimation of times of emergence and egg-laying difficult. The occurrence of pupae and of the largest-sized last instars throughout most of the sampling period suggest that emergence took place the year round (Fig. 8). This is further borne out by observations made in the field. The adults and pupae of this species are very conspicuous by their size and these were noted on the October-November and March-April sampling dates as well as during the spring and summer. Emergence during the winter months probably was not very great.

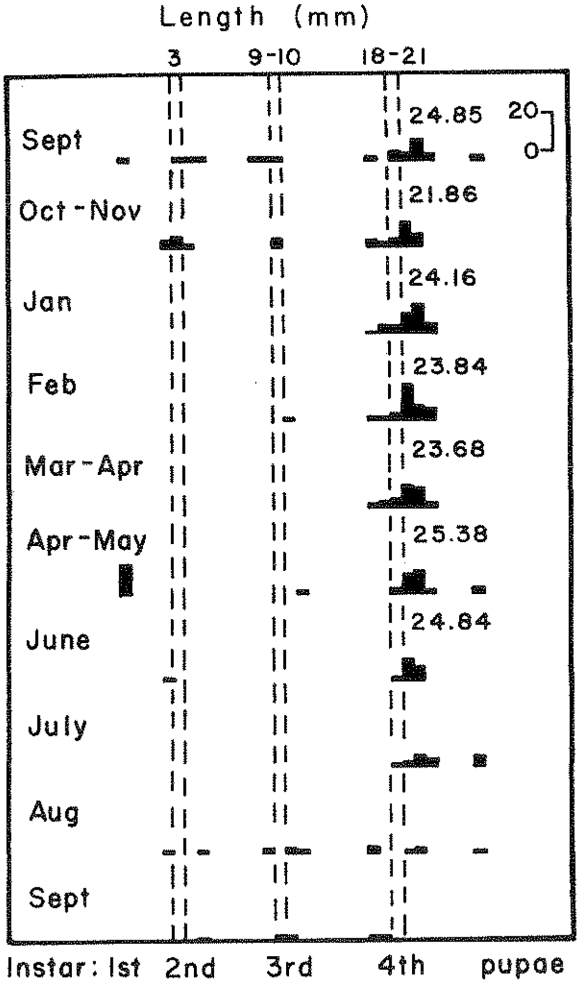

FIG. 8. Seasonal changes in instar and length frequency of *Chironomus plumosus*. Numbers to the right of histograms are the mean lengths for a given instar on a given sampling date.

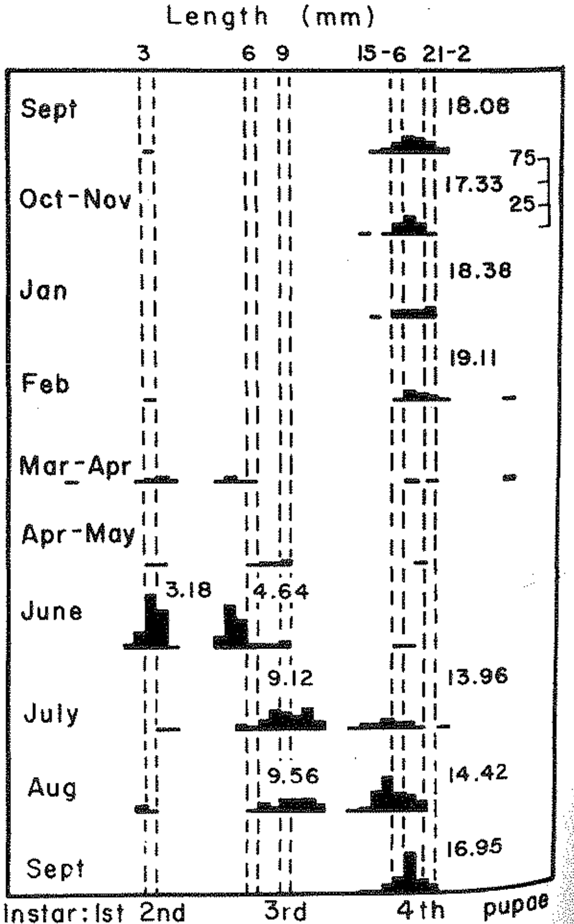

FIG. 9. Seasonal changes in instar and length frequency of *Chironomus* sp. (nr. *ferrugineovittatus*).

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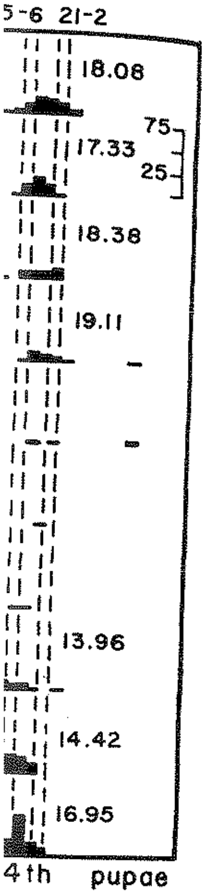

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ineovittatus).

Although few pupae were recovered, the emergence pattern for *Chironomus* sp. is fairly obvious (Fig. 9). During the period September through February, the number of 4th instars decreased while the mean length increased. A pupa was found in February and an adult noted in the field in January. By the end of March, last instars were virtually absent. In June, 2nd and 3rd instars were dominant; in July, 3rd instars; and, by August, the 4th instars were most common. It would appear then that *Chrinomus* sp. had a single generation per year and the breeding season extended from September through March.

Polypedilum spp.

The 2 species of the widespread genus *Polypedilum* were common along the study transect. Their considerable numbers and size made both of them important contributors to the total biomass. *Polypedilum* sp. (nr. *fallax*) was 1 of the 3 characteristic species encountered at the deep stations.

These 2 species construct mud-tubes which protrude a short distance above the surface of the substrate. Anchored by their posterior prolegs, they extend from these tubes and draw out salivary threads with their anterior prolegs. The animals return to their burrows and the threads are dragged over the surface of the mud and are eaten together with any particles which have adhered to them. The guts of *Polypedilum* were generally filled with black, amorphous material.

Although most abundant between 20 and 30 m, *Polypedilum* sp. (nr. *fallax*) occurred in considerable numbers at almost all depths in Lake Washington (Fig. 10). Although not indicated in Fig. 10, there was a tendency for the earlier instars of this species to be concentrated at the shallower depths. The distributions for the 2nd and 3rd instars were essentially the same with a definite peak at 20 m. The 4th instars were most abundant at 30 m. It would appear then that there was a considerable shift to deeper water after the 3rd instar. The distribution of *Polypedilum* sp. was nearly the same at all instar stages. The 2nd and 3rd instars were concentrated at 15 and 20 m; the 4th at 20 m. Both species were common between 15 and 30 m, however, only *Polypedilum* sp. (nr. *fallax*) was found in large numbers below 30 m. This was particularly true of the last instars of this species.

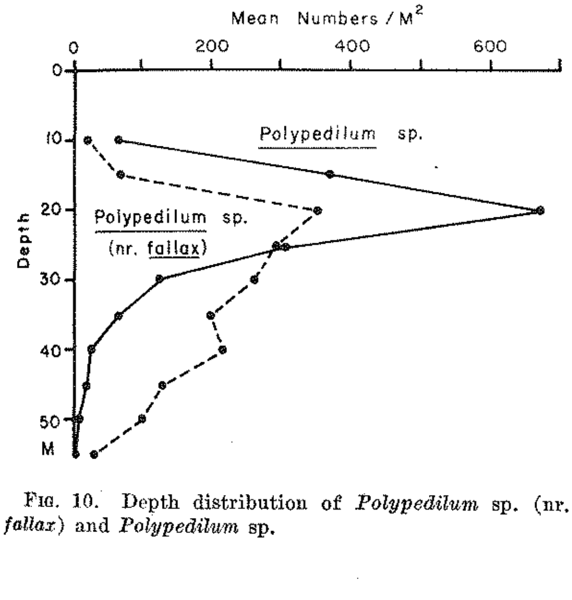

FIG. 10. Depth distribution of *Polypedilum* sp. (nr. *fallax*) and *Polypedilum* sp.

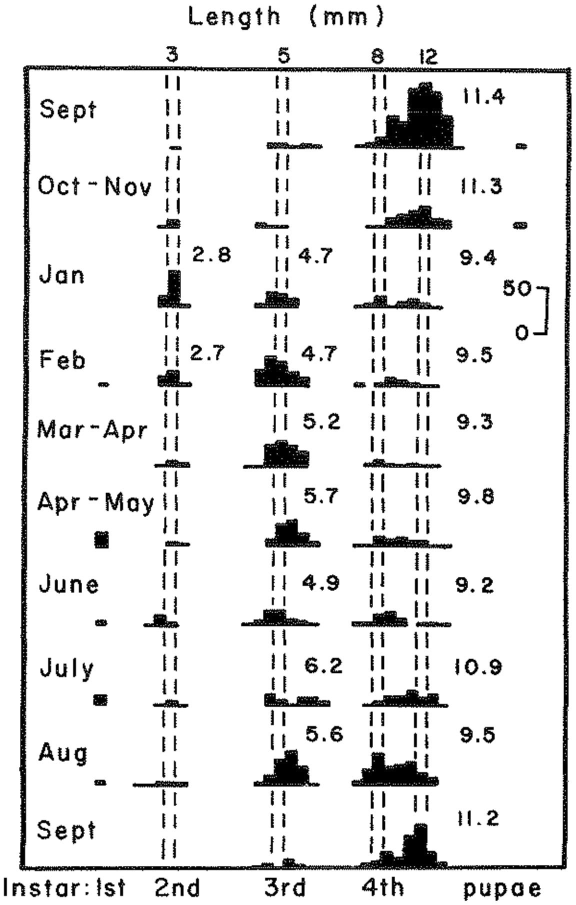

FIG. 11. Seasonal changes in instar and length frequency of *Polypedilum* sp. (nr. *fallax*). Numbers above and to the right of histograms are the mean lengths for a given instar on a given sampling date. For additional explanation, see Fig. 6.

There was a large population of late 4th instars of *Polypedilum* sp. (nr. *fallax*) in September of 1963; their numbers decreased rapidly thereafter (Fig. 11). Pupae were found on the September and October-November sampling dates only. In January, 2nd instars were dominant; in February, 3rd instars became dominant and continued to be so until June. By September of 1964, the population was in about the same situation as the previous September. Emergence appears to have occurred primarily from September to November. However, the presence of 1st instars and large last instars from February through August suggests emergence at a lesser level through this period as well.

Polypedilum sp. (nr. *fallax*) was the most commonly encountered chironomid in the open water (Table 3), especially in the summer (July to September). Like *Procladius culiciformis*, the larvae recovered were all last instars nearing pupation. Unlike *P. culiciformis*, larvae were captured by the trawl in the daylight hours but in only half the numbers captured at night. It has been suggested that chironomid larvae are passively brought into the open water by water currents. However, almost all of the larvae were taken from the open water when the lake was stratified and when mixing could not reach the depths at which most of the *Polypedilum* sp. (nr. *fallax*) larvae were found. *Polypedilum* sp. larvae were not recovered from the open water.

The second instars of *Polypedilum* sp. were dominant in September of 1963 but there was also a small population of very large fourth instars (Fig. 12). The dominant role shifted to the 3rd instars by the October-November sampling dates and remained as such until the April-May sampling dates. The 4th instars were most abundant thereafter. By September of 1964, a considerable number of 4th instars was still left but of a smaller size than in September of 1963; there were fewer second instars as well. The sequence of events seems to have been later in 1964.

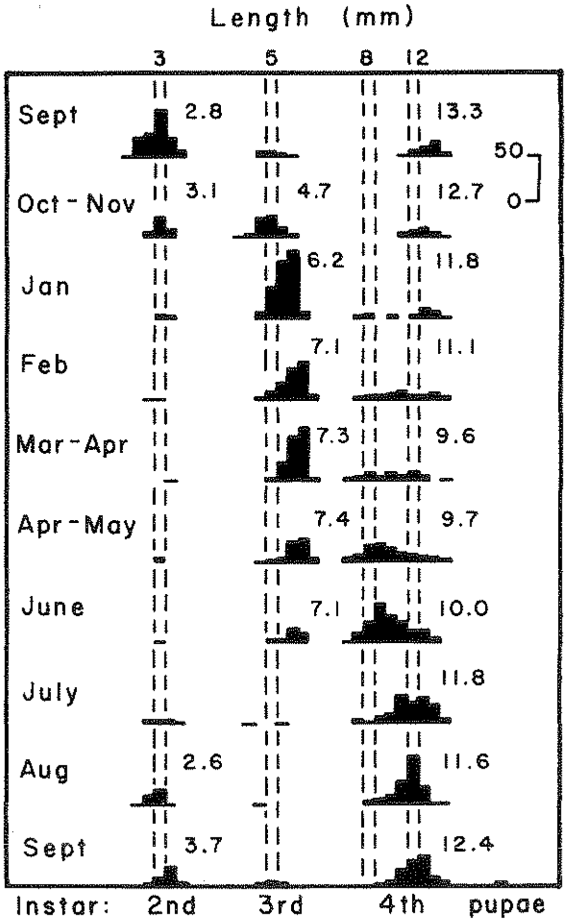

FIG. 12. Seasonal changes in instar and length frequency of *Polypedilum* sp.

Any estimation of the time of emergence is difficult as few pupae and no first instars were discovered. However, looking at the late 4th instars and at the 2nd instars, it might be guessed that emergence occurred at the greatest levels from June through October. The presence of 2nd instars throughout the sampling period suggests that emergence took place the year round although at a lesser rate in the winter and spring.

Glyptotendipes sp. (nr. *lobiferus*)

Glyptotendipes sp. occurred in shallow water only, but in enormous numbers—up to 2,650 fourth instars/m² and up to 19,300 third instars/m². This species generally accounted for more than half of the total number of organisms at the 10-meter station. *G. lobiferus* is a versatile species; it can function as a leaf-miner on aquatic plants or can live in a loose mud burrow from which it extends and col-

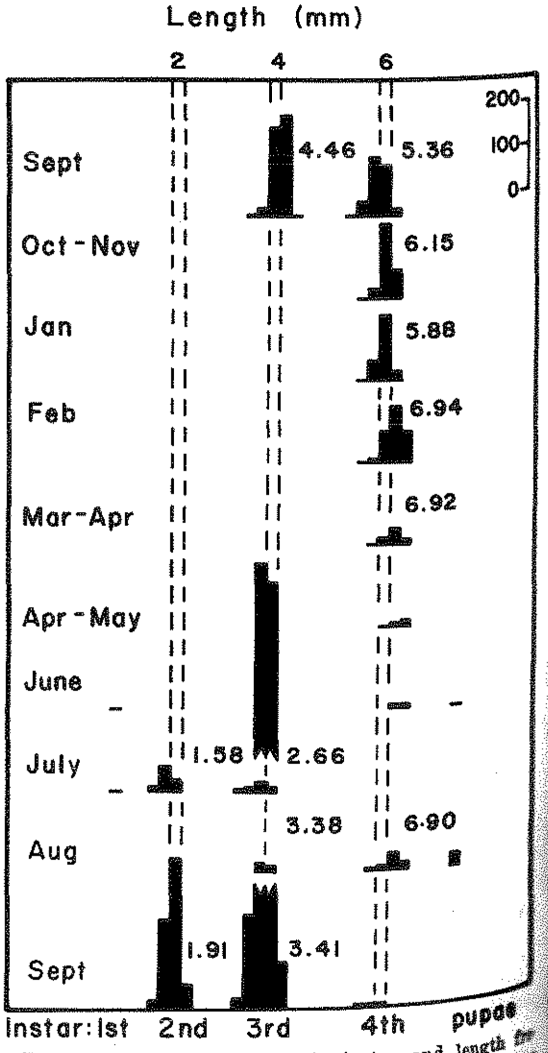

FIG. 13. Seasonal changes in instar and length frequency of *Glyptotendipes* sp. (nr. *lobiferus*). Numbers to the right of histograms are the mean lengths for a given instar on a given sampling date.

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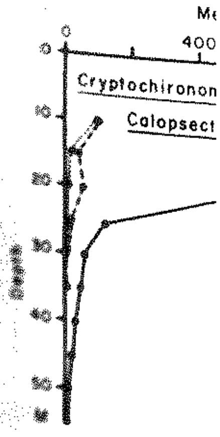

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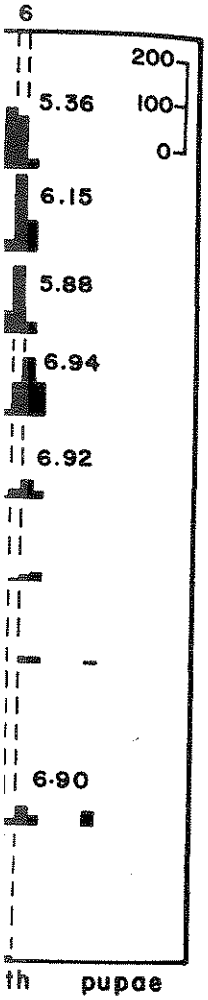

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lects detritus from the surface of the substrate. The species in Lake Washington behaves in this latter way.

Species of *Glyptotendipes* are typically shallow-water forms owing in part to a low tolerance for low oxygen concentrations. In Lake Washington, they averaged 4,431/m² at 10 m and 211/m² at 15 m—only 2 animals were taken at the greater depths. It is probable that their numbers in water shallower than 10 m were also very high.

In September of 1963, there were large numbers of both 3rd and 4th instars; by November, only 4th instars were found (Fig. 13). These gradually grew larger in size and became fewer in number; by May, they were virtually absent. This gradual disappearance of 4th instars suggests that the highest rates of emergence occurred from February through April. From April through June, *Glyptotendipes* sp. was very scarce. In July, they made an appearance; in August, there was a sudden shift to 3rd and 4th instars and pupae. In September of 1964, enormous numbers of early instars appeared, contrasting with the previous September.

The above suggests that this species had 2 generations per year. One emerged from February through April and gave rise to another which completed development in only a few months owing to the relatively warm temperatures that prevailed in the summer at the shallow depths at which *Glyptotendipes* sp. occurred. This summer generation then gave rise to the generation which appeared as early instars in September and emerged the following winter and spring.

Cryptochironomus spp.

Cryptochironomus sp. (*Harnischia* group) was infrequently encountered. The larvae are very small, seldom exceeding 4 mm in length. They were only found at the 10- and 15-meter stations but it is likely that larger numbers occurred in the shallow sublittoral. Unlike the other chironomids, the 4th instars were the most difficult to find. There is a suggestion that the earlier instars were distributed a little deeper than the later; 73% of the 2nd instars, 76% of the 3rd, and 94% of the 4th were found at 10 m. It is possible then that larger numbers of the last instars were to be found in water shallower than 10 m. Too few animals were recovered to get a consistent life history pattern.

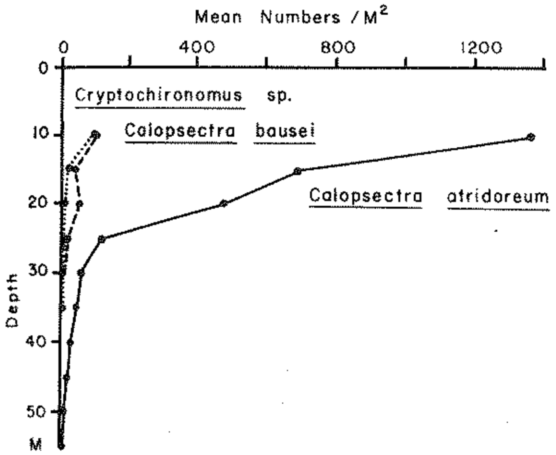

FIG. 14. Depth distributions of *Cryptochironomus* sp. (*defectus* group), *Calopsectra atridoreum*, and *Calopsectra bausei*.

Cryptochironomus sp. (*defectus* group) is totally unlike the above; it is large (up to 14 mm) and is the other chironomid predator in Lake Washington. It has been reported to feed upon the same kinds of things as *Procladius*. Like *Procladius*, the digestive tracts were generally empty or nearly so. It was found in about the same numbers and had about the same depth distribution as the other species of *Cryptochironomus* (Fig. 14).

Calopsectra spp.

Calopsectra atridoreum was very abundant at some times of the year in the shallow-water areas. It is a medium-sized animal; the larvae reach a length of 8 mm. They construct rambling mud-tubes of con-

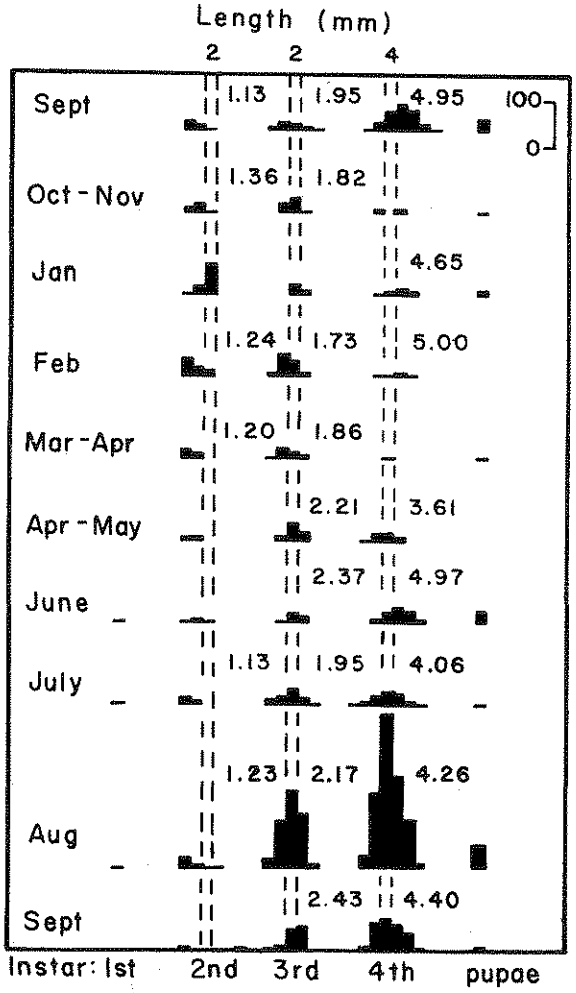

FIG. 15. Seasonal changes in instar and length frequency of *Calopsectra atridoreum*.

siderable length on or immediately below the surface and feed on the material that has settled there.

The largest numbers of this species occurred at 10 m, but there were considerable numbers at 15 and 20 m as well (Fig. 14). There was a tendency for the 4th instars to be concentrated in water slightly deeper than the earlier instars. The life history data do not reveal a very consistent pattern (Fig. 15). Pupae were found on practically every sampling date indicating that emergence took place to some extent throughout the year. 4th instars were most abundant in the summer (June through September) and emerging adults were probably most abundant at this time as well. Like *Glyptotendipes* sp., there was a sampling date, this time August, when an anomalous number of larvae suddenly appeared. These large numbers were found at 10 and 15 m. The only answer would appear to be a large-scale migration of larvae from the shallow sublittoral to these depths.

Calopsectra bausei was the smallest (only up to 3 mm) and one of the least common species taken along the transect. This species is unusual among the Chironomidae in that it lives in a portable case made of sand grains much like certain caddis larvae. It carries this case along while moving on the surface of the substrate feeding on the material that has settled there.

C. bausei was another shallow-water form with its greatest numbers at the 10-meter station; it was found in small numbers down to 25 m (Fig. 14). The last instars tended to be concentrated at greater depths than the 3rd instars. Too few animals were recovered to get a consistent life history pattern, however, data for the 4th instars and pupae suggest an emergence peak in August and September and only a single generation per year. 3rd instars were most common through a good part of the year.

Hydrobaenus spp.

The genus *Hydrobaenus,* although large and diverse, is largely unknown. The larvae of this genus are probably herbivores which burrow into the superficial layers of the mud and feed on the surface; they do not construct mud-tubes. Examinations of the stomach contents of individuals of the 2 species in Lake Washington revealed the same dark organic material found in the other deposit-feeders. *H.* (*Eukiefferiella*) sp. was also discovered feeding on periphyton in very shallow water. The periphyton was growing on glass slides suspended at some distance from the bottom, thus the larvae must be fairly mobile.

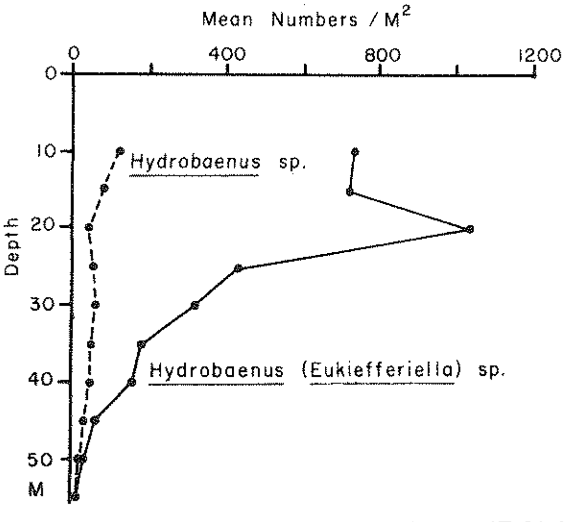

FIG. 16. Depth distribution of *Hydrobaenus* (*Eukiefferiella*) sp. and *Hydrobaenus* sp.

H. (*Eukiefferiella*) sp. was one of the more common chironomids in Lake Washington. The larvae are medium-sized (up to 8 mm). Like so many of the other chironomids, this species was found in the largest numbers at 20 m (Fig. 16); it was quite common at 10 and 15 m and in fair numbers down to 40 m. The 2nd instars were most common at 15 and 20 m and the 3rd and 4th instars at 20 m.

The life history data indicate 2 peaks of emergence—in September through October and in April (Fig. 17). On these dates, the pupae were common and the last instars had attained their largest size.

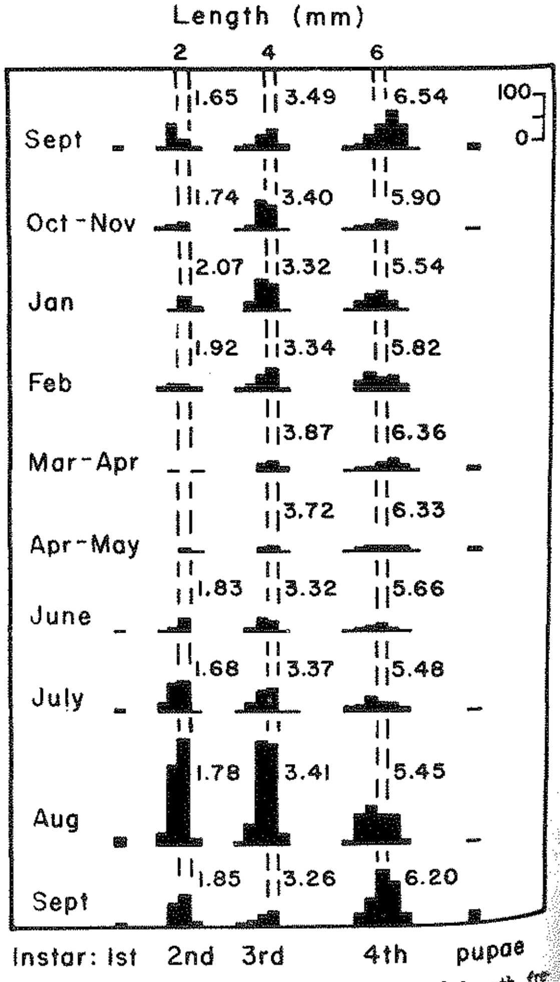

FIG. 17. Seasonal changes in instar and length frequency of *Hydrobaenus* (*Eukiefferiella*) sp.

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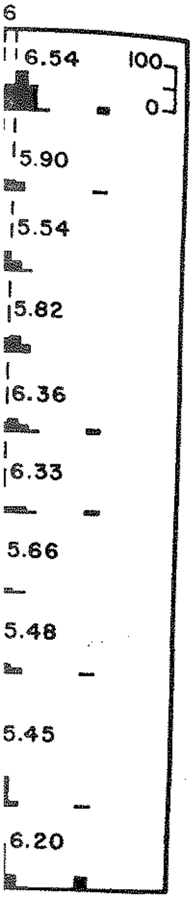

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However, pupae and early instars were found throughout the year and emergence probably occurred to some extent the year round. The 2 emergence peaks may be indicative of 2 generations per year but emergence and hatching were apparently so poorly synchronized that one cannot be sure on this point.

The larvae of *Hydrobaenus* sp. are large (up to 16 mm) and were found in moderate numbers along the transect. This species of *Hydrobaenus* is quite unlike the other, especially as regards its size and the structure of its mouthparts. *Hydrobaenus* sp. was found from 10 to 55 m but was somewhat more abundant in shallow water (Fig. 16). However, there was a distinct notch at 20 m, especially for the 4th instars. This is the same depth at which so many chironomid species reached their maximum numbers, including *H.* (*Eukiefferiella*) sp. There was a considerable shift away from the 20- and 25-meter stations by the 4th instars. There were too few of this species recovered to derive a consistent life history pattern. Emergence did appear to be heaviest in the autumn and the large size of the larvae and their prevalence in the cooler water of the hypolimnion would suggest that this species had only 1 generation per year.

Only 2 or 3 specimens of *Paratendipes* sp. were recovered; the same was true for the family Ceratopogonidae.

Oecetis sp. was found in small numbers at the 10-meter station. Caddis larvae are generally found in the littoral and sublittoral and the few recovered probably represented only a small part of a much larger population.

NEOMYSIS AWATCHENSIS

A few specimens of *Neomysis awatchensis* were collected with the Ekman dredge. The Mysidacea are only temporary members of the benthic community. During the day, they live in the meter or so of water immediately above the bottom or on the bottom itself; at night, they become a part of the plankton. Mysids comprised a considerable portion of the diet of the bottom-feeding fish, *Cottus asper*.

PONTOPOREIA AFFINIS

Another animal which frequents both the open water and the bottom is *Pontoporeia affinis*. This was recovered in fair numbers by dredging. This animal has been studied in Lake Washington by Waldron (1953); the study is primarily morphological but life history data are presented. Unlike the majority of amphipods, *P. affinis* is characteristically found in the profundal zone of deep, cold lakes. It has been found as deep at 300 m in Lake Superior. When on the bottom, they feed on the flocculent material on the mud surface. Their only important predators are fish; a few were found in the stomachs of *Cottus asper*.

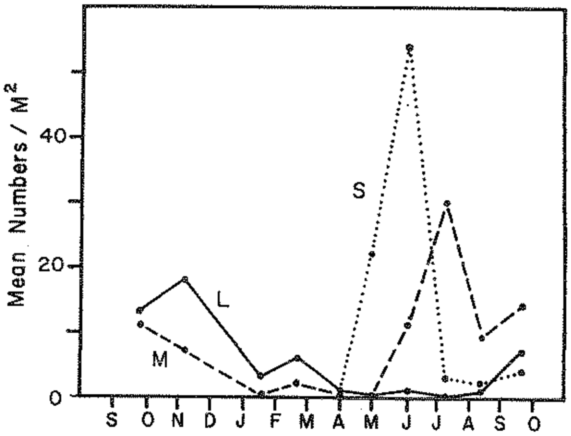

FIG. 18. Seasonal changes in numbers of three size classes of *Pontoporeia affinis*.

In the study of Waldron, gravid females were found from January through June. Young were released from March through July with a peak in early June. He concluded that the life span of *P. affinis* in Lake Washington is shorter than in the typical North American lake, one year instead of two, and that the mature animals die after producing one brood of young.

As a study on the life history of *Pontoporeia affinis* had already been made, little effort was expended in this direction. The animals were counted and placed into 3 subjective categories: large, medium, and small (Fig. 18). Large animals were dominant from September of 1963 to April; their numbers gradually decreased during this time reflecting post-reproductive mortality. As indicated by the number of small individuals, release of the young occurred from April through July with a peak early in June just as Waldron had concluded. The medium-sized category peaked in July and the number of large individuals began to climb in September. There is no indication that the animals survived for more than a year. The depth distribution of *P. affinis* showed two obvious

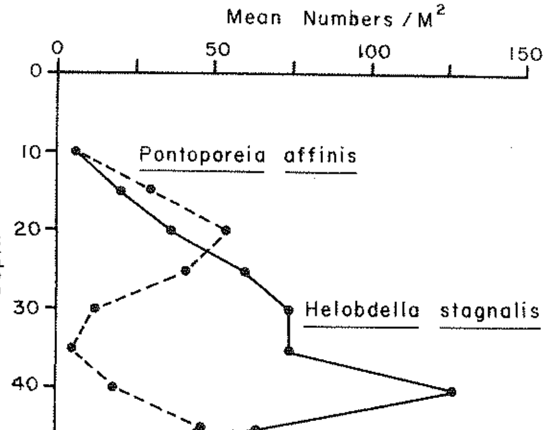

FIG. 19. Depth distributions of *Pontoporiea affinis* and *Helobdella stagnalis*.

zones of concentration: at 15 to 25 m and at 45 m (Fig. 19).

GYRAULUS SP.

The molluscs constituted only about 11% of the total biomass of the bottom fauna of Lake Washington. This contrasts with many other lakes where a considerable percentage of the total biomass may be tied up in the form of large bivalves.

The Gastropoda are more typical of small lakes and the littoral region than of the area in this study. However, fairly large numbers of the planorbid, *Gyraulus* sp., were encountered at the deeper stations. There is some precedence for this; Planorbidae have been taken from some of the deep Eurasian lakes at depths of 40 to 350 m. They are generally associated with hard substrates or emergent vegetation where they graze on the attached "Aufwuchs" and, in the latter case, on the plant tissues themselves. On the soft sediments in Lake Washington, the snails glide on the surface ingesting the seston which has settled there. Their principal predators are generally fish. Leeches probably account for some small percentage of the predatory mortality.

The freshwater Gastropoda are hermaphroditic and reproduce either by cross- or self-fertilization. The fertilized eggs are attached in a mass to some hard substrate. The paucity of such substrates in the profundal zone of Lake Washington leads them to seek out small scraps of wood, pieces of cellophane, or, most often, each other. Most egg masses were found on either the occupied or unoccupied shell of some snail. The average number of eggs per mass was about 10 with a range of 4 to 21.

Gyraulus sp. showed a marked concentration zone between 45 and 55 m (Fig. 20). The only other mollusc found, the bivalve *Pisidium casertanum*, exhibited a similar distribution pattern.

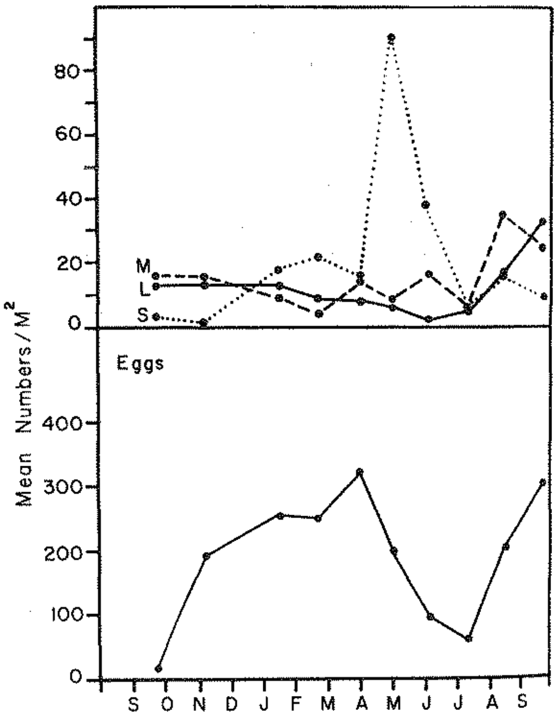

FIG. 21. Seasonal changes in numbers of three size classes of *Gyraulus* sp. and of the eggs of *Gyraulus* sp.

The specimens recovered were counted and subjectively classified into 3 categories: large, medium, and small. The number of eggs was also determined (Fig. 21). The large animals showed a steady decrease in numbers from September of 1963 through June. The medium-sized individuals showed a similar decrease through February. This general decline was probably due, in large part, to post-reproductive mortality—egg-laying was maximal during this period. While the numbers in the 2 larger categories were decreasing, the number of small animals was markedly increasing. By February, the medium-sized category, reflecting the effects of growth from the small class, showed slight gains. By July, small specimens were scarce. A month later, the bulk of this new generation was medium-sized. In September, large individuals showed signs of dominating as medium-sized ones began to decline.

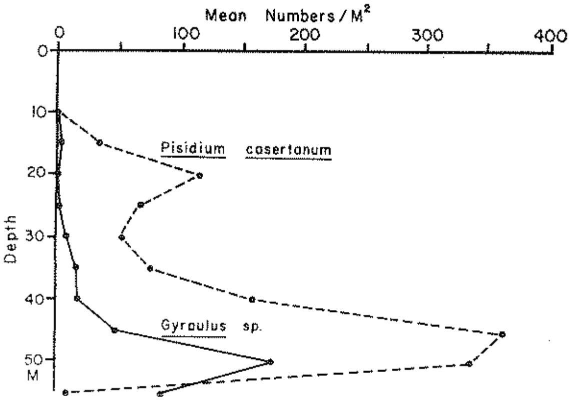

FIG. 20. Depth distributions of *Gyraulus* sp. and *Pisidium casertanum.*

The egg counts reveal that reproduction occurred the year round. The number of eggs found per m² corresponded fairly well with the appearance of small animals, preceding the inflections for these by about a month. *Gyraulus* sp. appears to have had a single generation per year, although individuals were beginning their life cycles throughout the year. There was a 2nd peak of egg production in September of 1964. There was a considerable difference between the 2 September dates, especially in the number of large animals and eggs. The dissolved oxygen concentration, particularly of the deeper water, was substantially lower in 1963 than in 1964.

PISIDIUM CASERTANUM

In many lakes, the Pelecypoda contribute the major portion of the total benthic biomass, especially in the form of large mussels. In the sublittoral of Esrom Lake, the live weight of *Dreissensia polymorpha* reached as high as 11 kg/m² or 99.8% of the total biomass (Berg, 1938). In Lake Washington,

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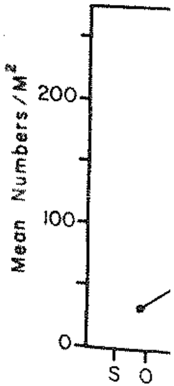

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however, there appears to have been only a single small species in the study area, *Pisidium casertanum,* which contributed little to the total biomass, 2 to 3%. *P. casertanum* is a ubiquitous species which exhibits a number of varieties. According to H. B. Herrington (pers. comm.), the variety in Lake Washington is one of the "short forms." He also noted that this species has been reported to exhibit considerable variation in dimensions within the same lake with "shorter forms" being found in deeper water. A cursory look at the Lake Washington specimens gave no indication of this.

Pisidium belongs to the family Sphaeriidae, members of which are often represented in the profundal zone of lakes. These animals live in the superficial layers of the bottom where they filter particles from the overlying water. They have a unique mode of reproduction, producing very few young at a time and carrying these until they reach a considerable size and of the adult form in a marsupium formed by the inner gill.

P. casertanum was most abundant at 45 and 50 m with a subsidiary peak at 20 m (Fig. 20).

Each of the specimens recovered was measured to the nearest tenth of a millimeter. The number of young in the marsupia and their length were also determined.

Marsupial clams were found throughout most of the year; their numbers were lowest in the late spring and early summer (Fig. 22). The counts for the 2 September dates contrast sharply with the much higher values of 1964 recalling the situation for *Gyraulus* sp. This difference appears to have been due to a higher fecundity at this later date. The numbers of adult clams recovered on these 2 dates were similar—97 in September of 1963 and 138 in September of 1964. However, the percentage contributed by individuals of a size 2.0 mm or more—the smallest individual found bearing young was 2.0 mm—was 16% in September, 1963 and 34% the following September.

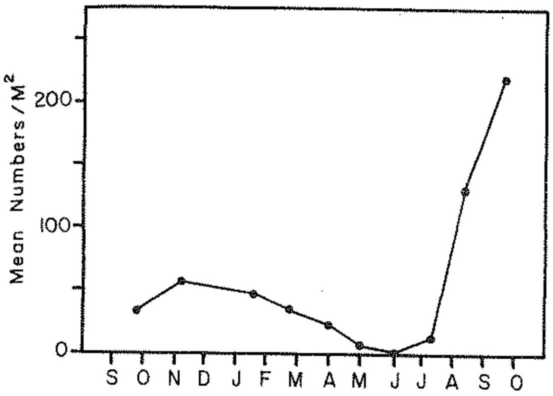

FIG. 22. Seasonal changes in numbers of marsupial clams of *Pisidium casertanum.*

The larger the size of a specimen of *P. casertanum,* the more likely it was to be carrying embryos. Only 2% of the individuals 2.0 mm in length bore embryos whereas 30 to 33% of those between 3.0 and 3.6 mm—the maximum size attained—bore embryos. Embryos were discovered as large as 1.2 mm. There must be a considerable latitude in the size at which embryos are released as animals were found free which were only 0.6 mm and 0.8 mm individuals were quite common. As many as 25 embryos were found in a single marsupium with an average of 8.

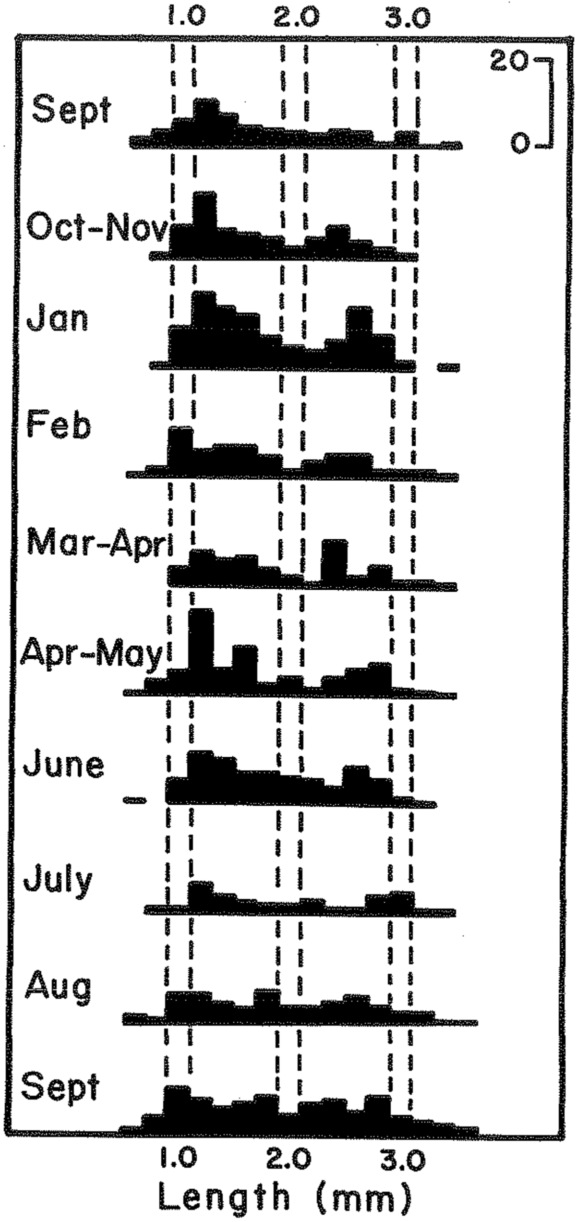

FIG. 23. Seasonal changes in length frequency of *Pisidium casertanum.*

The numbers of *P. casertanum* remained fairly constant throughout the sampling period, exhibiting no apparent trend (Fig. 23). The histograms demonstrate a marked tendency toward a bimodal distribution. This is especially marked for the earlier sampling dates. This same tendency was noted in the study of Foster (1932) for *Sphaerium solidulum,* a related species. He was able to attribute the bimodality to the existence of two periods of accelerated reproduction in each year. This was ascertained both by counts of marsupial young and by noting the presence of 2 distinct size classes of young in most of the marsupia. Neither circumstance occurred in the Lake Washington population.

Probability paper was utilized to facilitate the interpretation of these distributions (see Harding, 1949 and Cassie, 1950). This procedure removes some of the subjectivity involved in deciding what constitutes a distinct sub-population.

From September through January, there were 2 sub-populations of mean size, 1.4 mm and 2.5 to 2.7 mm. In February, a 3rd sub-population became evident formed by the splitting of the smaller into 1.0 to 1.2 mm and 1.5 to 1.6 mm components. This situation remained through the April-May sampling date. During this period, the largest-sized sub-population remained at about the same mean length but increased from 20% of the total population to 36%. In June, there was a considerable shuffling of the population, probably reflecting the absence of any number of young to supplement it. There were three sub-populations of mean sizes, 1.3 mm, 2.1 mm, and 2.7 mm. The first 2 gradually decreased to means of 1.0 mm and 1.6 mm. This coincided with the increase in the number of marsupial young.

OLIGOCHAETA

The Oligochaeta was an important component of the lake benthos. About one-half of the total number of organisms and about 1/3 of the total biomass were contributed by the Oligochaeta. Only 4 species have been recognized from Lake Washington: *Tubifex tubifex, Limnodrilus hoffmeisteri, Peloscolex variegatus* and *Ilyodrilus frantzi*—all members of the family, Tubificidae. This species list for the Oligochaeta should not be considered complete. 33 species have been reported from Lago Maggiore (Brinkhurst, 1963) and 22 from Esrom Lake (Berg, 1938). Most certainly more detailed collections and identifications for Lake Washington would turn up similar numbers.

Both *T. tubifex* and *L. hoffmeisteri* are very common species, especially abundant in eutrophic or organically polluted lakes where the water may be oxygen-depleted. *T. tubifex* is generally found in fringe habitats, in very clean or grossly polluted water (Brinkhurst, pers. comm.). In lakes, it is found at all depths and in all tpes of substrata. *L. hoffmeisteri* is found in all kinds of aquatic habitats; in lakes, it is frequently restricted to the littoral and sublittoral. The other 2 species, *P. variegatus* and *I. frantzi,* are very rarely encountered. *P. variegatus* has been reported on only 2 other occasions: in 1852, it was found in the Philadelphia area—and designated as the type for the genus *Peloscolex*—and, more recently, in the Great Lakes. *I. frantzi* had previously been reported only from Lake Tahoe and San Francisco Bay in California.

Aquatic oligochaetes, like their terrestrial counterparts, ingest indiscriminately all the particles composing the sediment below a certain limiting size and digest some fraction of these particles. Most of their feeding is done at a depth of 2 or 3 cm under the surface of the sediment. Bacteria are believed to be their primary food source.

The aquatic oligochaetes are capable of both sexual and asexual reproduction. This latter process is accomplished by budding and is not commonly found among the Tubificidae. The Oligochaeta are hermaphroditic and generally engage in cross-fertilization. The fertilized eggs are placed in a cocoon and the young emerge some time afterward. Stephenson (1930) reported that *Tubifex* requires 10 to 20 days to complete development, but at low temperatures such as are found in the hypolimnion of Lake Washington, may take much longer.

Due to the difficulty of distinguishing one species of Oligochaeta from another, they were dealt with as a group. For each sample, the oligochaetes were counted, their dry weight determined, and the number of eggs in cocoons counted. There appeared to be 3 morphologically different kinds of cocoons, each with a characteristic number of eggs, 2, 3, and 4. These are about half the values given for the Tubificidae in other reports; Stephenson states that 4 to 9 is typical.

The depth distribution curves of numbers and dry weight for the Oligochaeta were essentially the same, hyperbolic with the largest values occurring at the greatest depth (Fig. 24). This kind of depth distribution for the oligochaetes is typical of medium-deep lakes provided there is not a period of oxygen depletion in the deeper water. In very deep lakes or in shallow ones, there is generally a maximum at some intermediate depth. The relation to depth of the Oligochaeta was almost directly opposite to that of the Chironomidae, the other important group of animals in the Lake Washington benthos.

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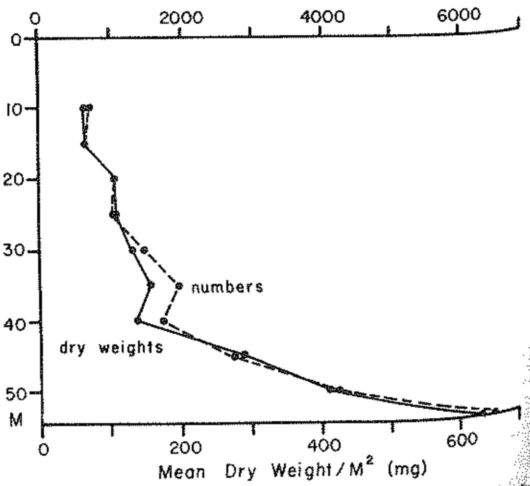

FIG. 24. Distribution with depth of mean numbers and of mean dry weights of the Oligochaeta.

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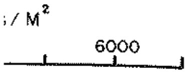

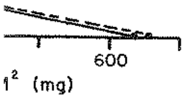

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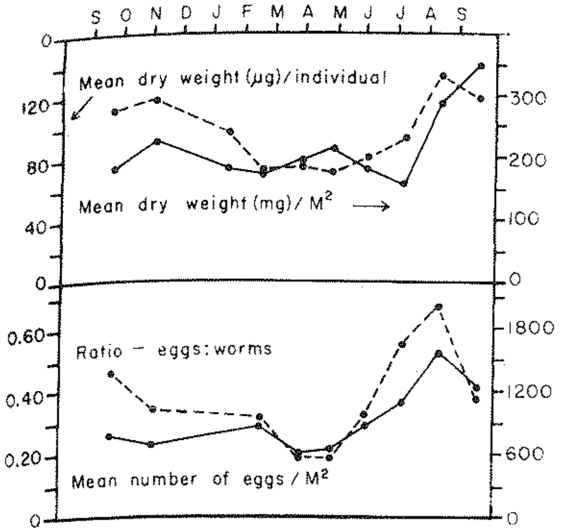

FIG. 25. Seasonal changes in mean dry weight/individual, mean dry weight/m², mean number of eggs/m², and ratio of eggs to worms.

117 μg on the October-November sampling date to around 70 μg in the winter and early spring (Fig. 25A). The mean weight then steadily increased to 133 μg in August. The value for September of 1964 was very near that of September of 1963, 118 and 110 μg, respectively.

The ratios of eggs to worms described a curve similar to the above (Fig. 25B). The ratio dropped from 0.458 in September to around 0.190 in the early spring and then rose to 0.671 in August. The hatching of large numbers of small worms in the summer together with the post-reproductive mortality of the adults accounted for the diminution of the mean weight in the autumn and winter. Sexual reproduction occurred throughout the year although it was considerably higher in the summer. The various species of Oligochaeta in Lake Washington probably had one generation per year with the dominant species reproducing primarily in the summer.

HELOBDELLA STAGNALIS

Two or three species of Hirudinea belonging to the family Glossiphoniidae were encountered in this study but only one, *Helobdella stagnalis,* was at all common. It comprised about 95% of the total leech fauna and will be the only one considered in detail.

H. stagnalis is perhaps the most common leech in the world. It occurs in a wide variety of habitats, including polluted waters, and is known to survive at low temperatures and at low oxygen concentrations. It functions as a scavenger or predator, feeding primarily on snails, especially the Planorbidae, and chironomid larvae. Hilsenhoff (1963) reported on laboratory experiments in which *Helobdella stagnalis* fed upon *Chironomus plumosus*. He concluded that *H. stagnalis* exerts a considerable influence on *C. plumosus* populations in any lake where both occur. In examining the material from Lake Washington, only 1 specimen of *H. stagnalis* was arrested in the act of feeding, a small individual feeding on an ostracod, but the gut contents of many specimens were of a dark red color which Hilsenhoff considered to be the presence of haemoglobin from the *Chironomus*.

The Glossiphoniidae have an unusual mode of reproduction where, after cross-fertilization, the eggs are carried in membranous capsules on the ventral surface of the body. After hatching the young attach to the venter of the parent by means of their suckers and, subsequently, let go. These leeches may have 2 generations per year depending on the temperature.

H. stagnalis had a very definite maximum at 40 m and occurred in relatively large numbers from 20 to 45 m (Fig. 19). This contrasts with the depth distributions reported for the Hirudinea in almost all other studies. Generally, leeches are found in the shallow littoral associated with emergent vegetation. They have been found in rare instances in small numbers down to 15 m (in Lake Erie) and isolated individuals have been recovered at depths of up to 50 m. Although this species is known to be capable of surviving at the low oxygen levels and low temperatures encountered in the hypolimnion of Lake Washington, there would seem to be some difficulty in moving about and searching out prey. Their usual mode of locomotion is by inchworm movements accomplished by alternate use of the oral and caudal suckers on some hard substrate. They are capable of only weak swimming movements.

The specimens of *H. stagnalis* were subjectively

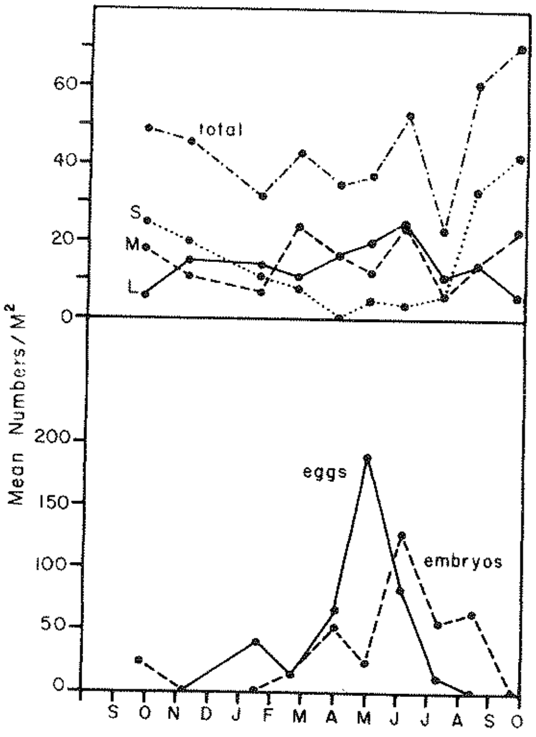

FIG. 26. Seasonal changes in numbers of 3 size classes of *Helobdella stagnalis* and of numbers of eggs and embryos.

classified into 3 size categories: large, medium, and small. These were enumerated as well as the numbers of eggs or young borne by adults (Fig. 26). These data suggest that *H. stagnalis* took one year to complete its life cycle. In September of 1963, small animals dominated. These gradually gave rise to medium and large individuals with the large ones dominating from April through July. Beginning in January, egg-bearing individuals were present; they achieved their largest numbers in early May. Adults bearing young animals appeared somewhat later, February, and reached a peak in June. Coincident with this, the number of small individuals rose—beginning in July—such that they again dominated the total population in September. In June, the number of large adults began to decline indicating the reported mortality of post-reproductive adults. The mean number of young borne by adults was 14.5 with a range of 6 to 36.

DISCUSSION

Although the effect of artificial eutrophication on the productivity of the benthos of Lake Washington cannot be assessed on the basis of the collections made in the restricted time period covered by this study, comparisons drawn to other lakes, especially those of similar morphometry, can provide the basis for some calculated guesses. If such comparisons are to be meaningful, the methods utilized in the studies must be similar and such differences as exist must be noted and their effects considered. One commonly disregarded limitation to comparing benthic studies arises from the use of different-sized screens in washing the bottom samples. Considerable differences in the retentive capabilities of screens of larger and smaller aperture sizes for early instars of insects and for small invertebrates of all kinds have been demonstrated. For example, Lauer (1963) showed that 2.5 times as many 1 and 2 mm *Pelopia* larvae were retained by a screen of 0.20 mm gauge than by one of 0.57 mm gauge. Comparisons drawn on a strictly numerical basis will be valid only if the screens used are of comparable mesh size. However, due to the small increment contributed to the total biomass by very small organisms, comparisons on a weight basis should be worthwhile regardless of the screens used.

Measures of biomass have been made on both a dry and a wet weight basis; the latter has been slightly the more popular owing to the relative ease with which it can be accomplished. The organisms are merely blotted on absorbent paper and weighed. The difficulty arises with this technique that the amount of water retained by the organisms will vary depending on a large number of factors. Consequently, the dry-weight technique, where the organisms are dried to constant weight, was utilized in this study.

In order to be in a position to compare the Lake Washington study to the many studies which derived wet weight measures, correction factors must be used. A number of correction factors have been proposed: Rawson suggested multiplying the dry weight by 6.7 to approximate the wet weight; using the data of Scott, *et al.* (1928) and accounting for the relative proportions of the organisms in Lake Washington, one arrives at a figure of 9; using the data of Ricker (1952) and treating it as above, at a figure of 8. This latter figure will be used as the correction factor with the understanding that it could be anywhere from 7 to 9.

The weighted mean dry weight for the profundal zone of Lake Washington during the period of study was 8.03 kg/ha. This figure accounts for the contributions to the total area of the lake made by each of the depth profiles. The mean dry weight of biomass ranged from 4.54 kg/ha at 35 m to 10.60 kg/ha at 55 m and from 6.43 kg/ha in July to 10.39 kg/ha in September of 1964. Using the correction factor, the weighted mean wet weight was about 64 kg/ha.

Mean benthic wet weights were compiled by Deevey (1941) for some 262 lakes from 7 geographical areas of the world. This compilation can be considered to be fairly representative of temperate zone freshwater lakes. There was considerable latitude in the way the various studies were conducted, but comparisons made with this compilation should still be of some value. The figure of 64 kg/ha for Lake Washington falls at about position number 168 of 262 in an ascending scale or somewhat above the median.

Among lakes of comparable depth in North America, the benthic standing crop of Lake Washington appears to be about average. Green Lake in Wisconsin (a mean depth of 33.1 m and 2,973 ha in area) has had wet weight values of approximately 216 kg/ha reported; Paul Lake in British Columbia (32.1 m and 630 ha) 61 kg/ha; Lake Athabaska in Alberta and Saskatchewan (26.0 m and 790,000 ha) 33 kg/ha; and Minnewanka Lake in Alberta (38.1 m and 1,330 ha) 36 kg/ha (Deevey, 1941 and Rawson, 1955). Thus Lake Washington appears to be a lake which maintains a benthic standing crop of average to slightly above average proportions. The standing crop before the influx of treated sewage was probably something less than average—considering the statement of Scheffer and Robinson (1939) that the lake was "distinctly oligotrophic."

Table 4 presents the percentage composition of the most important groups of benthic organisms for Lake Washington and other lakes of similar morphometry. Lake Erie was chosen to demonstrate the before and after cultural eutrophication situations; the other 4 were chosen as examples of lakes with profundal zones like that of Lake Washington both in depth and relative consequence to the lake as a whole, but which were little or not at all affected by pollution at the time of the study.

The most striking change in Lake Erie, whose recent history has been very much like that of Lake Washington, between 1929 and 1958 was the disappearance of *Hexagenia* and the assumption of the dominant role in the benthos by the Oligochaeta (Beeton, 1961). The Oligochaeta became more than twice as abundant as the next most common group, the Chironomidae. In 1929, although neither was very common, the Chironomidae were present in

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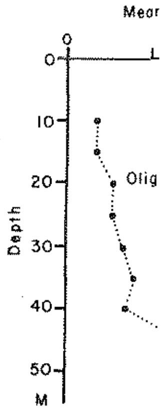

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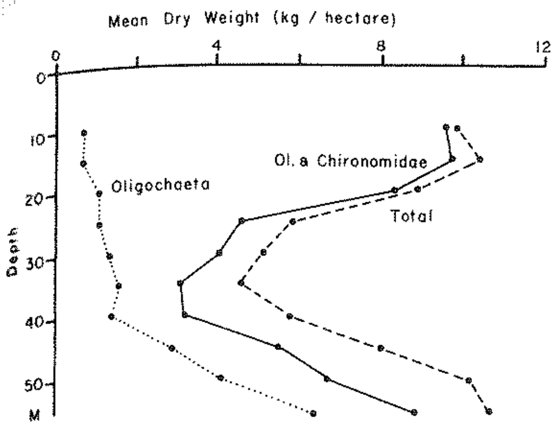

FIG. 27. Distribution with depth of the mean dry weights/ha of the Oligochaeta, of the Oligochaeta and Chironomidae, and of the total bottom fauna.

almost 10 times the numbers of the Oligochaeta. In the 4 isolated lakes, the Chironomidae occurred in numbers 2 to 3 times those of the Oligochaeta. Lake Washington has a larger percentage of Oligochaeta than Chironomidae and thus compares more closely with Lake Erie in 1958 than with any of the other examples. Lundbeck (1936) observed that culturally influenced lakes showed a proliferation of oligochaetes. He also noted that the Sphaeriidae increased in numbers in such lakes. This does appear to have occurred in Lake Erie; the data are not sufficient to draw any conclusions regarding Lake Washington.

The biomasses of the Oligochaeta, of the Oligochaeta and the Chironomidae, and of all the organisms taken together at each of the depths sampled are presented in Fig. 27. By noting the displacement of each line from that on its left, the contributions of the Oligochaeta, of the Chironomidae, and of all the other organisms combined to the total biomass at each depth can be determined.

The plot for total biomass shows a low point at 35 m with large steady increases as the stations become shallower and deeper than that at 35 m. At the shallow stations (10 to 20 m), the Chironomidae constituted the bulk of the biomass. With the progressive decrease of Chironomidae biomass and the increase of the biomasses of the Oligochaeta and the "other organisms" with greater depth, the situation was realized at 35 m where each of the 3 components contributed equally to a low total biomass. Moving to the deeper stations, the biomass of the Oligochaeta and of the "others" increased markedly and the biomass of the Chironomidae remained at about the same level with the net result of a steeply increasing biomass with increasing depth. At the deeper stations, the Oligochaeta were dominant. The Hirudinea were the primary contributors to the "others" at the mid-depths; the Gastropoda at the deeper. Neither was very consequential at the shallow depths.

In contemporary ecology, the study of the interactions between populations within a community has received a great deal of attention. This is especially true for the study of interspecific competition. The subject of competition, and the concomitant density-dependent factors, is a controversial one. It has been fairly well documented for terrestrial plants, birds, and some intertidal invertebrates and poorly documented for the plankton and the marine and freshwater infauna.

TABLE 4. Relative percentages of Oligochaeta, Chironomidae, and Sphaeriidae for selected lakes.

	% Oligochaeta	% Chironomidae	% Sphaeriidae
Lake Washington	51	43	3
Lake Erie (1929-30)*	1	10	2
Lake Erie (1958)**	60	27	5
Cultus Lake (B.C.)***	34	65	
Convict Lake (Calif.)****	31	65	
Lake Constance (Calif.)	20	57	20
Lake Dorothy (Calif.)	23	69	3

*mostly *Hexagenia*, a burrowing mayfly.
**Beeton, 1961.
***Ricker, 1952; all samples from 30 to 40 m.
****Reimers, *et al.*, 1955.

If, indeed, there is interspecific competition for some density-dependent resource among the benthic invertebrates of Lake Washington, the considerable number of species coexisting in a homogeneous environment such as that of the profundal zone of a lake is rather surprising. However, there are a number of devices which tend to isolate one species from another in their respective requirements. These are summarized in Table 5.

There were 4 different modes of feeding: predation, filter-feeding, feeding on the material deposited on the substrate surface, and ingesting the substrate itself. Further, among the deposit-feeders, there were a variety of ways in which this was accomplished. This variety might have allowed the different species to exploit subtle differences in the environment to their advantage.

Temporal separation is important in that the amount of a resource utilized by a population of univoltine animals generally increases as the population grows older. For example, Teal (1957) has demonstrated that the many small larvae of *Calopsectra dives* found in Root Spring early in the year assimilated only a third of the amount of food that the fewer large larvae assimilated later in the year. Thus a difference of only 2 or 3 months in the onset of the life cycles of 2 closely related species will assure that their periods of maximum food utilization will not coincide. The life cycles of the 2 species of *Polypedilum* began about 2 months apart; the 2 most important predators in Lake Washington, *Procladius culiciformis* and *Helobdella stagnalis*, were similarly separated. Most of the Chironomidae emerged in the summer and fall. The favorable weather to be found at this time of year undoubtedly reduces adult mortality. *H. stagnalis* and *Pontoporeia affinis* began

TABLE 5. Summary of the life histories of the benthic macrofauna of Lake Washington.

Species	Depth Distribution	Feeding Habits	Time of Reproduction	Generations /Year
P. culiciformis	10 to 25m	predaceous	IV.-IX.	1
C. plumosus	<10 to 20m	filter-feeder	ext.	?
C. sp. (nr. *ferrug.*)	30 to >55m	filter-feeder	IX.-III.	1
P. sp. (nr. *fallax*)	15 to 50m	deposit-feeder	IX.-XI.	1
Polypedilum sp.	10 to 35m	deposit-feeder	VI.-X.	1
Glyptotendipes sp.	<10 to 15m	deposit-feeder	II.-IV.& VI.-IX.	2
Cryptoc. (*Harn.*) sp.	<10 to 15m	?	?	?
Cryptoc. (*def.*) sp.	<10 to 15m	predaceous	?	?
C. atridoreum	<10 to 25m	deposit-feeder	ext.	?
C. bausei	<10 to 25m	deposit-feeder	VIII.-IX.	1
H. (*Eukief.*) sp.	<10 to 40m	deposit-feeder	ext.	?
Hydrobaenus sp.	<10 to 55m	deposit-feeder	IX.-XI	1
P. affinis	10 to 50m	deposit-feeder & planktonic	IV.-VII.	1
Gyraulus sp.	45 to >55m	deposit-feeder	ext.	1
P. casertanum	15 to 50m	filter-feeder	ext.	1
Oligochaeta—spp.	10 to >55m	substrate-feeder	ext.	1
H. stagnalis	15 to 45m	predaceous	II.-VI.	1

their life cycles in the spring. The remainder of the benthos had rather diffuse reproductive patterns.

The pattern of vertical distribution affords another means whereby species can apportion the environment. This was perhaps most obvious for certain of the congeneric species and for the predators. The 2 *Chironomus* species were distinctly separated with very little overlap in their vertical distributions, at least in the area where the sampling was done. The 2 *Polypedilum* species demonstrated a certain degree of spatial divergence although it was not nearly as marked. It should be noted that the earlier instars of the two *Polypedilum* species were distributed in almost identical fashion. There was a considerable difference among the 4th instars. If this difference was the result of interspecific competition, then it was an active and immediate response to this pressure, either by emigration from congested areas or by differential mortality from one area to the next, rather than a long-term evolutionary response such as deposition of eggs by the adults on water over different depths. The species belonging to the genera of *Hydrobaenus* and *Calopsectra* were quite distinct from one another. Both of these genera are very large and include very diverse larval forms. The depth distributions for the three predators showed peaks at 10, 20, and 40 m for *Cryptochironomus, Procladius,* and *Helobdella* respectively. Again, the distributions suggest some degree of spatial diversity and might serve to explain an other wise anomalous distribution for the leech.

Considerations such as the above can only suggest the role played by competition in the Lake Washington benthos. The problem awaits a carefully conceived experimental approach.

SUMMARY

1. The macroscopic bottom fauna of the profundal zone of Lake Washington was studied from September of 1963 to September of 1964. Lake Washington is a large, deep lake located near the city of Seattle. Between 1941 and 1966, the lake received large quantities of treated sewage. The sewage, rich in phosphates and nitrates, has caused striking changes in the chemistry and in the amounts and kinds of phytoplankton of Lake Washington.

2. Ten stations were sampled with an Ekman dredge at approximately monthly intervals. Isaac-Kidd midwater trawl samples were made available by the College of Fisheries of the University of Washington by which the pelagic phase of the life history of certain benthic animals was studied.

3. Lake Washington is a warm monomictic lake with a mixing period extending from December to April in most years. The epilimnion generally extends to about 10 m. The seston values for 1964 were higher than those for 1963 early in the year but essentially the same once the lake stratified. In deeper water, the 1964 oxygen values were substantially above those of 1963 when they fell to as low as 1.2 mg/liter in October.

4. 24 species were recognized from the profundal zone of Lake Washington, 13 of which were Chironomidae.

5. The Chironomidae were the most numerous of the bottom fauna constituents, accounting for about 45% of the total. The larvae were most common at the shallow-water stations and became progressively less abundant with an increase in depth. All of the species studied showed a tendency for the earlier instars to be found in greater numbers at the shallower depths with a progressive shift of the depth distribution toward deeper water as the animal passed into later instars. *Procladius culiciformis,* most abundant at 15 and 20 m, emerged in the greatest numbers in May and June. It had a single generation in the year's span and was one of the 2 chironomid species frequently encountered in the trawl samples. *Chironomus plumosus,* the largest chironomid in Lake Washington, was most common at the shallow-water

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stations. *Chironomus* sp. (nr. *ferrugineovittatus*), a closely related species, was most common at the deeper stations. *C. plumosus* emerged throughout the year; *Chironomus* sp. from September through March. Both species of *Polypedilum* were most abundant at 20 m. *Polypedium* sp. (nr. *fallax*), the other chironomid whose larvae were recovered from the open water, emerged primarily from September to November; *Polypedilum* sp. primarily from July to September. *Glyptotendipes* sp. (nr. *lobiferus*) occurred in enormous numbers, up to 19,300/m^2, in shallow water. A period of peak emergence probably took place from February through April. *Calopsectra atridoreum* was concentrated in shallow water; adults emerged throughout the year but especially in the summer. *Hydrobaenus* sp., most common at 10 and 15 m, had two emergence peaks, in the autumn and in the winter. *Hydrobaenus* (*Eukiefferiella*) sp., most common at 20 m, also appears to have had two emergence peaks, in the summer and in the spring.

6. *Neomysis awatchensis* and *Pontoporeia affinis* are only part-time members of the benthic community. *P. affinis* had 1 generation per year; the young were released from April through July. *P. affinis* was most abundant at 20 m and at 45 m.

7. *Gyraulus* sp. was concentrated between 45 and 55 m. Due to its large size, this species made a considerable contribution to the total biomass. Reproduction occurred throughout the sampling period with peaks in April and September of 1964.

8. *Pisidium casertanum* was most abundant at 45 and 50 m. The length- frequency histograms for this species were generally bimodal. The young are carried in marsupia in numbers which averaged about 8; marsupial clams were present throughout most of the year with a peak in September of 1964.

9. The Oligochaeta comprised about ½ of the total number and ⅛ of the total biomass of the profundal fauna. Four species were identified but there were probably many more. The Oligochaeta were found in the greatest numbers and biomass at the greatest depth sampled, 55 m; their abundance progressively declined with a decrease in depth. Sexual reproduction occurred throughout the year although it was considerably higher in the summer. The average weight per individual was very low in the winter and quite high in the summer just before the cocoons were deposited in their greatest numbers.

10. *Helobdella stagnalis* was most abundant at 40 m but was frequently encountered from 20 to 45 m. *H. stagnalis* had only a single generation per year with a peak in releasing young in June.

11. The weighted mean dry weight for the profundal zone of Lake Washington during the period of study was 8.03 kg/ha. Among lakes of comparable depth in North America, the benthic productivity of Lake Washington appears to have been about average. The large contribution made by the Oligochaeta to the total bottom fauna of Lake Washington is similar to the situations reported for other lakes which have undergone cultural eutrophication. The depth distributions of the 2 *Chironomus* species, the 2 *Polypedilum* species, and the 3 species which are predatory suggest that competition may play a role in determining the spatial distribution of benthic animals.

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