A SURVEY OF THE BENTHIC MACROINVERTEBRATE COMMUNITY OF LAKE PEPIN AND A STUDY OF THE INFLUENCE OF VARIOUS PHYSICAL FACTORS ON THE DISTRIBUTION OF SELECTED TAXA

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ABSTRACT

The macroinvertebrate community of Lake Pepin on the Upper Mississippi River was sampled twice during the summer of 1977 in order to determine the taxonomic groups present and what portion of the total standing crop each group represented. Using a petite Ponar dredge, 118 and 127 samples were collected during Sampling Periods I and II, respectively. A total of 38,874 individuals, representing 54 taxa, were collected. It was determined that the family Chironomidae comprised 56% of the benthic standing crop. *Chironomus* sp., and more specifically the pollution-tolerant midge *C. plumosus*, represented over 53% of the total number of individuals. Other dominant taxa were the Oligochaeta (40.37%), the Sphaeriidae (1%), and the Hirudinea (0.23%). The remaining taxonomic groups represented 5.43% of the standing crop. Only 18 nymphs of the genus *Hexagenia* were collected during the study. The pronounced domination of the benthic community by *C. plumosus* and the rare occurrence of the once prominent mayfly, *Hexagenia*, reflects the continued perturbation of the influent water of Lake Pepin.

In addition to the survey, correlation coefficients were calculated in order to determine the relationship between seven selected taxonomic groups and various physical factors (substrate particle size, dissolved oxygen, depth, and the % total sediment organics). Statistical analyses indicated that invertebrate distribution was effected by the physical factors examined and was often a function of feeding habit, physiological adaptations, and stage of larval development. Multiple correlation analyses determined that the physical factors investigated played a significant role in influencing the selected taxa.

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INTRODUCTION

Lake Pepin, which is located 111 km south of Minnespolis-St. Paul, Minnesota, markedly influences the downstream ecological characteristics of the Upper Mississippi River. Because of its great depth in comparison with the rest of the river, the lake acts as a settling basin by trapping much of the suspended material carried by the inflow. Historically, Lake Pepin supported a very large population of pollution-sensitive burrowing mayflies, *Hexagenia* spp. Reports made during the past 50 years concerning the lake and its aquatic community have indicated that Lake Pepin has been subjected to organic pollution and that the macroinvertebrate fauna has become dominated by the pollution-tolerant midge, *Chironomus plumosus*. However, the extent of decline in *Hexagenia* spp. populations and degree to which *C. plumosus* dominates the benthic community has not been documented. Because of the continued perturbation of the Upper Mississippi River, such information is necessary to assess the impact of further contamination. The present study was conducted to provide the needed baseline data. The main objectives of this study were to:

1. Complete the first comprehensive survey of the benthic macroinvertebrate community of Lake Pepin.
2. Determine the extent to which *Chironomus plumosus* dominates the benthic macroinvertebrate community.
3. Assess the degree of decline in *Hexagenia* spp. populations.
4. Evaluate the relationships between selected benthic macroinvertebrate taxa and dissolved oxygen, depth, substrate type, and organic content of the sediments.

DESCRIPTION OF STUDY AREA

The Mississippi River in Wisconsin extends from Prescott, Minnesota, to Dubuque, Iowa, a distance of 417 km. It drops in elevation a total of 26 km and has a slope of 6.3 cm/km. From a point above the mouth of the St. Croix River to Alma, Wisconsin, the river flows through the geological region known as the Older Drift Area (Martin 1965). Lake Pepin is located within this reach of the Mississippi. The major inlet of the lake lies 111 km downstream from the Minneapolis-St. Paul area. Lake Pepin is bordered by Goodhue and Wabasha counties in Minnesota and Pierce and Pepin counties in Wisconsin (Fig.1). Towns and villages located on the lake shores include, from north to south, Red Wing, Lake City, and Read's Landing, Minnesota; and Bay City, Maiden Rock, Stockholm, and Pepin, Wisconsin (Fig.1).

Lake Pepin, formed by an alluvial dam composed of bedload from the Chippewa River, is an enlargement of the Mississippi River. The Chippewa enters the Mississippi at the southeastern end of the lake. The delta was formed because of the inability of the Mississippi, with its lower grade, to move this alluvial deposit downstream. Water consequently backed up into the Mississippi River corridor, forming Lake Pepin. Deposition of suspended materials by the Mississippi is occurring at the upstream end of the lake. There are indications that this process will continue, eventually filling the entire basin (Martin 1965).

The shoreline of the lake is dominated by three main land formations: the high rock bluffs of the Mississippi gorge, modern deposits made by streams and waves, and terraces formed by the depositional and erosional activities of the early Mississippi River. Tributaries entering the lake include Isabel, Bogus, Lost, Wells, Gilbert, and Miller Creeks and the Rush River (Fig.1). Two small deltas are formed by the Rush River and Isabel Creek (Martin 1965).

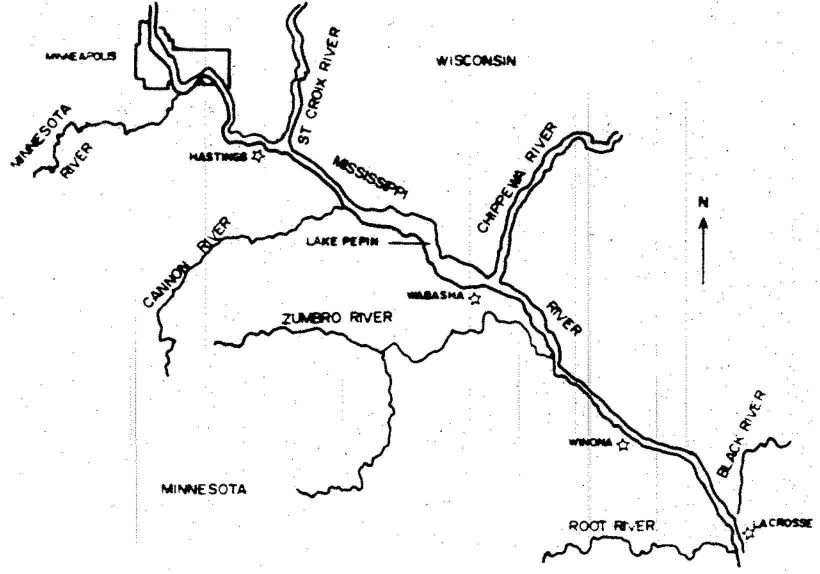
This S-shaped lake is 35 km long and 1.64 to 4.0 km wide and has a surface area of 101.17 km^2. The maximum depth is 17.1 m, with a mean depth of 5 m. The drainage area encompasses 146,593.94 km^2. Lake Pepin has an average retention time of 9 days (da) and an average inflow of 659 m^3/sec. Secchi disc readings average 0.8 m (USEPA 1975). The lake is ice-covered from November to late March or early April and prevailing winds are from the west. A survey by the USEPA (1975) reported the following average summer values for various physical and chemical characteristics of Lake Pepin water:

Alkalinity	3.000 meq/L
Conductivity	438.000 μmhos/cm
Total Phosphorus	0.185 mg/L
Ortho-Phosphorus	0.140 mg/L
Inorganic Nitrogen	1.090 mg/L

Areal loading rates of nutrients from various municipal, industrial, and non-point sources total 34.38 g phosphorus/m^2/yr and 468.8 g nitrogen/m^2/yr. Lake Pepin annually retains 11% of the incoming phosphorus while there is a net loss of nitrogen. Nitrogen has been determined to be the limiting algal nutrient in the lake (USEPA 1975).

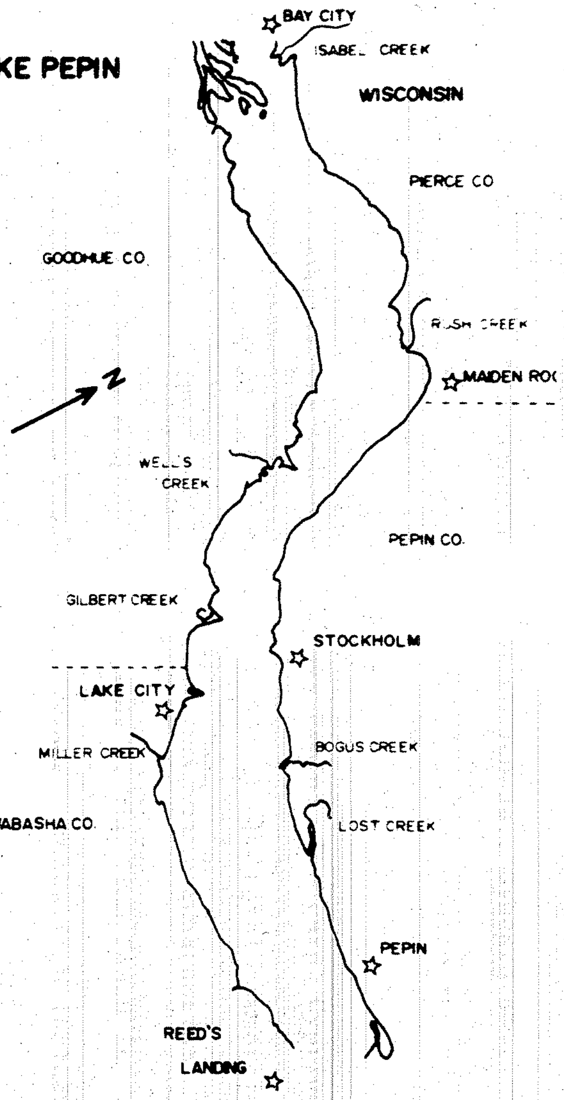
Phytoplankton in Lake Pepin is much more abundant than in the Mississippi above and below the waters of the lake. The average summer chlorophyll a concentration is 14.9 μg/L (USEPA 1975). The phytoplankton

Fig. 1. The Upper Mississippi River and Lake Pepin.



UPPER MISSISSIPPI RIVER

LAKE PEPIN



is lake-like in character and blue-green algae are abundant (Eddy 1963). Among the various phytoplankters found in Lake Pepin are *Aphanocapsa* sp., *Aphanizomenon flos-aquae*, *Microcystis* sp., *Dinobryon* sp., *Synedra* sp., *Cocconesis* sp., *Merismopedia* sp., *Kirchneriella* sp., and *Chroococcus* sp. (USEPA 1975, Galtsoff 1924).

Commercial fisheries are important in Lake Pepin. The carp, *Cyprinus carpio*, is heavily harvested and accounted for 93% of the total commercial catch in 1961 (Rademacher 1964). The lake also supports a substantial recreational walleye fishery (Waters 1977). Many of the fish found in Lake Pepin are characteristic of large river systems. These fish include the paddlefish, *Polydon spathula*; the shovelnose sturgeon, *Scaphirhynchus platorynchus*; and the flathead catfish, *Pylodictus olivaris* (Eddy 1963). Other species of fish found in Lake Pepin are the quillback carpsucker, *Carpiodes velifer*; the redhorse sucker, *Moxostoma aureolum*; the common sucker, *Catostomus commersonii*; the channel catfish, *Ictalurus punctatus*; and the buffalo, *Ictiobus cyprinellus* (Johnson and Munger 1931).

LITERATURE REVIEW

The Upper Mississippi River is defined as that section of the river extending from Lake Itasca, Minnesota, to the mouth of the Ohio River near Cairo, Illinois. This portion of the river has been investigated on numerous occasions since 1900. Information concerning its biological components and its physical and chemical characteristics, although scattered, does exist. Fish food habit studies by Hoopes (1960) documented the importance of mayfly nymphs of the genus Hexagenia sp. and various caddisfly larvae in the diets of several species of Mississippi River fishes. Prior to the establishment of the present lock and dam system, Ellis (1931) conducted a survey that provides a thorough description of many factors affecting important Upper Mississippi River fisheries. Lake Pepin and Lake Keokuk were extensively examined in that study. The molluscan population of the Upper Mississippi River has been studied by Grier (1922). He collected molluscs from various sites between Red Wing and La Moille, Minnesota, in order to ascertain the effects of pollution and excessive harvesting on this resource. At that time, Lake Pepin was the clamming center of the upper river. Grier reported that in 1920 between 190-238 tons of clams were removed from the lake. Dawley (1947) and van der Schalie and van der Schalie (1950) also compiled species lists of molluscs found in the Mississippi River. The mussel fauna of the Mississippi Valley (also known as the Interior Basin Fauna) has been found to be strikingly uniform, containing no species from other faunal regions. However, its own members have invaded other faunistic areas (van der Schalie and van der Schalie 1950). The most recent study of the Upper Mississippi River molluscan fauna was a 1978 survey of selected sites in the 9-foot navigation channel (Fuller 1978). The study revealed that channel maintenance-dredging had little impact on mussels. Instead, the noted decline in the number of molluscan species was more likely due to the impact of such factors as agricultural, industrial, and municipal wastes (the Twin Cities area was cited as an important contributor of industrial and municipal contaminants), increased river bedload, inadequate glochidial host oppurtunities, and the introduction of the Asiatic clam Corbicula fluminea (Fuller 1978).

Galtsoff (1924) presented data on the physiography, water chemistry, and planktonic populations from that portion of the Mississippi River extending from Hastings, Minnesota, to Alexandria, Missouri. He found the plankton of Lake Pepin to be dominated by crustaceans and rotifers; Grier (1922) noted that Aphanizomenon flos-aquae (Class Cyanopyceae; Order Nostocales) was the dominant phytoplankter in Lake Pepin and throughout the Mississippi River. Investigations by Wiebe (1927), Johnson (1929), Ellis (1931), and Johnson and Munger(1931) detailed the effects of pollution on aquatic life in the Upper Mississippi River, particularly above Lake Pepin. The river from Lake Pepin to the Minneapolis-St. Paul area was marked by a paucity of fish, very low oxygen content, and a limited benthic community dominated by pollution-tolerant organisms. This condition was produced as a result of the introduction of heavy organic loads from the Twin Cities region (Wiebe 1927). Johnson (1929) and Johnson and Munger (1931) examined factors contributing to the dominance of the pollution-tolerant midge larvae Chironomus plumosus in

Lake Pepin. These studies noted that within approximately ten years C. plumosus had replaced nymphs of the mayfly genus Hexagenia sp. These mayfly nymphs are known to be intolerant of low dissloved oxygen conditions (Nebecker 1972).

Although Lake Pepin was not believed to be seriously polluted, the abundance of midge larvae apparently resulted from enrichment of the sediments with organic contaminants entering the river at the Twin Cities (Johnson and Munger 1931). A similar replacement of a Hexagenia sp. dominated community with one dominated by C. plumosus occurred in the Illinois River and was attributed to increased organic perturbation (Richardson 1928). Its slow current and great depth in relation to the rest of the river enables Lake Pepin to trap large quantities of suspended materials, resulting in their accumulation on the lake bottom (Wiebe 1927, Ellis 1931, Johnson and Munger 1931, Fuller 1978). Ellis (1931) noted that soil erosion, and thus the amount of suspended colloidal materials carried by the river, greatly increased just prior to his study. He contended that this class of fine sediments had a high affinity for organic materials such as municipal sewage; therefore, when these sediments settled, two major effects were produced. Not only did the silt settle and inundate the benthic organisms faster than they could recover but the adsorbed organic material that settled with it created an oxygen demand that severely depleted hypolimnetic oxygen concentrations. Recent studies by Fremling (1964b) and Hilsenhoff and Narf (1968) indicated that the benthic community was still dominated by C. plumosus and contained few mayfly nymphs; the presence of this type of community structure supported the theory Ellis proposed concerning siltation. However, contrary to the above studies, Carlson (1968) did not find the increased C. plumosus and declining Hexagenia sp. populations in Pool 19 (Lake Keokuk) to be a reaction of the benthic community to serious pollution. Instead, he contended this shift in dominance was indicative of a natural, highly productive aquatic system.

As reported above, the two most important members of the invertebrate fauna of Lake Pepin are the abundant, pollution-tolerant midge larvae Chironomus plumosus and the more sensitive and less frequently encountered mayfly nymph Hexagenia sp. A review of their life histories is provided below. For information concerning the other invertebrates found in this study, the following references may be consulted: Usinger (1956), Brinkhurst and Jamieson (1971), Hart and Fuller (1974), Hilsenhoff (1975), Fuller (1978), Merritt and Cummins (1978), and Pennak (1978).

Life Histories

The Chironomidae

Members of the Family Chironomidae are among the most important components of the benthic fauna in freshwater ecosystems (Lindeman 1942, Jonasson 1965, Sublette and Sublette 1965, and Paterson and Fernando 1970). According to Sublette and Sublette (1965) and Oliver (1971), no other group of aquatic insects is more ubiquitous, inhabiting practically all ecological niches from mountain torrents to the anaerobic ooze of deep eutrophic lakes. Brundin (1966) suggested that the Chironomidae arose in cool, spring-fed mountain streams. Based on studies of Dipteran mouthparts, this group is believed to have descended from biting and suctorial ancestors (Downes 1974). Although over 5,000 chironomid species have been classified, there is no reliable estimate of the total number of species in this family. In addition, the living species in large sections of Asia and Africa have yet to be described (Oliver 1971).

The classification within the Chironomidae has long been confusing. Part of this difficulty originated from usage of two different familial names. In 1963 the International Commission on Zoological Nomenclature suppressed the names established by Meigen in 1800. Thus, the family name "Tendipedidae" was officially replaced with the name "Chironomidae" (China, 1962, Fittkau 1966). The name "Chironomidae" was derived from the plumose nature of the adult male antennae (Bryce and Hobart 1972). At present, seven subfamilies are recognized: Tanypodinae, Podonominae, Chironominae, Corynoneurinae, Diamesinae, Orthocladiinae, and Clunioninae (Bryce and Hobart 1972). Another obstacle to chironomid taxonomy is their holometabolous (i.e. a complete metamorphosis) life cycle. In response to the diverse habitats occupied by the larvae, numerous physiological and biological adaptations have given rise to a vast array of morphological forms. In contrast, the short-lived adults are more uniform in appearance, existing only long enough to reproduce. Therefore, the environmental influences on their morphology have been few. However, the development of unique adult male reproductive organs allowed identification at the specific level (Acton 1956, Oliver 1971). Much difficulty remains in identifying the larvae to species. Progress has been made by utilizing the banding pattern on the large salivary gland chromosomes for taxonomic purposes (Acton 1956). In addition, recent investigations have dealt with complete life history studies (e.g. Hilsenhoff 1966), allowing the larvae to be associated with positively identified adults. Such studies can potentially lead to delineation of taxonomically distinct characteristics in immature forms (Oliver 1971).

Oviposition by adult female chironomids occurs at the water surface. The eggs absorb water, swell to several times their original diameter, and sink to the bottom. Hatching takes place on the sediments. Ford (1959) found the possession of four larval instars predominant among the Chironomidae. Oliver (1971) generally concurred, although he did note that some exceptions have been reported for Tanypodinae. McCauley (1974) attributed the occurrence of more than four instars to the exposure of larvae to low or extremely low temperatures and/or to pollutants. This exposure would lead to a lengthening of the time required to complete the life cycle, resulting in additional numbers of instars. Hilsenhoff (1966) reported *Chironomus plumosus* was typical of most Chironomidae in having four instars. Instar differentiation is accomplished utilizing measurements of head capsule width (Hilsenhoff 1966, McCauley 1974).

First instar larvae become planktonic after hatching. Hilsenhoff (1966) noted that such was the case for the first instar *C. plumosus* larvae. He attributed this behavior to positive photoreactivity and a possible initial contact with unfavorable substrate types. Swimming behavior of all four instars of *C. plumosus* was recorded during both day and night by Yamagashi and Fukuhara (1971). Davies (1976) reviewed chironomid entry into the water column and discussed the importance of this behavior in aiding the dispersal of larvae throughout a body of water.

Members of the subgenus Chironominae construct tubes in sediments and line them with material woven from salivary gland secretions. Walshe (1947) found that members of *Chironomus* ~~*plumosus* built U-shaped burrows,~~ but studies by McLachlan and McLachlan (1971) and McLachlan and Cantrell (1976) indicated that three different tube types (U-shaped, J-shaped, and horizontal) existed, depending on the depth of sediment development.

Jonasson and Kristiansen (1967) observed that *C. anthracinus* built chimney-shaped tubes of varying heights. Variation in tube shape among *C. anthracinus* larvae was thought to be closely but not exclusively related to hypolimnetic oxygen concentration as well as degree of larval development. The shape of tubes built by *C. plumosus* was correlated with characteristic feeding habits of their inhabitants (McLachlan 1977). Larvae in horizontal tubes fed at the substrate surface on bottom deposits while those in J-shaped tubes combined surface feeding with somewhat inefficient filter feeding. Larvae inhabiting U-shaped tubes were particularly well suited for filter feeding. Walshe (1947) presented a detailed description on the feeding behavior of larvae in U-shaped burrows. Larvae create a water current via body undulations and materials are trapped in a cone-shaped net woven at one end of the tube. At regular intervals the larva turns in its burrow, consumes the net and its contents, weaves another net, and repeats the process. Occasionally the formation of a net is abandoned and the sides of the burrow are scraped instead. Similar behavior was noted in *Glyptotendipes glaucus*, a leaf-burrowing chironomid (Burtt 1940).

Larvae of *Chironomus* sp., particularly *C. plumosus*, have been described as being indiscriminant feeders, consuming any material trapped in their nets (Walshe 1947, Hilsenhoff 1966, Biever 1971, Alfred 1974). However, numerous studies indicated that larvae exhibit a great deal of food selectivity and will preferentially feed on a certain species of algae even though the alga is not the predominant phytoplankter in the lake (Sadler 1935, Provost and Branch 1959, Armitage 1968, Kajak and Warda 1968, Jonasson 1969, Jonasson and Kristiansen 1967). Provost and

Branch (1959) contended that high utilization of green algae was probably due to their large size, increasing the likelihood of their being retained by the nets. Results of a study on the feeding of high Arctic Chironomidae indicated that these larvae possessed a marked preference for certain food types and displayed a variable assimilation efficiency for those foods (Davies 1975). If this is true, "the current theoretical bases of many feeding studies concerning chironomids may be unsound" (Davies 1975).

In addition to feeding on living and partially decomposed algae, chironomid larvae have been found to consume chironomid eggs and smaller instars (Hilsenhoff 1966, Jonasson 1969, Biever 1971), bacteria (Kajak and Ryback 1970), amorphous organic matter (Kajak and Dusoge 1967), oligochaetes (Loden 1974), protozoa and rotifers (Burbanck and Mozely (1969), and materials excreted by clams (Izvekora and Liora-Katchanova 1972). Larvae in turn serve as major food items for invertebrates such as the leech *Helobdella stagnalis* (Mann 1957, Hilsenhoff 1963). Chironomid larvae have long been known to form a major portion of the diet of freshwater fish (Hayne and Ball 1956, Kajak 1963, Cook et al 1964, Burbanck and Mozely 1969, Kajak and Ryback 1970, Bryce and Hobart 1972, Guzuir and Wielgosz 1975). Czeczuga (1974) studied seasonal changes in concentrations of carotenoids, particularly astaxanthin, in larvae of *Chironomus annularis*. He demonstrated that midge larvae serve as an important source of vitamin A for fish. Midge larvae obtain carotenoids from dying plant matter and are consumed in turn by fish; carotenoids are then converted to vitamin A in the alimentary ~~tract of the fish.~~

In order to survive under physiologically rigorous environments such as streams polluted by acid mine drainage or in the profundal zones of lakes, midge larvae of the genus Chironomus sp. have developed several unique adaptations, the most striking of which is their use of hemoglobin (Lindeman 1942; Walshe 1947, 1948; Mundie 1957; Czeczuga 1959; Jonasson 1965; Nebeker 1972). Walshe (1947, 1948) found that chironomid larvae utilized hemoglobin to maintain a constant rate of oxygen consumption, and therefore a stable metabolic rate, even as the oxygen concentration in the water diminished. It has been demonstrated that this constancy in O_2 consumption is a result of increased hemoglobin concentrations with decreasing oxygen pressure (Czeczuga 1959). Nebeker (1972) found that Tanytarsus dissimilis was able to tolerate 30-day exposures to dissolved oxygen concentrations as low as 0.6 mg/L, while Lindeman (1942) found Chironomus plumosus capable of surviving in water devoid of oxygen for a period of 120 days. Members of the genus Chironomus are among the few animals capable of fermentation (Lindeman 1941, 1942; Augenfeld and Ness 1961; Augenfeld 1967). Large amounts of glycogen were discovered in the larvae. Chironomids surviving anoxic conditions had glycogen levels that never fell below 5% of their body weight (Augenfeld 1967). Harp and Campbell (1967) found that C. plumosus was capable of surviving in waters with extremely low pH and that larval development was not hampered by the degree of acidity except in waters with a pH less than 3.0. In these waters, emergence from the pupal stage was unsuccessful. The ability of chironomid larvae to survive extremes in temperature, i.e. from temperatures as high as 38°C to the extreme low temperatures encountered in the Arctic, was reported by Walshe (1948) and Danks (1971).

Activities of burrowing larvae play a significant role in the interactions between nutrients in sediments and overlying water. Ganapati (1949) discovered that burrowing activities of abundant Chironomus plumosus larvae in a sand filter of the Madras Water Works contributed significantly to the concentration of nutrients, particularly free ammonia and phosphate, in the water column. An increase of ammonia in the overlying water, resulting from larval activities, was also reported by Edwards (1958). Chironomid larvae were also responsible for large accumulations of Fe^{+2} and NH_4^+ in the hypolimnion. The chemical oxygen demand of these nutrients was high enough to produce a significant oxygen depletion at the mud-water interface (Rossolimo 1939). Larval burrowing activities resulted in an increased pH in bottom sediments. Undulating larvae created irrigation currents that removed microbially-produced acidic metabolites. Additionally, chironomid activity was found to be important in determining the width of the oxidized microzone in sediments (Edwards 1958).

The annual number of chironomid generations is somewhat variable and is determined by a number of interacting factors that differ in each lake. Lindeman (1942) reported three generations of C. plumosus in a shallow senescent northern Minnesota lake whereas two generations per year were reported in Lake Winnebago (Hilsenhoff 1966, 1967). Mundie (1957) found that C. plumosus larvae inhabiting the profundal zone of an English reservoir had an annual life cycle, while larvae living at shallower depths of the same reservoir produced two generations per year. Carter (1976) also recorded an annual cycle for C. plumosus larvae in Lough Neagh, Scotland. Danks (1971) reported that the majority of larvae which overwintered did so as fourth instar larvae. Pupation occurs in the larval burrow and the duration of the pupal stage is dependent on substrate temperature (Hilsenhoff 1966). The pupal stage for C. plumosus will last only one day at a temperature of 24°C; this is equivalent to the mud temperature in Lake Winnebago in August (Hilsenhoff 1966). At lower temperatures such as those reported for Lake Winnebago in May (10°C), the pupal stage lasted 6-10 days (Hilsenhoff 1966). According to Johnson and Munger (1931), a similar pupal duration was noted for Lake Pepin. Emergence cannot take place unless larvae have achieved a minimum threshold weight (Jonasson 1965, Hilsenhoff 1966). However, even with proper temperature and weight conditions, emergence may be delayed under high larval densities. Ikeshoji (1973) observed that during periods of overcrowding, larvae produced chemical factors that retarded growth of younger instars. This retardation subsequently delayed and produced irregular emergence.

When all conditions for emergence are favorable, pupae leave their burrows and rise to the water surface. Once at the surface, emergence is completed in 15-30 sec as the pupal integument splits in the mediodorsal portion of the thorax. The adult fly climbs out of the exuvium and flies to shore (Hilsenhoff 1966). Emergence is reported to occur just prior to sunset (Buckley and Sublette 1964, Hilsenhoff 1966), although some species will emerge at sunrise (Oliver 1971).

Flies are sexually mature at emergence but pass through a teneral period before mating. The teneral period, which lasts approximately 12 hr, is spent resting on structures near the shoreline until the exoskeleton hardens (Hilsenhoff 1966). Mouthparts of chironomid adults are vestigial and a lack of feeding is reported by most authors. However, Downes (1974) observed representatives of 26 genera (including *Chironomus* sp.) feeding on honeydew. This saccharin material is deposited on plant leaves by aphids. Downes hypothesized that the consumption of some type of sugar meal is widespread and may even be viewed as a routine crepuscular activity among Chironomidae.

Mating-swarms, which consist of several thousand adult male flies, are generally formed and are most prevalent at dusk and dawn although they frequently occur throughout the day (Hilsenhoff 1966, Oliver 1971). The size of the swarm varies greatly; however, a typical *Chironomous plumosus* swarm may be 8 feet high, 10 feet wide, and 30 feet long with a density of 10-20 flies/ft^3 (Hilsenhoff 1966). Chironomids form swarms in relationship to markers (Downes 1969) such as haystacks, trees, and buildings. The horizontal shape of the swarm usually assumes that of the object over which it hovers (Hilsenhoff 1966). Undoubtedly, the main function of the swarm is to bring the two sexes together (Downes 1969). Larger-bodied female flies enter the swarm and copulation is initiated. The pair drops from the swarm to complete copulation; the male returns to the swarm and the female rests momentarily on the ground (Hilsenhoff 1966). In the case of *C. plumosus*, oviposition occurs 2-5 days later; the adult female will fly to the oviposition site and deposit an egg mass on the water surface (Hilsenhoff 1966, Oliver 1971).

The presence of large chironomid populations becomes obvious to the general public during periods of emergence, swarming, and oviposition. In Lake Winnebago *C. plumosus* was observed to emerge twice a year; a major emergence took place in early May followed by a second, smaller emergence in July and August (Hilsenhoff 1966). Chitinous exuviae are quite resistant to decomposition and have been known to accumulate in windrows along the shore of Lake Pepin (Johnson and Munger 1931). An offensive odor produced by decomposing bodies of millions of dead flies severely affects the seasonal recreational business of Lake Pepin

(Johnson and Munger 1931). Not only do large numbers of midges, which resemble mosquitoes, produce an esthetically displeasing site, but they are known to be responsible for interfering with industrial operations and reducing property values (Grodhaus 1963, Anderson et al 1965). Additionally, inhalation of chironomid fragments can initiate an allergic response in humans (Grodhaus 1963).

Ephemeroptera: Hexagenia

Representatives of the order Ephemeroptera are found along the entire length of the Mississippi River. Extremely large numbers of emerging adults, particularly *Hexagenia* sp., have often been reported (Burks 1953, Fremling 1960). In Lake Pepin, *Hexagenia bilineata* is the species most frequently encountered although *H. limbata* has been reported (Fremling 1964b). Life histories of these two species have been extensively investigated in two major studies. Hunt (1953) documented the life history and economic importance of *H. limbata* while Fremling (1960) examined that of *H. bilineata*. Briefly, the two species have a one-year life cycle with eggs usually being deposited in June. Eggs sink to the bottom and hatch, producing first instar nymphs. Although it has not been positively determined, Hunt (1953) believed that the number of instars through which nymphs pass ranges from 27 to 30. The nymphs shed their old exoskeleton when molting between instars occurs. Before the new chitinous exoskeleton can harden (a period of 3 to 5 min), nymphs undergo a rapid expansion in body size via ingestion of large quantities of air.

Nymphs live in U-shaped burrows and exhibit a distinct preference for muddy substrates (Morgan 1911, Lyman 1943, Hunt 1953, Fremling 1960, Eriksen 1964, Hilsenhoff 1975). They are well adapted for life in such substrates, possessing highly developed fossorial claws on prothoracic legs (Lyman 1943). Similar to tubiphilous members of the Chironomidae, they also create water currents in their tubes via body undulations. However, unlike the Chironomidae which depend on cuticular respiration, Hexagenia spp. utilize gills to passively absorb oxygen from water. Also unlike the Chironominae, nymphs are very intolerant of low oxygen concentrations (Fremling 1960, Eriksen 1964, Swanson 1967, Hilsenhoff 1970, Nebeker 1972, Roback 1974). Shapas and Hilsenhoff (1976) reported that ephemeropteran nymphs generally consume plant matter. Hunt (1953) and Fremling (1960) often found the alimentary tracts packed with an amorphous organic mud detrital material. Hexagenia nymphs are not completely sedentary and various instars have been recovered from the water column (Mundie 1957). Lyman (1943) described their swimming activities.

When the nymphs are ready to emerge, they rise to the surface. Their bouyancy is produced via the formation of a gaseous space between the nymphal and subimaginal cuticles (Hunt 1953, Fremling 1960). A schism forms in the nymphal skin, and the subimago (a life stage unique to the Ephemeroptera) emerges. The subimago then flies to shore. Approximately 24 hr after emergence, another molt occurs and the subimago becomes a sexually mature imago. Figley (1940) termed the exuvium a pellicle. Like the Chironomidae, male Hexagenia spp. form mating swarms, usually at dusk. These swarms are also oriented over landmarks. Females fly through the swarm and are pursued by males until copulation is initiated. The pair leaves the swarm; when copulation is completed, the male returns to the swarm while the female lands on the water surface and deposits two packets of eggs (Hunt 1953, Fremling 1960).

Both Hunt (1953) and Hoopes (1960) reported that nymphs of the large mayfly, *Hexagenia* spp., are very important in diets of fish. Nymphs of this genus are also important because their presence is indicative of waters free from organic pollution (Fremling 1964b, Roback 1974). Of particular interest is Fremling's observation that mass emergences of *H. bilineata* and *Pentagenia vittigera* have not been recorded in Lake Pepin and only one large emergence has been reported for *H. limbata*. The low numbers of mayfly nymphs in Lake Pepin have been attributed to the absence of oxygen in the hypolimnion (Fremling 1964b). According to this report, large amounts of sewage enter the Mississippi River from the Twin Cities area and are transported to Lake Pepin. The high-oxygen demand of this material depletes available oxygen in the water, especially at the mud-water interface (Fremling 1964b).

Environmental Factors Affecting Macroinvertebrate Distribution

The existence and distribution of organisms in a particular habitat is partially dependent upon the presence of suitable ranges of various physical and chemical constituents. These physical and chemical features include adequate dissolved oxygen concentrations, depth, water temperature, substrate organic content, and substrate particle size. Hunt (1953) found that, in addition to other factors, depth influenced the distribution of both *Hexagenia* spp. and Chironomidae. Studies have shown that various species of Chironomidae apparently exhibit depth preferences (Underhill and Cole 1967). Depth has been correlated with the density and variety of benthic organisms in Lake Erie (Krecker and Lancaster 1933). Harker (1953) found that within the particular stream he studied, the distribution of mayfly nymphs was generally related to relative depth, not absolute depth. Relative depths were arbitrarily defined as being the top 25%, 50%, and 75% of the absolute depth reported at any one station.

As previously mentioned, the distribution of Hexagenia spp. nymphs has been found to be closely associated with the presence of adequate concentrations of dissolved oxygen. Mundie (1957) observed that chironomid distribution in storage reservoirs was related to oxygen. A similar relationship was reported by Barber and Kevern (1974) in their study concerning the ecological factors influencing standing crops of many stream invertebrates. In a study on the benthic community in Lake Ontario, Johnson and Brinkhurst (1971) demonstrated that temperature could influence, either independently or together with lake trophic status, the diversity and hence the distribution of macroinvertebrates. Ide (1935) found that temperature limited the distribution of mayfly nymphs in stream habitats. However, in a study on the ephemeropteran nymphs in Douglas Lake, Lyman (1956) disagreed with Ide's conclusion. He determined that temperature appeared to have only a small effect on these organisms. In addition, he pointed out that the temperature within the littoral zone was quite uniform over a period of time. The uniform lake temperatures reported by Lyman contrasts with the stream situation studied by Ide where water tended to become warmer from the headwaters downstream to the mouth.

Although most work concerning the relationship between substrate particle size and macroinvertebrate distribution has been conducted in marine habitats, numerous freshwater investigations have been completed, particularly in the last two decades. Cummins et al (1966) provided an excellent review of the studies and a brief review is included below.

Several authors have studied benthic communities or benthic associations and found that distribution was apparently correlated with benthic sediment types. Several investigators indicated that distinct changes in the character of the substrate were often clearly reflected by changes in the macroinvertebrate fauna (Eggleton 1931). Beatty and Hooper (1958) described three biotic associations characteristic of certain sediment types. Based on the dominant organisms present, Shelford and Boesel (1942) were able to name three distinct communities in Lake Erie and correlated community distribution with the dominant substrate type. Data gathered in a study on the shoreline of Western Lake Erie revealed that the abundance and variety of benthic animals were closely correlated with the nature of the substratum (Krecker and Lancaster 1933). Similar studies concerning substrate preferences of single species of lacustrine macroinvertebrates have also been conducted. Substrate preferences of mayflies have been reported by Lyman (1943), Eriksen (1964), and Swanson (1967). Preferred sediment types have been reported for crayfish (Flint 1977), leeches (Mann 1957, Sawyer, 1974), molluscs (Harman 1972, Fuller 1978), and chironomids (Iygenar et al 1963, Iovino and Miner 1970, McLachlan and McLachlan 1971, McLachlan and Cantrell 1976). Laboratory studies have shown that the amphipod *Pontoporeia* sp. and a midge larvae were able to distinguish between various sediment types and demonstrated that these two organisms actually selected their preferred substrate (Gannon and Beeton 1969, 1971).

Investigations concerning the influence of substrate type on macroinvertebrates in lotic systems have also been completed. The distribution of midges in two rivers in Poland was recorded by Niedzwiecki (1970, 1974). Wene (1940) noted the relationship between chironomid distribution and five sediment types found in a small Ohio stream. Another study reported that the addition of medium-sized rubble (16.5 x 11.4 x 8.9 cm) to sandy bottoms greatly increased stability and thus productivity of an area (Wene and Wickliff 1940). Certain mayfly species were observed to select particular bottom types without respect to stream velocity (Linduska 1942). Chutter (1969) found that the introduction of unstable sand and silt greatly affected the composition of stream bottom fauna. In a similar investigation, increasing amounts of fine silts were shown to produce a community dominated by tubificids and chironomids (Nuttal and Bielby 1973). Both Cummins (1964), Cummins et al (1966), and Brusven and Prather (1974) arrived at the conclusion that substrate particle size was the most important environmental factor influencing stream macroinvertebrate distributions; all other factors appeared to be secondary. This view was further substantiated by Cummins and Lauff (1969). These authors concluded that although factors such as current velocity, temperature, or the concentration of a chemical may have limited the range of habitat tolerance (macrodistribution), it was substrate particle size that exerted the primary microdistributional influences. Other investigations have not clearly demonstrated the relationship between substrate and macroinvertebrate distribution. In studying stream populations of Trichoptera larvae, Scott (1958) found that substrate preference changed with life stage. Barber and Kevern (1974) reported even more confusing results. Their data indicated that the Ephemeroptera did not exhibit a consistent relationship with substrate type. The numbers of Coleoptera showed a similar trend although their biomass increased with increasing particle size. Similar trends occurred for both numbers and biomass of the Chironomidae and the Trichoptera. They hypothesized that larger substrates provided more interstitial spaces which could trap more detritus and thus provide food for stream invertebrates. Rabeni and Minshall (1977) drew similar conclusions. Egglishaw (1969) contradicted these findings, observing that it was the accumulation of plant detritus, regardless of substrate particle size, that was of primary importance in determining macroinvertebrate distributions. Macan (1974) and Hynes (1970) provided excellent discussions of the role played not only by substrate particle size but other factors thought to influence benthic communities.

METHODS AND MATERIALS

Field Procedures

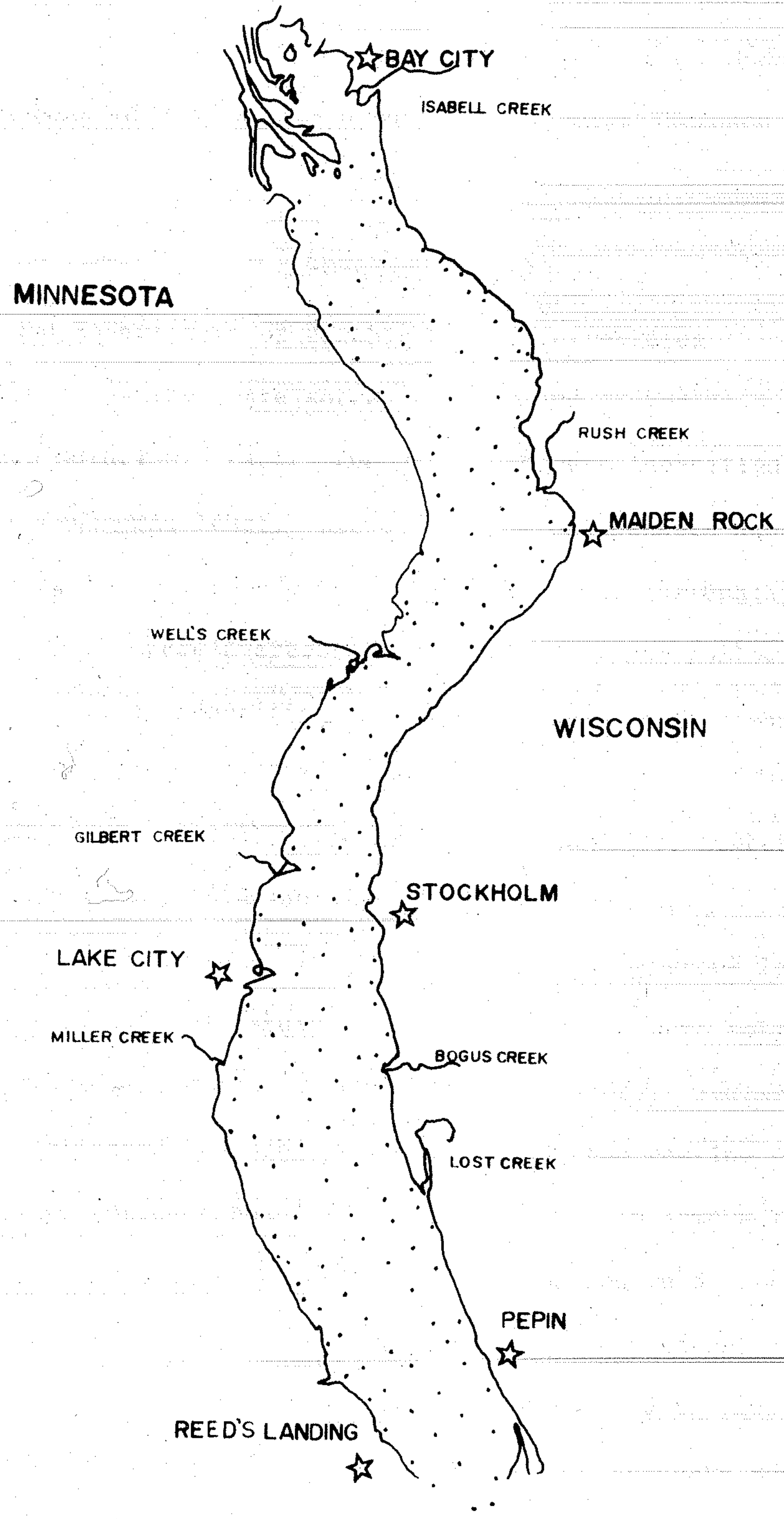
Station Location

The benthic community of Lake Pepin was sampled on May 20-21 and June 2, and July 21-22, 1977. Transects aligned on a north-south axis were established at 0.4-km intervals that began at the inlet of the lake and ended at the Chippewa River Delta. Sampling stations were located along each transect and were separated by a distance of 0.4-km (Fig. 2). In addition to these stations, several shoreline locations were also sampled. Of the 173 stations sampled during Sampling Period I and the 167 sampled during Sampling Period II, 125 and 118 stations, respectively, were completely analyzed for all organisms encountered and various physical variables (sediment type, depth, dissolved oxygen concentrations, and % total substrate organics). Only benthic identifications were completed on the remaining samples.

Sample Collection

A petite Ponar dredge (Wildlife Supply Company, Saginaw, Michigan) was used to collect benthic macroinvertebrate samples. Material collected in two succesive grabs (0.046 m^2) was pooled and represented a single benthic sample. Each sample was washed through a U.S. No. 30 brass screen (0.600 nm openings). Invertebrates were then contained in 70% ethanol.

Fig. 2. Lake Pepin and stations sampled May 20-21 and June 2, (Sampling Period I) and July 21-22 (Sampling Period II), 1977.


BAY CITY
ISABELL CREEK
MINNESOTA
RUSH CREEK
MAIDEN ROCK
WELL'S CREEK
WISCONSIN
GILBERT CREEK
STOCKHOLM
LAKE CITY
MILLER CREEK
BOGUS CREEK
LOST CREEK
PEPIN
REED'S LANDING

Sediment samples were collected and immediately frozen. Temperature (^{o}C) and dissolved oxygen concentrations (mg/L) were determined using a dissolved oxygen meter (Yellow Springs Instruments Co. Model 54). Depth determinations were made with a survey fathometer (Ratheon Corp. Model DE-719B).

Laboratory Procedures

Taxonomy and Enumeration of Benthic Macroinvertebrates

Benthic organisms were sorted by hand and stored in a 5% glycerin-70% ethanol solution. Later, the organisms were identified to the lowest attainable taxonomic level. Except for the Oligochaeta and Hirudinea, all determinations were made to the generic and occasionally to the specific level. Macroinvertebrate keys found in the following publications were used for identifications: Johannsen (1937), Pennak (1953), Usinger (1956), Roback (1957), Mason (1973), Hilsenhoff (1975), and Merritt and Cummins (1978). The number of taxa/site, number of organisms/site, and the number of organisms/taxon was recorded.

To determine the specific identification of numerous large chironomid larvae collected in this study, last instar larvae were collected during October 1977 and reared to adults in the laboratory. Sediments from Lake Pepin were collected and used as substrate for the rearing experiment; sediments were forced through a fine mesh screen to remove living organisms that may have interfered with the rearing and were then placed in one 10-gal aquarium and two 15-L assay jars. The sediment averaged 15.2 cm deep. Water from the Mississippi River was added to each container and aquarium aerators were employed to assure an adequate supply of oxygen. Approximately 200 larvae were placed in each container and were fed a moderate amount of finely ground commercial dog food (Hartz

Mountain Company). Adults were captured and stored in 70% ethanol. Hypogia of males were cleared in a 10% potassium hydroxide solution, neutralized with acetic acid, and washed in several dilutions of ethanol (95%, 70%, and 50% ethanol). Specimens were then mounted on glass slides in Hoyer's solution. Identifications were made utilizing a key to adults (Johannsen 1937).

Sediment Analyses

Determinations of % total organic content and sediment particle size were made on the sediment. Samples were thawed, homogenized in a blender, and dried in an oven (60°C). Dry material was then triturated using a mortar and rubber pestle.

Particle size analysis was accomplished utilizing the bouyoucos method (Day 1965). A 100 ml aliquot of a 5% polyphosphate solution (Calgon^R) was added to a 40-gm sediment sample. This mixture was then homogenized for a 5-min period. The solution was transferred to a 1-L sedimentation cylinder and water was added to bring the final volume to 1 L. Sediments were suspended by vigorous stirring of the solution for exactly 2 min. When agitation ceased, hydrometer readings were recorded at 0.5, 30, and 120 min. The percentages of sand, silt, and clay were determined using equations cited in Day (1965).

The % of total organic matter was determined using a modified H_20_2 oxidation process (Jackson 1962). Two-gram sediment samples were added to tared 125-ml erlenmeyer flasks. The flasks and their contents were then placed in drying ovens (100°C) for 12 hr, removed and cooled to room temperature in a desiccator, and the combined flask-sediment weights recorded. Reagent grade 30% H_20_2 was then added to oxidize the organic matter. Flasks were gently heated to accelerate the reaction. Oxidation was determined to be complete when the solution no longer produced rapid bubbling after addition of H_2O_2. The flasks were returned to the drying oven for 12 hr. After cooling the flasks to room temperature in a desiccator, the final flask weights were determined. The % of organic matter was determined by the following equation:

$$\%\ \text{total organic matter} = \frac{\text{initial flask wt} - \text{final flask wt}}{2\ \text{g (initial sediment wt)}}$$

Statistical Analyses

Statistical analyses were conducted to evaluate the relationship between selected benthic invertebrates and five independent variables. Both simple and multiple correlation coefficients were determined according to Zar (1974).

Prior to analysis, a log (x + 1) transformation was performed on all dependent variables i.e. benthic invertebrates. This procedure is recommended by Elliot (1971) in order to overcome the deviation from symmetry produced by the aggregated distribution of benthic organisms.

RESULTS

Physical and Chemical Constituents

A survey of the macroinvertebrate population of Lake Pepin was completed during the summer of 1977. The lake was shallower at the upstream end and gradually increased in depth downstream (Fig. 3). Samples were collected from stations with depths ranging from 0.5 to 12.2 m. Dissolved oxygen concentrations at the stations sampled ranged from 0.2 to 12.8 mg O_2/L. Concentrations of 1.5 mg O_2/L or less were encountered at 23.2% and 60.2% of the sites during Sampling Periods I and II, respectively. A marked stratification was noted at many sites during both sampling periods. Much of the severe stratification appeared to be confined to the middle portion of the lake where depths were the greatest.

Sediment samples were collected and analyzed for percent composition of clay, silt, sand, and total organic content. The distribution of sediment types is presented in Figures 4 and 5. Sites with a silt composition of 50% or greater prevailed in the upper portion of the lake, whereas the clay fraction dominated the mid-lake sediments. Although a few scattered stations of the upper portion of the lake had sediments dominated by sand, this particle fraction was more common in the lower reaches of the lake (Figs. 4 and 5). This condition reflects the influence of the Chippewa River bedload.

The % total organic content of sediment in Lake Pepin ranged from 0% to 12.96%. Low organic values were associated with sediments composed

Fig. 3. Lake Pepin and depth (in meters) of stations sampled May 20-21 and June 2, (Sampling Period I) and July 21-22 (Sampling Period II), 1977.

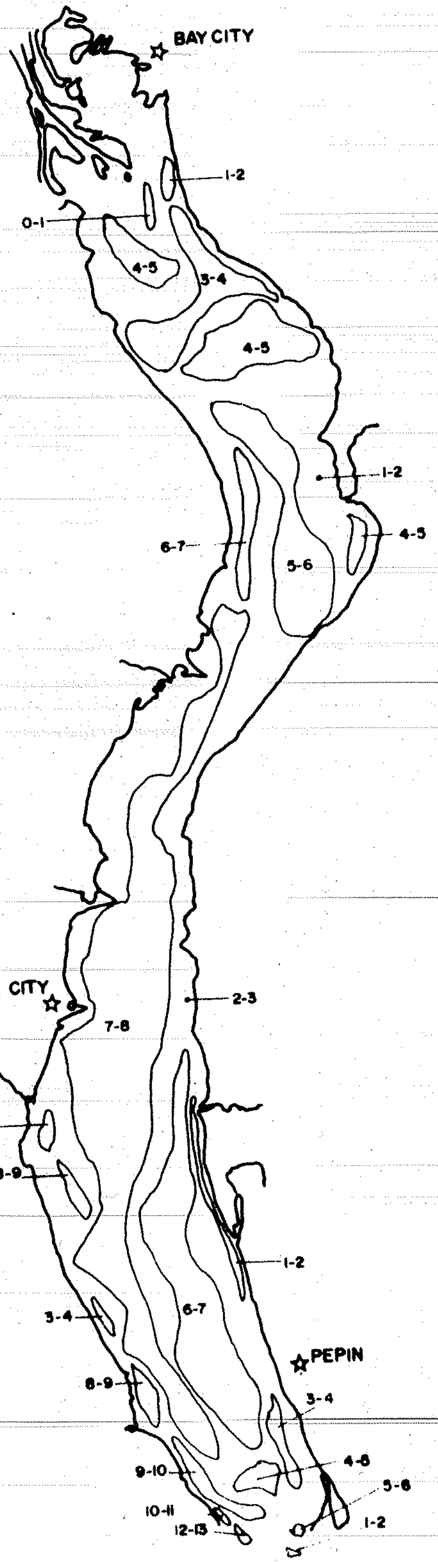
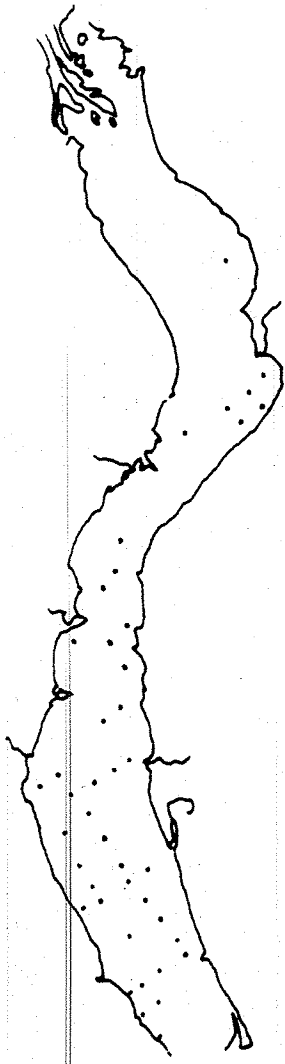
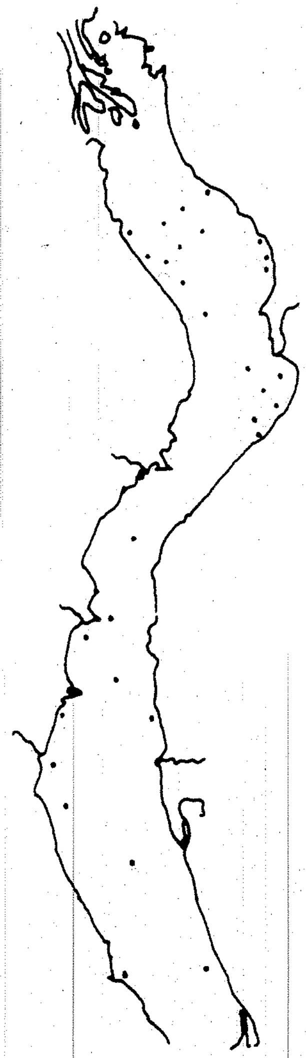

BAY CITY
1-2
0-1
4-5
3-4
4-5
1-2
4-5
6-7
5-6
LAKE CITY
2-3
7-8
5-6
8-9
1-2
6-7
3-4
PEPIN
8-9
3-4
9-10
4-5
5-6
10-11
1-2
12-13

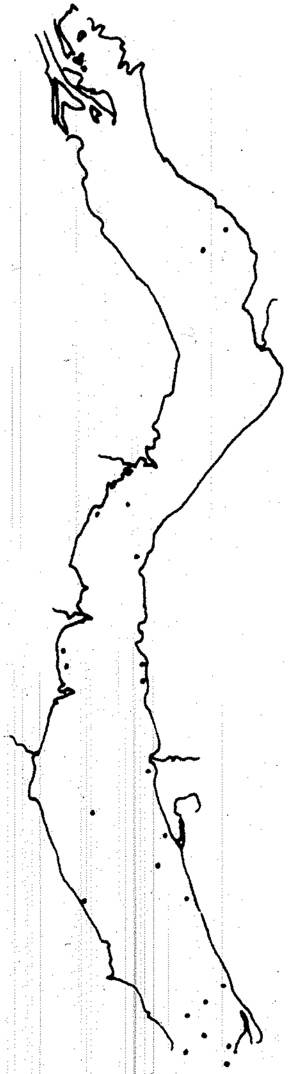
Fig. 4. Location of stations with sediments containing 50% or greater clay, silt, or sand; Sampling Period I.



50% CLAY

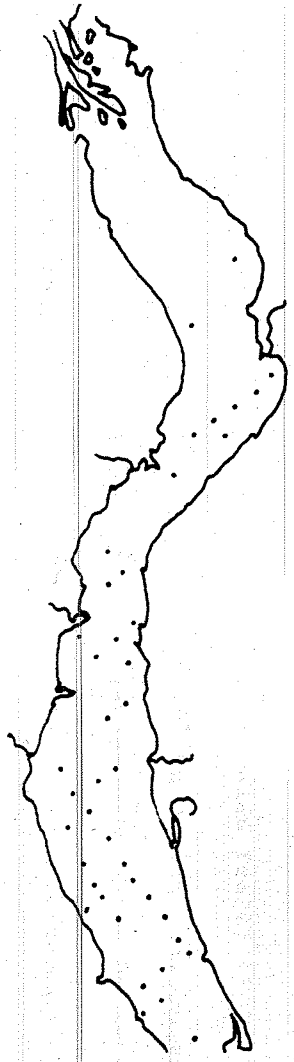


50% SILT

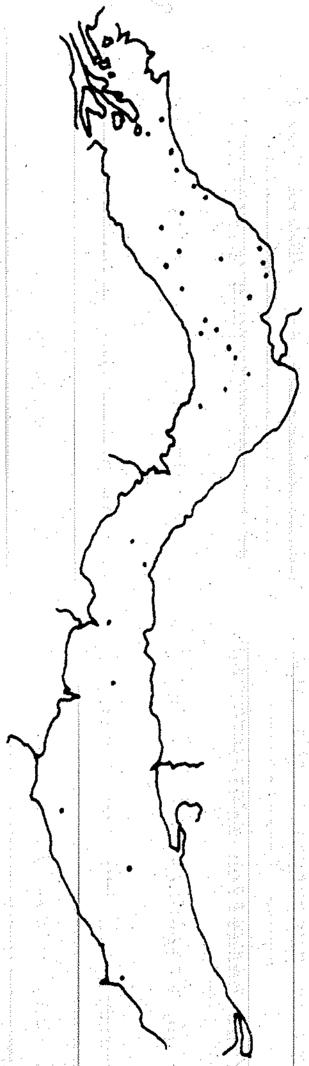


50% SAND

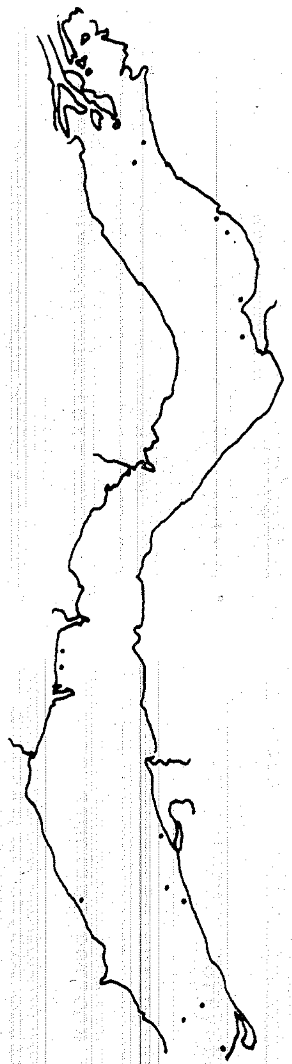
Fig. 5. Location of stations with sediments containing 50% or greater clay, silt, or sand; Sampling Period II.



50% CLAY



50% SILT



50% SAND

primarily of sand while high values were significantly correlated with clay-dominated sediments ($r_{SPI} = 0.427$, $r_{SPII} = 0.546$).

Biological Constituents

A total of 54 taxa were collected during the study. Forty-four taxa were collected during Sampling Period I and 33 collected during Sampling Period II. Twenty-six taxa were common to both sampling periods (Table 1). These taxonomic groups were represented by a total of 38,874 individuals. During Sampling Period I, 20,780 organisms were collected; the second sampling period yielded 18,094 individuals.

As indicated in Table 2, the family Chironomidae, which includes all the chironomid genera and species encountered, was the most abundant taxonomic group. It represented 66% of the total organisms collected during Sampling Period I and 46.9% of the organisms collected during Sampling Period II. In addition to the other less frequently encountered chironomid genera, two major groups, *Chironomus* sp. and *C. plumosus*, comprised the Chironomidae. Although all representatives of the genus *Chironomus* sp. were probably *C. plumosus*, the specific epithet was restricted to fourth instar larvae that could be identified with a large degree of confidence as *C. plumosus*. Fourth instar larvae were those with a head capsule width of 0.60 mm (Hilsenhoff 1966); the determinations were confirmed by the identification of adult males reared from these fourth instar larvae. During the first sampling period, *Chironomus* sp. was the most abundant organism observed; it appeared in 80.9% of the samples. This macroinvertebrate was thus the third most frequently encountered benthic organism. During Sampling Period II, *Chironomus* sp. appeared in 58.4% of the samples, was represented by only 1,148 individuals,

Table 1. Taxonomic list of benthic macroinvertebrates collected in Lake Pepin during the summer of 1977.

- NEMATODA
- ANNELIDA
  - Oligochaeta
  - Hirudinea
- ARTHROPODA
  - Crustacea
    - Malacostraca
      - ISOPODA
        - *Asellus* sp.
      - AMPHIPODA
        - *Hyalella* sp.
  - Insecta
    - EPHEMEROPTERA
      - Caenidae
        - *Caenis* sp. Stephens
      - Ephemeridae
        - *Hexagenia* sp. Walsh
    - ODONATA
      - Coenagrionidae
        - *Enallagma* sp. Charpentier
      - Gomphidae
        - *Ophiogomphus* sp. Selys
    - TRICHOPTERA
      - Unidentified Trichoptera pupae
      - Leptoceridae
        - *Oecetis* sp. Mc Machlan
        - *Ceraculea* sp. Stephens
      - Rhyacophilidae
        - *Rhyacophila* sp. Pictet

Table 1. cont.

COLEOPTERA

Elmidae
- *Dubiraphia* sp. Sanderson
- *Stenelmis* sp. Dufour
- *Optioservus* sp. Sanderson

Chrysomelidae
- *Donacia* sp. Fabricius

Dryopidae
- *Helichus* sp. Erichson

Hydrophilidae
- *Anacaena* sp. Thomson

DIPTERA

Nematocera

Chaoboridae
- *Chaoborus* sp. Lichenstein

Chironomidae
- Unidentified Chironomidae pupae
- *Chironomus* sp. Meigen
- C. *plumosus* Linneaus
- *Cryptochironomus* sp. Kieffer
- *Einfeldia* sp. Thienemann
- *Glyptotendipes* sp. Kieffer
- *Parachironomus* sp. Lenz
- *Polypedilum* sp. Kieffer
- *Coelotanypus* sp. Kieffer
- *Procladius* sp. (Skuse) Edwards
- *Psectrotanypus* sp. Kieffer
- *Tanypus* sp. Meigen
- *Prodiamesia* sp. Kieffer
- *Monodiamesia* sp. Kieffer
- *Paratanytarsus* sp. Bause.
- *Ablabesmyia* sp. Philippi
- *Pseudochironomus* sp. Malloch

Ceratopogonidae
- *Palpomyia* sp. Meigen

MOLLUSCA

Gastropoda

Ctenobranchiata

Amnicolidae
- *Amnicola* sp. Gould and Haldeman

Table 1. cont.

Valvatidae
  Valvata sp. Muller

PLUMONATA
  Physidae
    Physa sp. Draparnaud

  Planorbidae
    Gyraulus sp. Carpentier
    Helisoma sp. Swainson

Pelecypoda

  Unionidae
    Amblema sp.
    Truncilla sp.
    Proptera sp.

  Sphaeriidae
    Unidentified Sphaeriidae
    Musculium sp.
    Pisidium sp.
    Sphaerium sp.

and was the fourth most frequently encountered organism. Although only 2,180 *C. plumosus* larvae were collected during Sampling Period I, it was found at 87.7% of the stations and was the second most frequently encountered benthic invertebrate. This same frequency of occurrence was noted during the second sampling period (Table 2).

The only other taxonomic group to be collected in high abundance was the class Oligochaeta. These macroinvertebrates occurred with the greatest frequency during both sampling periods (Table 2).

Table 2 indicates that representatives of taxonomic groups other than those mentioned above were rarely encountered. Those most notably absent were members of the genus *Hexagenia*. These ephemeropterans were collected at two sites during Sampling Period I (3 nymphs) and at three sites during Sampling Period II (15 nymphs).

Physical and Biological Relationships

In addition to the survey work, an investigation into the influence of several physical variables on the distribution of seven taxonomic groups was conducted. The following seven taxa were selected for analysis primarily because of their abundance:

Chironomidae
C. plumosus
Chironomus sp.
Oligochaeta
Sphaeriidae
Hirudinea
Palpomyia sp.

Although present only in low densities, *Palpomyia* sp. and Hirudinea were included in the analysis to represent predaceous taxa for comparison with the other five non-predaceous groups. Data on the seven major invertebrate taxa were subjected to simple and multiple correlation analyses

Table 2. Total number of organisms collected, frequency of occurrence[1], and rank[2] for Sampling Periods I and II.

Taxonomic Group	Total # S.P. I	Total # S.P. II	Freq. Occur. S.P. I	Freq. Occur. S.P. II	Rank S.P. I	Rank S.P. II
Family Chironomidae	13,646	8,488	-	-	-	-
Chironomus sp.	10,845	1,148	80.9	58.4	3	4
C. plumosus	2,180	6,624	87.7	88.0	2	2
Oligochaeta	6,502	8,950	88.9	91.6	1	1
Procladius sp.	389	567	53.7	59.6	5	3
Chironomidae pupae	54	57	19.8	16.9	7	6
Polypedilum sp.	173	82	13.6	2.4	8	12
Cryptochironomus sp.	43	50	13.6	16.9	8	6
Monodiamesia sp.	80	18	4.9	2.4	12	12
Palpomyia sp.	80	18	28.4	7.8	6	9
Nematoda	6	17	3.7	7.8	14	9
Sphaeriidae	178	215	61.1	51.2	4	5
Psectrotanypus sp.	17	0	4.3	0	13	13
Chaoborus sp.	17	10	6.2	4.8	11	11
Pisidium sp.	23	54	8.0	9.0	10	8
Caenis sp.	11	4	3.7	1.8	14	13
Coelotanypus sp.	9	4	2.5	1.2	15	14
Hexagenia sp.	3	15	1.2	1.8	17	13
Parachironomus sp.	2	0	1.2	0	17	15
Tanypus sp.	12	37	1.2	2.4	17	12
Hirudinea	41	48	2.5	15.1	9	7
Musculium sp.	5	19	1.9	72.3	16	10
Dubiraphia sp.	7	3	0.62	1.8	18	13
Asellus sp.	1	5	0.62	2.4	18	12
Anacaena sp.	2	0	0.62	0		
Heilchus sp.	6	0	0.62	0		
Ophiogomphus sp.	1	0	0.62	0		
Paratanytarsus sp.	32	0	0.62	0		
Oecetis sp.	0	95	0	7.8		
Cryptochironomus sp,	0	1	0	0.6		
Hyalella sp.	20	5	1.23	1.8		
Stenelmis sp.	3	0	1.85	0		
Ceraculea sp.	1	0	0.62	0		
Einfeldia sp.	3	0	1.23	0		
Ablabesmyia sp.	0	1	0	0.6		
Valvata sp.	0	13	0	0.6		

Table 2. cont.

Taxonomic Group	Total # S.P. I	Total # S.P. II	Freq. Occur. S.P. I	Freq. Occur. S.P. II	Rank S.P. I	Rank S.P. II
Pseudochironomus sp.	15	32	1.85	1.8		
Ceratopogonidae pupae	0	1	0	2.4		
Trichoptera pupae	1	0	0.62	0.6		
Rhyacophila sp.	4	0	0.62	0		
Donacea sp.	1	0	0.62	0		
Optioservus sp.	1	0	0.62	0		
Tanypodinae	11	0	0.62	0		
Prodiamesia sp.	1	0	0.62	0		
Gyraulus sp.	1	0	0.62	0		
Proptera sp.	0	1	0	0.60		
Elliptio sp.	1	0	0.62	0		
Helisoma sp.	1	0	0.62	0		
Physa sp.	2	2	0.62	0.60		
Pleurocera sp.	2	1	0.62	0.60		
Amnicola sp.	0	1	0	0.60		
Enallagma sp.	0	1	0	0.60		
Glyptotendipes sp.	3	0	0.62	0		
Amblema sp.	0	1	0	0.60		
Truncilla sp.	0	1	0	0.60		
Total Number of Taxa	44	33				
Total Number of Organisms	20,780	18,904				

[1] Frequency of Occurrence: % of sites at which the organism was collected; based on 162 sites for Sampling Period I and 166 sites for Sampling Period II.

[2] Rank: organisms ranked by frequency of occurrence; only the 18 most abundant organisms were ranked.

with the following six physical features as independent variables:

Depth
Dissolved Oxygen Concentration
% Total Organic Matter
% Clay
% Silt
% Sand

During Sampling Period I, family Chironomidae was negatively correlated with high concentrations of clay and with depth, whereas it was positively correlated with dissolved oxygen at the mud-water interface (Table 3). No significant correlations were noted for the other three physical factors. Strong positive correlations between the family Chironomidae and % total organics, clay, and silt were observed during Sampling Period II. Significant inverse relationships occurred between sand, depth, and the Chironomidae during this same period (Table 3). Significant multiple correlation coefficients of 0.428 and 0.528, respectively, were obtained for Sampling Periods I and II.

Data on C. plumosus revealed significant ($\alpha = 0.01$) positive relationships with the % total organic content of sediment, clay, silt, and depth for both sampling periods (Table 3). Significant correlations existed between this species and both sand and dissolved oxygen concentrations during Sampling Periods I and II. The relationships between C. plumosus and sediment type are also indicated in Figures 6 and 7. The analysis revealed a highly significant relationship between all six physical factors and C. plumosus (Table 3).

Standing crops of Chironomus sp. were inversely related to clay, total organic matter, and depth (Table 3). During both sampling periods positive correlations were obtained between Chironomus sp. and dissolved oxygen concentrations. The associations between Chironomus sp. and the

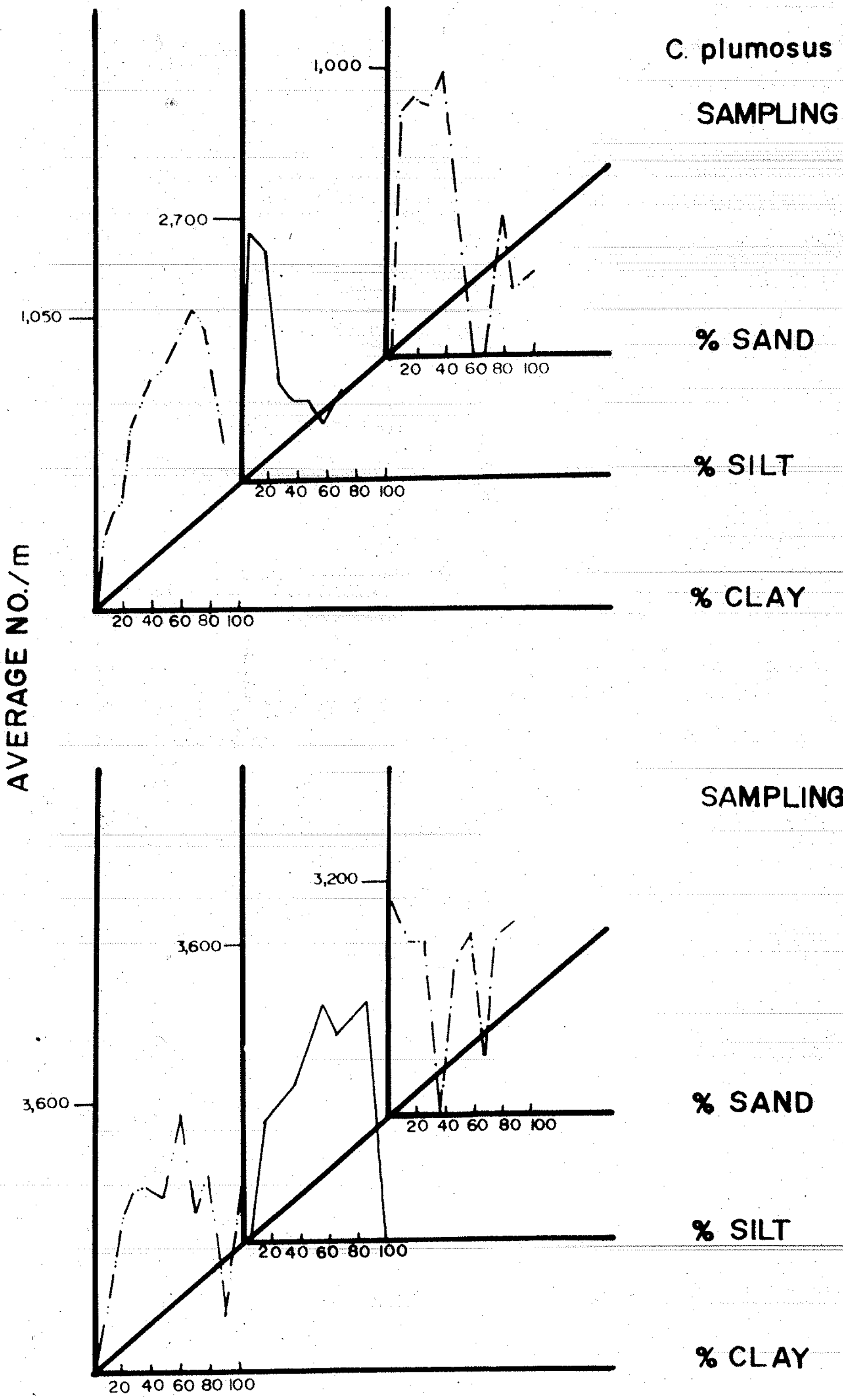
Table 3 . Simple linear[1] and multiple correlations of selected benthic dependent variables with physical factors. Samples were collected in Lake Pepin on May 21-22, June 2 (Sampling Period I) and on July 21-22 (Sampling Period II), 1977.

Taxonomic Group		% T.O.M.[2]	% Clay	% Silt	% Sand	Depth	D.O.[3]	multi-R
Family Chironomidae	I	-0.028	-0.233**	0.052	0.126	-0.355**	0.255**	0.428**
	II	0.303**	0.247**	0.478**	-0.486**	0.169	-0.183*	0.528**
Chironomus plumosus	I	0.429**	0.537**	0.402**	-0.563**	0.672**	-0.361**	0.752**
	II	0.480**	0.479**	0.526**	-0.688**	0.452**	-0.546**	0.735**
Chironomus sp.	I	-0.213*	-0.407**	-0.045	0.285**	-0.539**	0.329**	0.585**
	II	-0.070	-0.250**	0.130	0.072	-0.127	0.325**	0.451**
Oligochaeta	I	0.159	-0.032	0.215*	-0.058	-0.049	0.049	0.393**
	II	0.390**	0.414**	0.422**	-0.564**	0.358**	-0.454**	0.595**
Hirudinea	I	-0.365**	-0.278**	-0.182*	0.289**	-0.346**	0.283**	0.470**
	II	-0.294**	-0.246**	0.053	0.134	-0.328**	0.201*	0.380
Sphaeriidae	I	0.077	0.168	0.047	-0.107	0.215*	-0.233*	0.285*
	II	-0.093	-0.130	0.293**	-0.102	-0.288**	0.129	0.425*
Palpomyia sp.	I	-0.020	-0.273**	0.147	0.079	-0.376**	0.111	0.484**
	II	-0.102	-0.092	0.226**	-0.063	-0.207*	0.087	0.330

---

[1] Sampling Period I, 123 degrees of freedom; Sampling Period II, 116 degrees of freedom
[2] % T.O.M. = % total organic matter in the sediments
[3] D.O. = hypolimnetic dissolved oxygen concentrations
*Significant at the 0.05 level
**Significant at the 0.01 level

Fig. 6. Average number of *Chironomus plumosus* larvae/m^2 encountered in sediments with increasing % concentrations of either clay, silt, or sand.



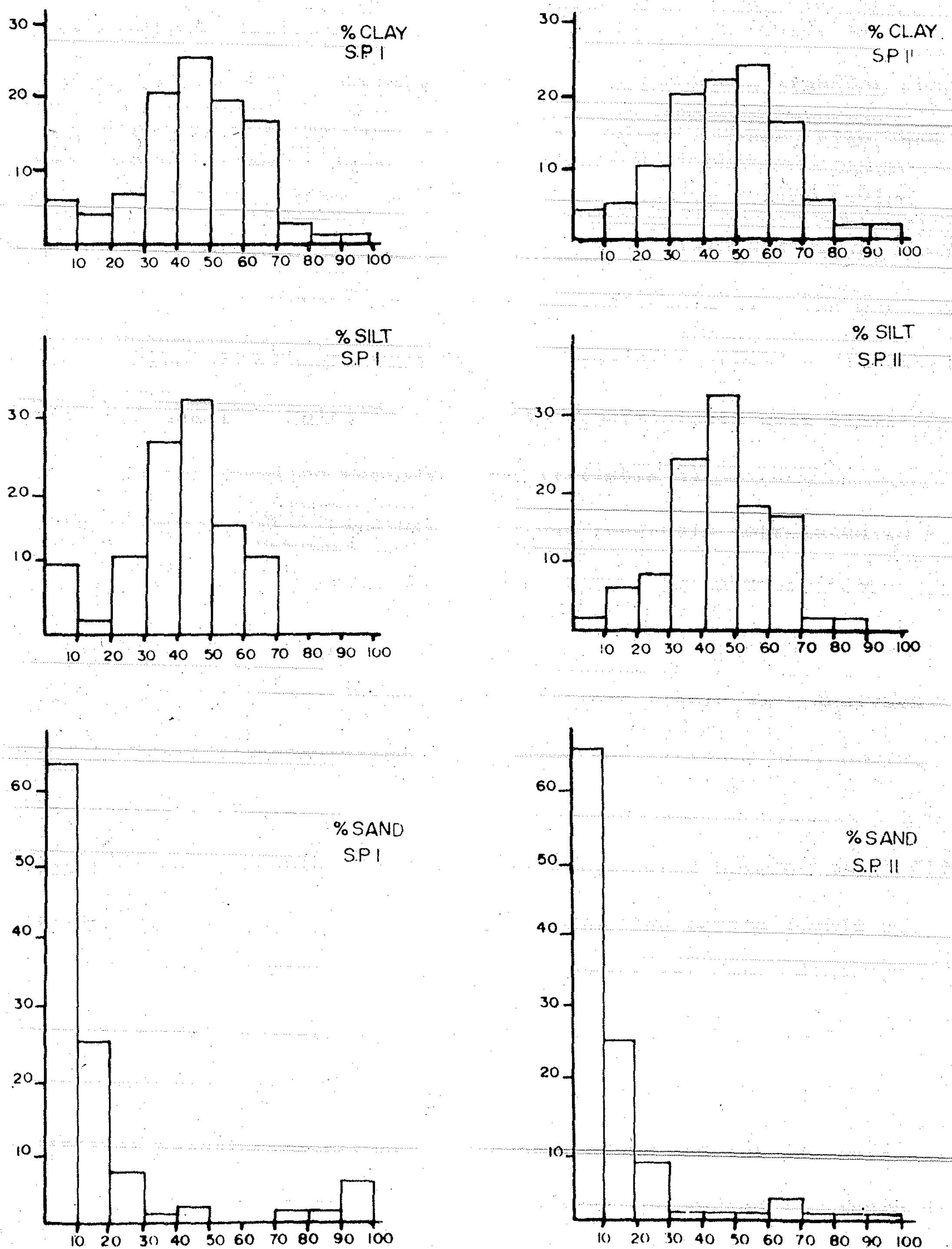
C. plumosus

SAMPLING PERIOD I

SAMPLING PERIOD II

Fig. 7. Number of Chironomus plumosus larvae encountered in sediments with increasing % concentrations of either clay, silt, or sand.

C. plumosus


% CLAY
S.P I
30
20
10
10 20 30 40 50 60 70 80 90 100
% CLAY
S.P II
30
20
10
10 20 30 40 50 60 70 80 90 100
% SILT
S.P I
30
20
10
10 20 30 40 50 60 70 80 90 100
% SILT
S.P II
30
20
10
10 20 30 40 50 60 70 80 90 100
% SAND
S.P I
60
50
40
30
20
10
10 20 30 40 50 60 70 80 90 100
% SAND
S.P II
60
50
40
30
20
10
10 20 30 40 50 60 70 80 90 100

three sediment types are illustrated in Figures 8 and 9. During both sampling periods significant multiple correlation coefficients were obtained (R = 0.0585, $\alpha = 0.01$; R = 0.451, $\alpha = 0.05$, respectively).

A significant positive association existed between Oligochaeta and silt during both sampling periods (Table 3). Oligochaeta standing crops were positively correlated with the % total organic content, clay, and depth during Sampling Period II. Significant negative relationships ($\alpha = 0.01$) were obtained between the Oligochaeta, dissolved oxygen, and the sand substrate for the same sampling period (Table 3). The association between the oligochaetes and the three sediment types is displayed in Figures 10 and 11. Multiple correlation coefficients were significant ($\alpha = 0.01$) during Sampling Periods I and II (Table 3).

Distribution of the order Hirudinea was inversely correlated to total organic content, % clay, depth ($\alpha = 0.01$), and to % silt ($\alpha = 0.05$). These invertebrates were positively associated with the amount of sand and hypolimnetic dissolved oxygen concentrations (Table 3). Analyses resulted in significant multiple correlation coefficients only during Sampling Period I (Table 3).

Positive relationships ($\alpha = 0.05$) were indicated between sphaeriid standing crops and depth during the second sampling period (Table 3). In contrast, negative inverse correlations ($\alpha = 0.05$) were obtained between sphaeriid populations and dissolved oxygen during Sampling Period I and between the Sphaeriidae and depth during Sampling Period II. A significant association between fingernail clams and the six physical factors examined was only indicated during Sampling Period II (Table 3). All associations between Sphaeriidae and the three sediment tyoes are illustrated in Figures 12 and 13.

Fig. 8. Average number of Chironomus sp. larvae/m^2 encountered in sediments with increasing % concentrations of either clay, silt, or sand.

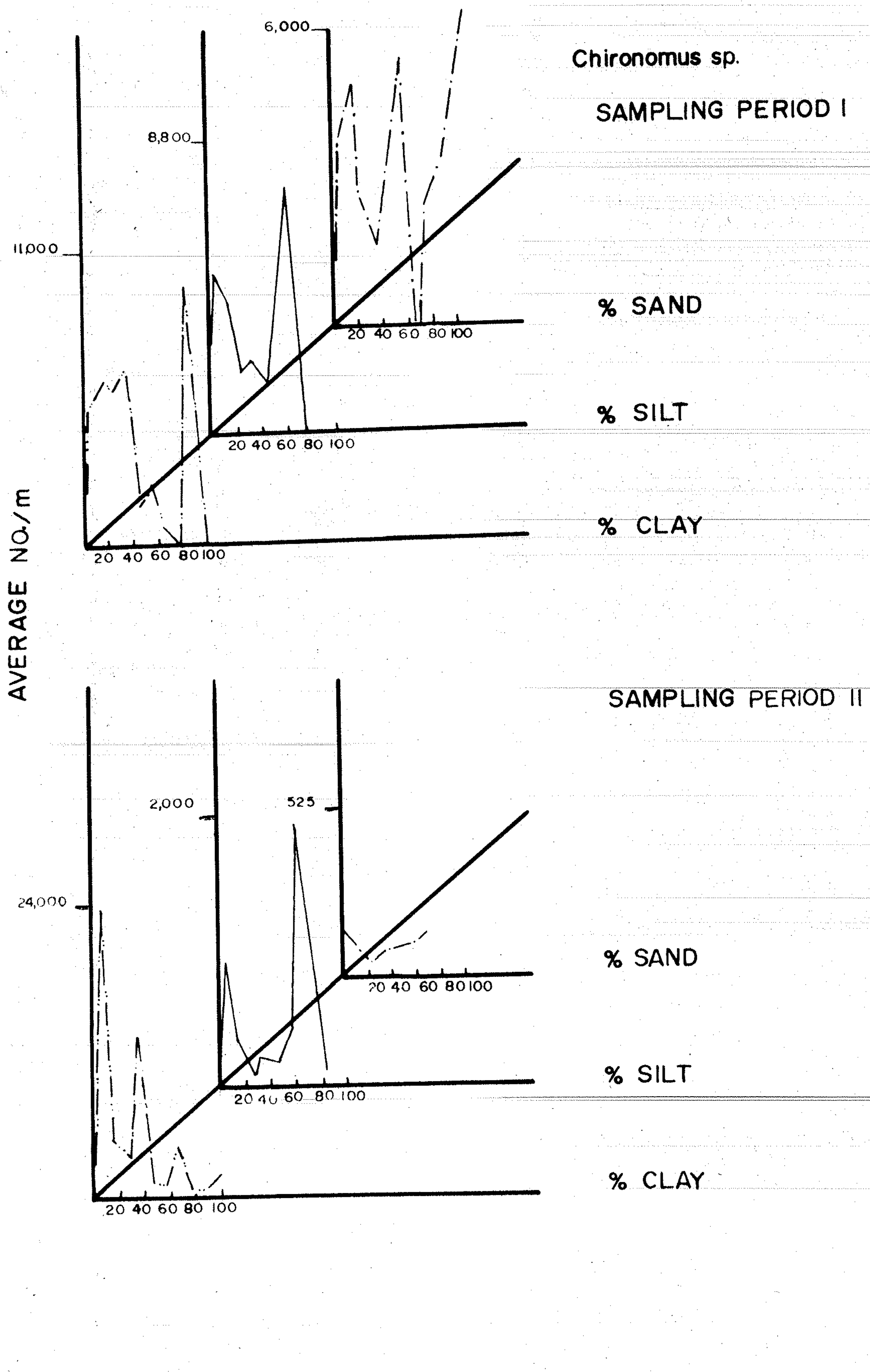

Chironomus sp.
SAMPLING PERIOD I
6,000
8,800
11,000
% SAND
% SILT
% CLAY
20 40 60 80 100
AVERAGE NO./m
SAMPLING PERIOD II
2,000
525
24,000
% SAND
% SILT
% CLAY
20 40 60 80 100

Fig. 9. Number of *Chironomus* sp. larvae encountered in sediments with increasing % concentrations of either clay, silt, or sand.

Chironomus sp.

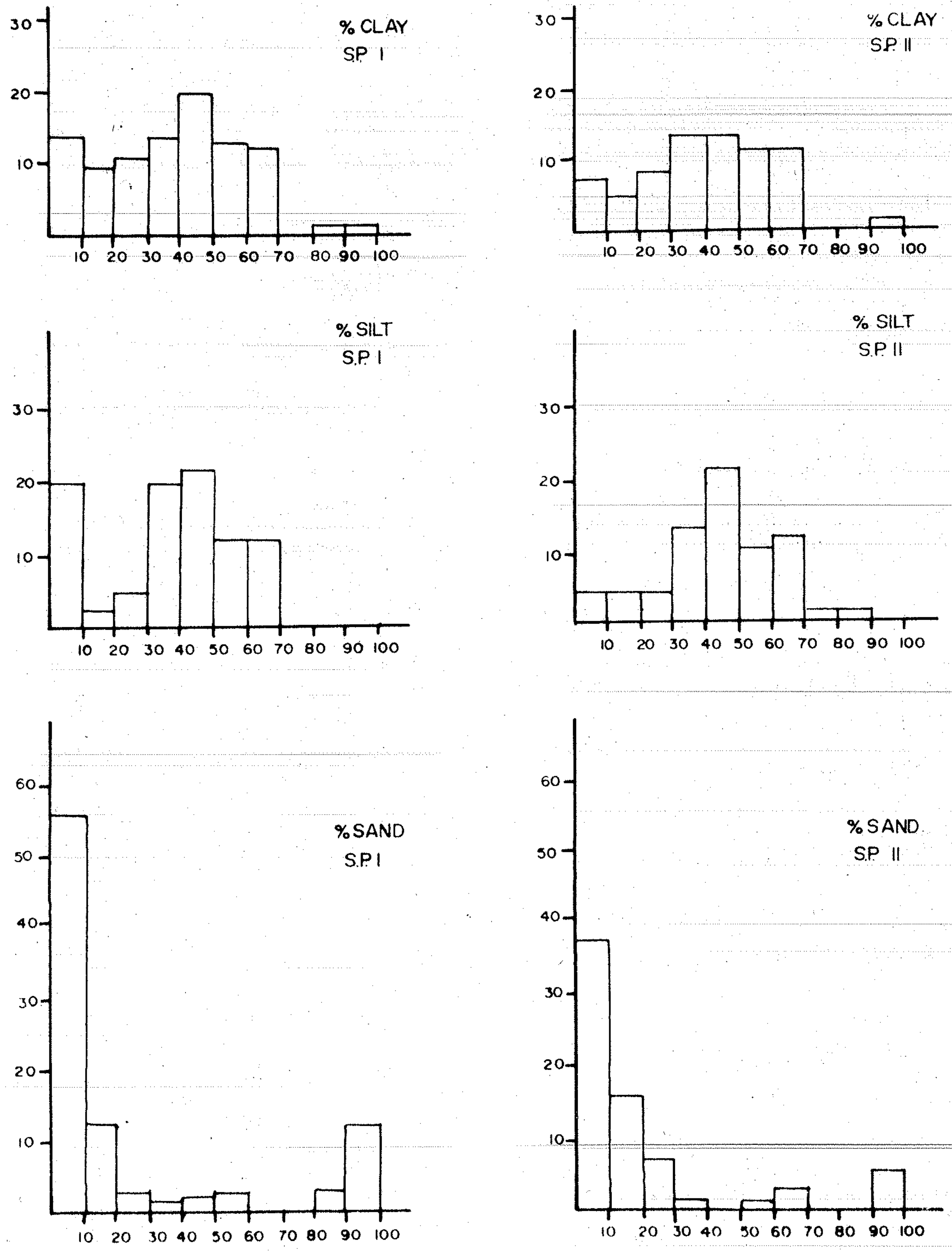
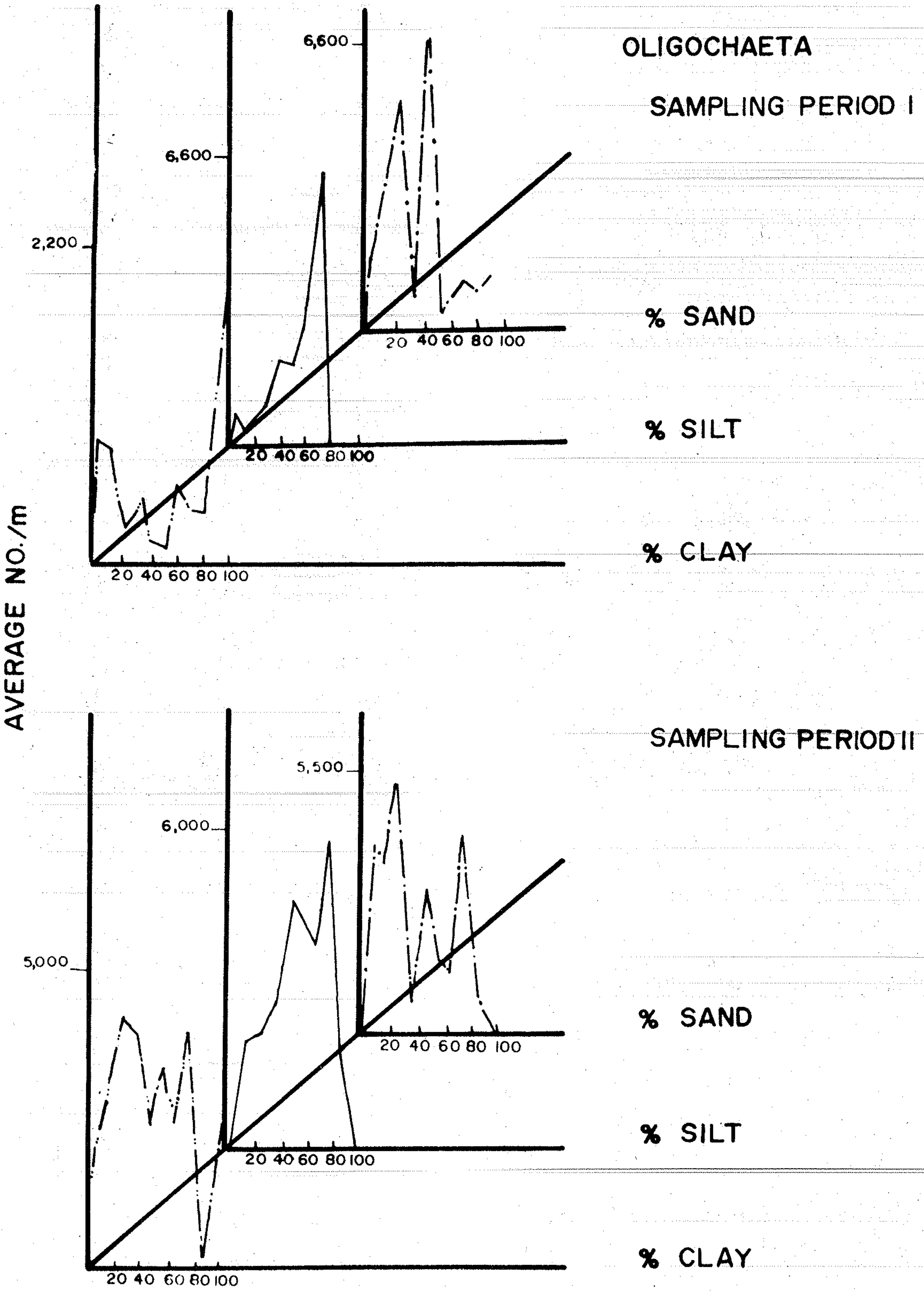


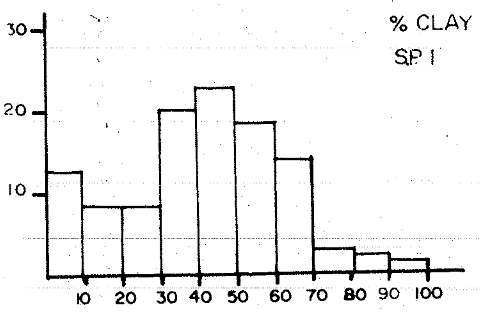
Fig. 10. Average number of Oligochaeta/m^2 encountered in sediments with increasing % concentrations of either clay, silt, or sand.

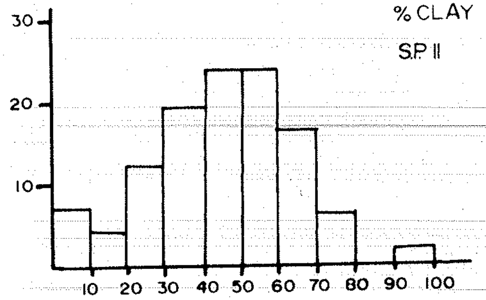


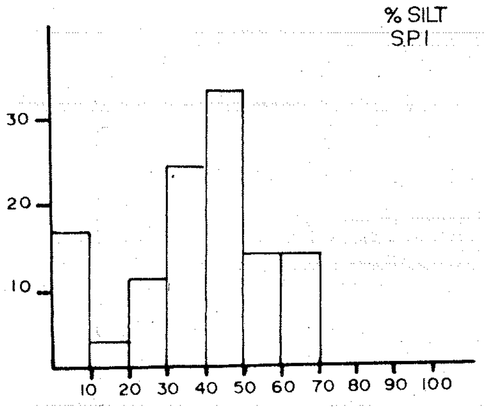
OLIGOCHAETA

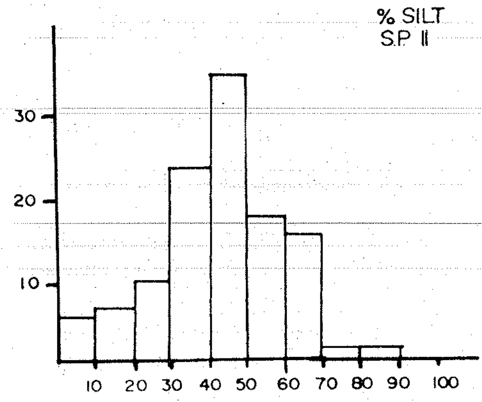
Fig. 11. Number of Oligochaeta encountered in sediments with increasing % concentrations of clay, silt, or sand.

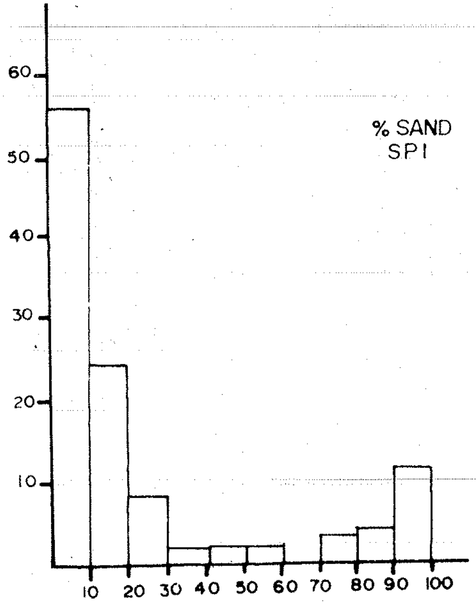
OLIGOCHAETA











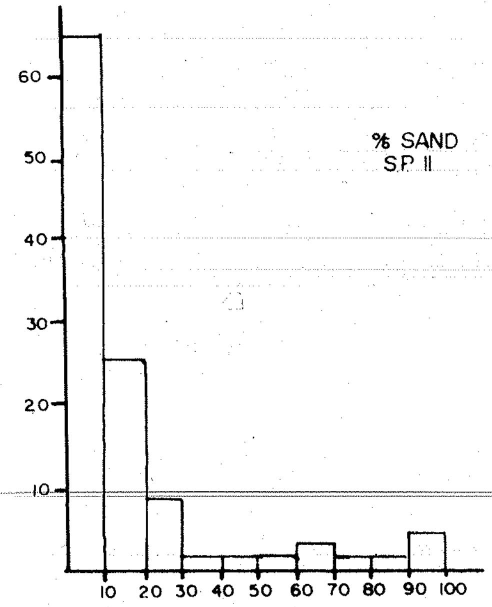


Fig. 12. Average number of Sphaeriidae/m^2 encountered in sediments with increasing % concentrations of either clay, silt, or sand.

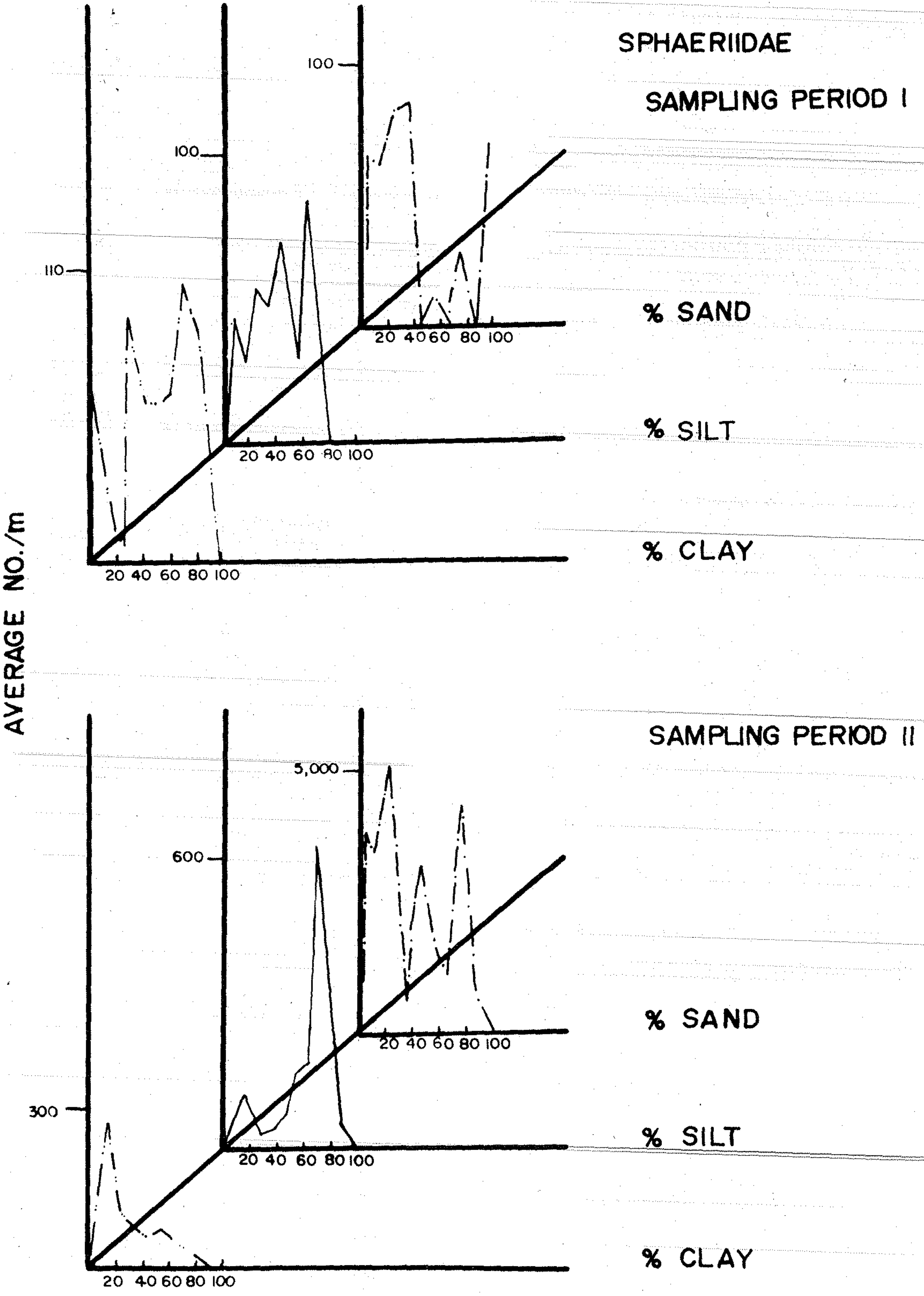
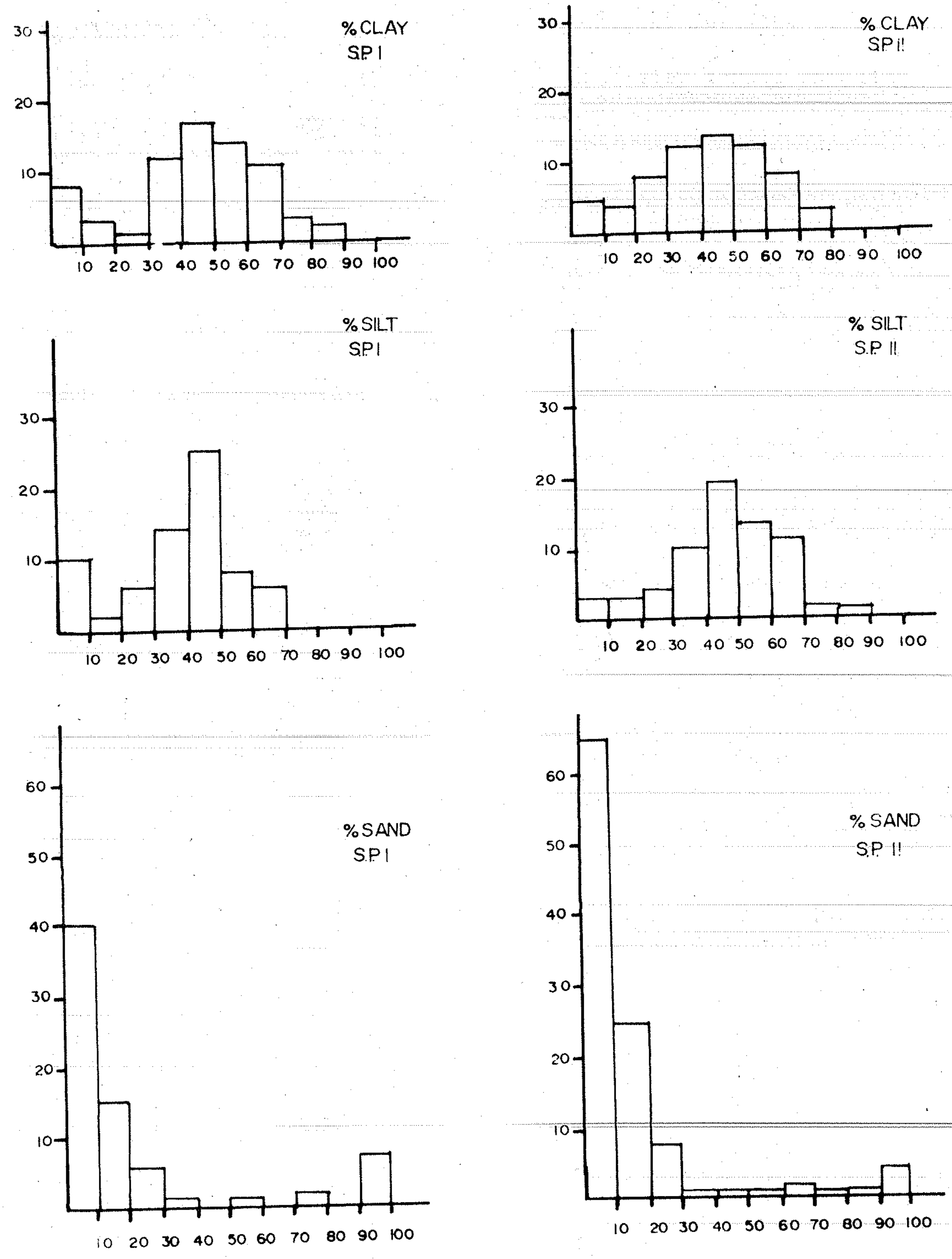

SPHAERIIDAE
SAMPLING PERIOD I
100
100
110
% SAND
20 40 60 80 100
% SILT
20 40 60 80 100
% CLAY
20 40 60 80 100
AVERAGE NO./m
SAMPLING PERIOD II
5,000
600
300
% SAND
20 40 60 80 100
% SILT
20 40 60 80 100
% CLAY
20 40 60 80 100

Fig. 13. Number of Sphaeriidae encountered in sediments with increasing % concentrations of either clay, silt, and sand.

SPHAERIIDAE



Significant negative correlations were observed between *Palpomyia* sp. and clay during Sampling Period I and with depth during both periods. The % clay and *Palpomyia* sp. standing crops were positively correlated during Sampling Period II (Table 3). A significant multiple correlation coefficient ($R = 0.484$; $\alpha = 0.01$) was indicated only during Sampling Period I.

DISCUSSION

The water quality of the Mississippi River between Minneapolis-St. Paul and the upper end of Lake Pepin has severely declined, apparently from heavy organic pollution and relatively high silt loads (Galtsoff 1924; Wiebe 1927; Johnson and Munger 1931; Ellis 1931, 1936; Fremling 1964b). Prior to 1938 the Minneapolis-St. Paul Metropolitan Wastewater Treatment Plant had no mechanism for removing high biochemical oxygen demand (BOD) materials. Between 1938-1966, BOD removal was accomplished by primary treatment only. A secondary treatment system was not operational until 1966 (Metropolitan Wastewater Commission Annual Report 1975). In addition to receiving a high organic load for the past several decades, Lake Pepin has also served as a deposition site for large quantities of silt (Ellis 1931,1936). The combined action of those two materials has long been implicated as the primary cause in the alteration of the aquatic community of the lake (Grier 1922; Ellis 9131, 1936; Johnson and Munger 1931; Fremling 1964b). The effects of erosion, siltation, and organic pollution are still of great concern, and recently chemical contamination of the lake (e.g. heavy metals and polychlorinated biphenyls) has been siginificant (Citizens for a Clean Mississippi Newsletter 1978, 1979).

Lake Pepin, with a mean depth of 5 m, is relatively shallow compared to other lakes. However, it does constitute the deepest reach of the Upper Mississippi River. The river above the lake is comparatively shallow and seldom exceeds 6 m. Its current velocity is greater than that in the lake. In a 1921 survey Galtsoff recorded a current velocity of 0.42 m/sec at a site one mile above the inlet of Lake Pepin. The current velocity in the lake ranged from 0.03 m to 0.25 m/sec (Galtsoff 1924). Thus the depth (maximum depth = 17.1 m), the slow current velocity, and a slope of 1.5×10^{-3} m/km all contribute to the trapping efficiency of Lake Pepin. According to several indices utilizing nitrogen and phosphorus loading (Sakamoto 1966, Vollenweider 1970, Carlson 1977), the surface water of Lake Pepin is a highly productive, eutrophic system. However, these indices do not consider lake flushing rates and retention times. Dillon (1975) devised a model which included these factors in addition to mean depth and areal loading. The model provided a method to calculate a corrected nutrient loading rate for lakes. The corrected loading rate for Lake Pepin is 0.755 g P/m^2/yr rather than 34.380 g P/m^2/yr as reported by the USEPA (1975). This corrected value is comparable to Lake Erie which has a phosphorus loading rate of 0.424 g/m^2/yr. Therefore, with the corrected P-loading value, Lake Pepin can still be categorized as a very eutrophic system. Without the short retention period of 9 da, the nutrient-rich water would remain in the lake for a more extensive period and would have a more profound effect on the trophic status of the lake. Although fluctuations in nutrient loads received by Lake Pepin occur, the lake receives significant nutrient input throughout the year from its tributaries. Large sporadic discharges of raw sewage by the Minneapolis-St. Paul Municipal Combined Sewage System also contribute substantial organic material to the Upper Mississippi River (Citizens for a Clean Mississippi Newsletter 1978).

The phytoplanktonic species composition and summer chlorophyll a concentrations are also characteristic of a highly productive, eutrophic system. The mean summer chlorophyll *a* concentrations (14.9 μg/L) reported for Lake Pepin (USEPA 1975) categorized the lake as eutrophic (Sakamoto 1966, Rhode 1969). The summer phytoplankton was dominated by members of the Cyanophyta, the blue-green algae. This group as a whole is characteristic of highly productive waters (Hutchinson 1967). During the warmer months, massive algal blooms composed in part by *Anacystis* sp. and *Aphanizomenon flos-aquae* develop in productive temperate lakes. These blooms are indicative of eutrophic systems and occur primarily in hard water containing sufficient concentrations of sodium. Blue-green algae have a relatively high sodium requirement, and sewage and stormwater runoff have high concentrations of this needed ion.

Two members of the Bacillarophyta, *Synedra* sp. and *Cocconeis* sp., are also found in Lake Pepin. In some seasons highly productive lakes of the temperate region are dominated by eutrophic diatom populations. *Synedra* sp. is one diatom included in this group (Hutchinson 1967, Palmer 1969). The green alga, *Kirchneriella* sp., which is usually encountered in fertile ponds and shallow lakes, is also abundant in Lake Pepin (USEPA 1975). In June 1972, *Dinobryon* sp. comprised a significant portion of the phytoplankton (USEPA 1975). This unicellular alga is often associated with oligotrophic systems (Rawson 1956); however, it is not unusual to find *Dinobryon* sp. in very productive waters during seasons of nutrient depletion such as that following spring diatom blooms (Pearsall 1932, Hutchinson 1967).

Data on the composition of the macroinvertebrate community substantiates the eutrophic status of Lake Pepin. The community surveyed during the present study was dominated by the family Chironomidae and by *Chironomus* sp. in particular (Table 2). The combined number of individuals represented by *Chironomus* sp. and *C. plumosus* comprised 63% of the total benthic community sampled in the first sampling period and 43% of the organisms collected during the second sampling period (Table 2). The other major macroinvertebrate group encountered in the survey was the Oligochaeta. Members of this class constituted 31.0% and 49.5%, respectively, of the invertebrates gathered during Sampling Periods I and II (Table 2). The 41 remaining taxonomic groups accounted for 6.3% of the organisms collected during Sampling Period I. Thirty-one taxa, exclusive of Oligochaeta, *Chironomus* sp. and *C. plumosus*, represented 7.6% of the individuals gathered during the second sampling period (Table 2). It is well established that stable, undamaged ecosystems support communities generally composed of numerous taxa representing various trophic levels. No single component of a community should be present in densities that create an obvious population imbalance. Roback (1974) reviewed data gathered from a number of studies on both damaged and undamaged systems. Undamaged systems were composed of insect families that represented 3%-23% of the total community. In damaged ecosystems, the percentages represented by certain families increased while others decreased. In addition, the number of species comprising each family decreased, and the community progressed toward the establishment of monotypic assemblages (Roback 1974). The depauperate pollution-tolerant macroinvertebrate community found in Lake Pepin during the present study clearly categorizes the lake as a damaged ecosystem.

The use of organisms as indicators of polluted and non-polluted biocenoses is controversial; however, the concept of indicator communities has merit if the user is aware of its limitations (Roback 1974). The macroinvertebrate assemblage found in Lake Pepin, which is dominated by the Oligochaeta and *Chironomus plumosus* with representatives of the Sphaeriidae and *Palpomyia* sp., is indicative of highly eutrophic systems (Nuttal and Bielby 1973, Olive and Smith 1975, Shiozawa and Barnes 1977).

The Sphaeriidae inhabiting Lake Pepin were primarily represented by *Sphaerium transversum* and smaller standing crops of *Pisidium* sp. *Sphaerium transversum* is a member of the group *Musculium* which is regarded by many malacologists as congeneric or subgeneric to *Sphaerium* (Fuller 1974). Presently, *Musculium* is regarded as a distinct genus, and *Musculium transversum* is considered the more correct designation (Fuller personal communication). These invertebrates were observed in the present survey but in low numbers (Table 2). In an earlier study Wiebe (1927) collected 3,013 sphaeriids/m^2 from a station located on the northern end of Lake Pepin. The Sphaeriidae represented only 0.99% and 1.6%, respectively, of the total macroinvertebrate fauna collected during Sampling Periods I and II. This organism responds positively to highly eutrophic systems such as those resulting from sewage effluent and is not adversely affected until the macroinvertebrate faunal variety is greatly reduced (Richardson 1928, Carr and Hiltunen 1965, Weber 1973, Fuller 1974). In view of the low macroinvertebrate variety and the reduced numbers of Sphaeriidae collected, it can be concluded that conditions in Lake Pepin have deteriorated since 1927. The system is no longer capable of supporting large populations of this pollution-tolerant organism.

Although no attempt was made to isolate or enumerate the Tubificidae collected, it was apparent that this family was the major representative of the class Oligochaeta. During Sampling Period I, the average oligochaete density was 1,729/m^2 while a density of 2,322/m^2 was recorded for

Sampling Period II (Table 2). Members of the class Oligochaeta are found in a wide variety of habitats. In North America freshwater oligochaetes are represented primarily by members of the family Tubificidae, which consists of approximately 60 spieces (Brinkhurst and Cook 1974). Members of this class feed on bacteria via ingestion of sediment. The quality and quantity of organic material reaching the sediments affects the bacterial community composition. Therefore, organic matter has a more significant role in governing which oligochaete species will be present in a particular habitat than other commonly measured chemical and physical variables (Brinkhurst and Cook 1974). The Oligochaeta, more specifically the family Tubificidae, are regarded as very tolerant to organic pollution (Richardson 1925, 1928; Gaufin and Tarzwell 1956; Brinkhurst 1962; Weber 1973; Brinkhurst and Cook 1974). Aquatic systems subjected to heavy siltation, a highly organic silt load, and associated deoxygenation tend to have sediments increasingly occupied by the Tubificidae (Brinkhurst and Cook 1974). Howmiller (1977) surveyed 26 Wisconsin lakes and recorded densities of Tubificidae found in each lake. He arbitrarily chose a density of 1,000 Tubificidae/m^2 as the value separating lakes with low and high oligochaete standing crops. Tubificid densities exceeding 1,000/m^2 are infrequently encountered except in the presence of organic pollution (Howmiller 1977). Howmiller (1974) collected approximately 1,000 tubificid worms/m^2 in Lake Pepin and grouped the lake with other eutrophic waters. The tubificid densities reported by Howmiller agree with the findings of the present study (Table 2) and also affirms that Lake Pepin is an enriched system receiving organic contaminants.

The macroinvertebrate fauna of Lake Pepin was dominated by *Chironomus* sp. during Sampling Period I and during Sampling Period II. This genus ranked second in frequency of occurrence behind the oligochaetes (Table 2). Associations between Oligochaeta and Chironomidae are quite common, particularly in aquatic systems receiving high silt and/or organic loads (Richardson 1925, 1928; Nuttal and Bielby 1973; Howmiller 1974, 1977; Shiozawa and Barnes 1977). The similar correlations between standing crops of Oligochaeta and Chironomus sp. and the various examined physical factors (Table 3) reinforce the fact that they have several common requirements that, when optimally met, result in the presence of substantial numbers of both groups (Howmiller 1977). The presence of large numbers of Chironomus plumosus is indicative of organic pollution and low oxygen conditions (Richardson 1928, Johnson 1929, Johnson and Munger 1931, Mundie 1957, Grodhaus 1963, Fremling 1964, Carr and Hiltunen 1965, Augenfeld 1967, Weber 1973). Lakes supporting large populations of chironomids generally have a mean depth of less than 15 m and receive a high concentration of nutrients from their watershed (Grodhaus 1963). Brundin (1958) devised a lake classification system based on the dominant species of Chironomidae in the benthic community. Accordingly, C. plumosus was indicative of extremely eutrophic systems. A more precise definition of the relationship between Chironomidae and the trophic status of lakes was proposed by Mundie (1957). The species of Chironomidae predominant in a lake is not determined by lake productivity, but by the oxygen deficiency of the hypolimnion. In most lakes, however, eutrophy is associated with a low, hypolimnetic oxygen concentration, which therefore results in a correlation between lake type and the predominant midge species (Mundie 1957). Based on nutrient input, oxygen regime, and the domination of the macroinvertebrate population by C. plumosus, Lake Pepin could be classified as a highly eutrophic lake.

The present survey of the macroinvertebrate community in Lake Pepin found 3 members of the genus *Hexagenia* during Sampling Period I and 15 nymphs during Sampling Period II. Lake Pepin historically had a macroinvertebrate community dominated by the burrowing mayfly, *Hexagenia*. Although commonly found in eutrophic lakes with silt-clay substrates, members of this genus are unable to withstand oxygen depletion (Hunt 1953; Lyman 1956; Swanson 1967; Nebecker 1972). Exposure to oxygen concentrations of 1.4 mg/L or less is fatal in 96 hr (Nebecker 1972). No major mayfly emergence occurred in Lake Pepin prior to the first sampling period, and even though mayfly emergences had taken place before Sampling Period II (Fremling 1964a), *Hexagenia* nymphs should have been encountered in far greater numbers even if only a small population were present. This survey found that the benthic assemblage of Lake Pepin was composed of *Chironomus plumosus*, Oligochaeta, and Sphaeriidae, and lacked representatives of *Hexagenia*. Therefore, the deterimental factors cited by Wiebe (1927), Johnson (1929), Johnson and Munger (1931), Ellis (1931), and Fremling (1964b), which were thought to have produced the initial change in the macroinvertebrate community in Lake Pepin, were still present and contributing to the decrease in water quality of this aquatic system.

Similar conversions of communities dominated by *Hexagenia* to those dominated by the *Chironomus*- Oligochaeta-Spaheriidae complex have occurred in other aquatic systems. Richardson (1925,1928) recorded the change in the macroinvertebrate fauna of the Illinois River above Peoria Lake. That section of the river was grossly contaminated by sewage from the Chicago area. In less than a 10-yr period, Richardson documented the complete disappearance of pollution-sensitive organisms such as *Hexagenia* bilineata and reported the establishment of a pollution-tolerant assemblage composed of Chironomus plumosus, Tubificidae, and Musculium transversum. The portion of river most severely contaminated was north of Havana, Illinois. In that area the current was slowest and the most extensive sedimentation occurred.

The following series of studies documented the changes which occurred in Western Lake Erie: Britt (1955 a,b), Beeton (1961), Carr (1962), and Carr and Hiltunen (1965). Samples taken in the lake indicated the presence of an abundant Hexagenia population with an average density of 139 organisms/m^2 (Carr and Hiltunen 1965). Prior to 1953, a Hexagenia sp. density of 400 nymphs/m^2 was recorded in the island region of the lake (Britt 1955a). A prolonged period of calm weather during late August and early September, 1953, resulted in thermal stratification and hypolimnetic oxygen depletion. Within a week after the development of the above conditions, Hexagenia densities decreased to 44 nymphs/m^2 (Britt 1955a). Subsequent sampling revealed a rapid recovery in 1954 (Britt 1955b), but by 1957 the population again declined to 39 nymphs/m^2 (Beeton 1961). Failure of the population to recover by 1961 was further substantiated by investigations of Carr and Hiltunen (1965). Concurrent with the decline of Hexagenia sp., increases in Musculium transversum, Oligochaeta (Carr and Hiltunen 1965) and Chironomus plumosus (Beeton 1961) were reported. These shifts in the benthic community were attributed to increased organic enrichment of the sediments.

Similar to Lake Erie, Oneida Lake in New York is a relatively shallow lake with a mean depth of 7.6 m (Clady 1975). The lake drains a nutrient-rich watershed and is surrounded by flat terrain, fully exposing its surface to prevailing winds (Clady 1975). Between 1956 and 1964, periods of calm weather occurred, producing temporary thermal stratification and subsequent oxygen deficits that caused a decline in the *Hexagenia* population (Jacobsen 1966). This decrease was accompanied by an increase in the *Chironomus* population (Jacobsen 1966, Clady 1975) which indicated that enrichment of the lake occurred.

Events that have taken place in Lake Pepin are similar to those that occurred in the above aquatic systems. Johnson and Munger (1931) reported that the succession from a community dominated by *Hexagenia* to one dominated by *Chironomus plumosus* occurred in less than 10 yrs. The present study clearly indicates that the Lake Pepin *Hexagenia* population, like that of Lake Erie, has not recovered (Table 2). Lake Pepin resembles the section of the Illinois River studied by Richardson (1925, 1928) in that the current velocity in both systems decreases and allows sedimentation to take place. Furthermore, Lake Pepin and the portion of the Mississippi River to its north have historically received organic effluents from a large metropolitan area. Reports indicate that the Minneapolis-St. Paul Metropolitan Sewage Treatment Plant repeatedly exceeds the National Pollutant Discharge Elimination System Regulation (Permit No. MNS029815) limits of 40 mg/L BOD and 40 mg/L TSS (total suspended solids). During April 1979 BOD and TSS averaged 67/mg/L and 116 mg/L, respectively, which means during that period 189,602 kg of solids entered the river per day (Citizens for a Clean Mississippi Inc. Newsletter 1979). A 0.64 cm rainfall in the Twin Cities area resulted in stormwater effluent containing 5,443 kg BOD, 1,814 kg oil and grease, and 15,876 kg of TSS (Citizens for a Clean Mississippi Inc. Newsletter

1978). The amounts of salt, heavy metals, fertilizers, and untreated wastes leaving the sewage treatment plant were not documented.

The dramatic oxygen deficit observed in Lake Pepin during the two sampling periods was undoubtedly produced by large amounts of organic material and silt reaching the lake. The oxygen demand of this material was sufficient to severely reduce hypolimnetic oxygen. This situation, like that documented for Lakes Erie and Oneida, can become particularly severe during periods of calm weather such as those experienced during Sampling Period II. During this period over 60% of the stations sampled had hypolimnetic concentrations $\leq$ 1.5 mg O_2/L. *Hexagenia* sp. are incapable of surviving longer than 30-48 hr when exposed to 1.0 mg O_2/L (Hunt 1953). Thus, the benthic community of Lake Pepin continued to be dominated by organisms such as *C. plumosus* and oligochaetes that can survive periods of low dissolved oxygen or even anaerobic conditions.

Benthic Community Relationships

The distribution of the family Chironomidae was positively correlated with % total organic material in sediments and with silt particles. Negative correlations were calculated between this family and sand and depth (Table 3). Upon examination, however, conflicting results concerning the relationship between the Chironomidae, clay, and hypolimnetic oxygen content were obtained. Because greater than 90% of the members of this family were represented by *Chironomus* sp. and *C. plumosus*, analyses of these taxa were conducted to delineate and reconcile these contradictory correlated coefficients.

According to taxonomic determinations made in this study, *Chironomus* sp. was composed of larvae that could not be positively identified as

C. plumosus. Based on rearing studies, however, it is reasonable to conclude that these larvae represented first, second, and third instars of *Chironomus plumosus*. In this study the epithet *C. plumosus* was arbitrarily limited to larvae having head capsule widths greater than 0.75 mm. The contention that all members of *Chironomus* sp. can be categorized as *C. plumosus* is supported by data reported by Hilsenhoff and Narf (1967) who found that greater than 96% of the larvae identified as *Chironomus* sp. were *C. plumosus*.

Larger fourth instar larvae were strongly correlated with total substrate organic matter, depth, clay, and silt. The standing crop of *C. plumosus* was inversely related to sand and oxygen concentrations (Table 3, Figs. 6 and 7). Their strong association with substrates such as clay and silt and negative correlation with inpenetrable, unstable sand is reasonable because of the burrowing and tube-building habit of *C. plumosus* larvae. Eggleton (1931) found few benthic macroinvertebrates in sand sediments of Douglas Lake. McLachlan and McLachlan (1971) reported that high concentrations of coarse sand had an adverse affect on midge larvae. McLachlan and Cantrell (1976) did not find *Chironomus plumosus* in sand but only in sediments where they could burrow and build tubes. Large quantities of chironomid larvae have been collected from sand sediments (Arshad and Mulla 1976, Barber and Kevern 1973). However, these reports described stream systems and not lakes. In addition to providing a suitable habitat, sediments dominated by silt and clay also have an affinity for organic matter, which can act as a nutrient source for larvae. Although *C. plumosus* is usually reported as a filter-feeding organism, several studies indicated that these invertebrates feed, at least in part, on sediment detritus (Jonasson 1965, Kajack and Warda 1968, Bryce and Hobart 1972). Furthermore, filter-feeding is probably restricted to the shallower littoral zone (Kajack and Warda 1968).

The positive relationship between *C. plumosus* and depth observed in this study is well documented (Dugdale 1955, Czeczuga 1960, Buckley and Sublette 1964, Kajak and Warda 1968, Burbanck and Mozely 1969, Davis 1971, Carter 1976). The increase in standing crop with increasing depth coincides with the negative correlation between larvae and dissolved oxygen. These relationships indicate that the distribution of *C. plumosus* is not dependent on oxygen concentrations because the larvae can withstand low oxygen conditions. Migration to the profundal zone allows *C. plumosus* to escape potential predators whose presence is excluded by lack of sufficient oxygen.

A difference in habitat preference with larval age was documented in the present study. Scott (1958) observed that habitat requirements of trichopteran larvae changed with the age of larvae. Czeczuga (1960) indicated that older *C. plumosus* instars were found in deeper layers of the substratum than were younger instars. The relationships between *Chironomus* sp. and the physical factors examined differ greatly from the associations between the older fourth instars and the same physical features (Table 3). A positive association existed between the standing crop of the younger instars represented by *Chironomus* sp. in Lake Pepin and substrates containing sand. Additionally, this taxon was strongly correlated with dissolved oxygen concentrations. Clay sediments, % total organics, and depth were negatively associated with *Chironomus* sp. (Table 3). The relationship between *Chironomus* sp. and various sediment types was supported by the number of individuals associated with varying concentrations of clay, silt, and sand but not by the occurrence at these same concentrations (Figs. 8 and 9). The negative association between *Chironomus* sp. and sediment organic content, depth, and clay can be partially attributed to low dissolved oxygen associated with each of these factors. Jonasson (1971) observed that the ability of larvae to penetrate the microstratification which occurs at the mud-water interface is related to the irrigation current produced by larvae. Smaller-bodied larvae producing weak currents are found in areas with relatively high dissolved oxygen, whereas larger-bodied larvae, capable of producing stronger currents, are able to tolerate low dissolved oxygen.

The initial distribution of chironomid larvae is determined by egg deposition which generally occurs along the shoreline (Davies 1976). In Lake Pepin, stations with sediments ≥50% sand were located mainly along the shoreline (Figs. 4 and 5). The strong positive correlation between *Chironomus* sp. and sand indicated that these young larvae did not have time to migrate to other areas. Because of their inability to tolerate low dissolved oxygen, sandy sediments with low organic concentrations probably provided a more suitable habitat for them. The low nutrient concentrations in sand apparently did not significantly influence the distribution of the larvae because younger instars would have been able to obtain sufficient food via filter-feeding at these shallower depths.

Young instars often exhibit clumped distributional patterns and disperse as they mature (Underhill and Cole 1967). Hatching of an egg mass in one area results in strong competition between first instar larvae for food and space. This situation would be particularly severe in a sandy substrate. Accordingly, the larvae become planktonic and are passively distributed by wind-induced currents or the pumping action of seiches (Davies 1976). Several studies documented planktonic first instar larvae (i.e. Sadler 1935, Hilsenhoff 1966). Older instars tend to be more closely associated with the substrate and thus are more static. However, under certain conditions such as environmental deterioration, older instars also entered the water column (Mundie 1957; Hamilton 1965; Lellack 1965; Davis 1971; Oliver 1971; Davies 1973, 1976). As the larvae mature, they become more evenly distributed and located at greater depths. Tolerance to low oxygen enables older larvae to evade predators and competitors. At greater depths they also tend to feed on sediment detrital materials rather than on suspended matter.

Analysis of data gathered during Sampling Period I revealed five significant correlations between *Chironomus* sp. and the six physical factors examined (Table 3). In contrast, only two significant relationships were detected among data collected during the second sampling period. These results partially reflected the *Chironomus* sp. population structure during the two separate sampling periods. Younger instars were far more prevalent during the first sampling period with a total of 10,845 organisms as compared to the second sampling period with a total of 1,147 organisms (Table 2). An emergence occurred in late April and early May 1977 and the larvae collected during Sampling Period I represented the offspring of the imagos (Hilsenhoff 1966). Few fourth instar larvae (a total of 2,180 organisms) were present (Table 2). A second smaller emergence occurred in late July and early August 1977. Thus, by the second sampling period, most of the larvae had reached the fourth instar, the final larval stage prior to pupation. As a result, far more larvae were identified as *C. plumosus* (6,624 individuals) and fewer larvae were categorized as *Chironomus* sp. . For this reason, fewer data points were obtained to allow for tests of significant relationships between *Chironomus* sp. and the six physical factors during the second sampling period.

The Oligochaeta (composed primarily of Tubificidae) were positively associated with clay, silt, % total organics, and depth. Their distribution was inversely related to dissolved oxygen and sand (Table 3). The relationship between Oligochaeta standing crop and the three sediment types is also indicated in Figures 4 and 5. The positive association between oligochaetes and total organic matter, silt, and clay, as well as their inverse relationship with sand, reflects the burrowing habit of these organisms and their mode of feeding. Oligochaetes derive most of their nutrition from bacteria and must ingest large volumes of sediment in order to extract sufficient nutrition (Brinkhurst and Cook 1974, Howmiller 1977). Oligochaetes, especially the Tubificiade, are noted for their ability to withstand considerable oxygen depletion. Like the Chironomidae, the oligochaetes exhibited an inverse relationship with oxygen concentration and a positive correlation with increasing depth. Such relationships indicate that these two invertebrates were able to tolerate the low oxygen concentrations found in deeper water, thus avoiding predation and possible competion. Brinkhurst and Cook (1974) have reported similar findings for the Oligochaeta. The comparable environmental requirements of these two groups found in this study has often been reported (e.g. Nuttal and Bielby 1973, Shiozwa and Barnes 1977). In addition, the standing crops recorded for the Oligochaeta and C. plumosus (Table 3) indicate that when their requirements are met, these invertebrates coexisted in large numbers. Howmiller (1977) made the same observation.

The Hirudinea collected in the study were dominated by the pollution-tolerant form, Helobdella stagnalis. An inverse relationship was established between the distribution of these invertebrates and clay, silt, depth, and the sediment organic content. The leeches were positvely correlated with sand and dissolved oxygen (Table 3). According to Sawyer (1974), the two most important factors influencing the distribution of freshwater leeches are the availability of prey items and the presence of a solid substrate. Aquatic insect larvae such as Chironomus sp. and members of the Oligochaeta are most often included in the diet of H. stagnalis (Hilsenhoff 1963, Sawyer 1974). As shown in Table 3, Hirudinea and Chironomus sp. exhibited similar relationships with the physical features examined. A similar relationship was not observed between the Hirudinea and their other prey item, the oligochaetes. This lack of a correlation was probably due to the strong relationship between the oligochaetes and soft clay-silt sediments; such substrates are unsuitable for the Hirudinea. In contrast, both Chironomus sp. and the leeches were positively associated with sand. Thus the distribution of the Hirudinea in Lake Pepin was most strongly influenced by the distribution of Chironomus sp. and the presence of a firm, coarse sand substrate.

The Sphaeriidae, represented primarily by Musculium transversum and Pisidium sp., were positively correlated with the silt components of the sediments and were inversely related to oxygen concentrations (Table 3). The relationship between Sphaeriidae and silt is also indicated in Figures 12 and 13. These same associations have been reported by

Elstad (1977) and Gale (1971). There is strong evidence that substrate type is one the major factors influencing the distribution of molluscs (Harman 1972). The ability of the Sphaeriidae, especially M. transversum to withstand low oxygen conditions was reflected in their negative correlation with dissolved oxygen. During Sampling Period I (Table 3), oxygen was not a factor in sphaeriid distribution. This was further substantiated by the positive association between these invertebrates and depth during the same sampling period. However, a negative correlation between sphaeriid densities and depth was observed during Sampling Period II. It is conceivable that the Sphaeriidae were unable to withstand the severe oxygen depletion that occurred throughout the lake during this period. Over 60% of the hypolimnetic samples collected Sampling Period II had concentrations of less than 1.5 mg O_2/L.

Palpomyia sp. represented the family Ceratopogonidae (biting midges) in Lake Pepin. These predaceous larvae were inversely correlated with depth and clay and positively associated with silt. Palpomyia sp. have been reported tolerant of less than 4.0 mg O_2/L (Roback 1974). Therefore a positive association between these larvae and depth would have been anticipated. In a study of 41 backwater areas on the Mississippi River, Palpomyia sp. was positively correlated with depth (Elstad 1977). In the present study, the distribution of Palpomyia sp. was probably influenced more strongly by the location of Chironomus sp., a potential prey item.

Multiple correlation analyses were conducted to determine the combined influence of the six selected physical factors on the distribution of the seven taxa examined. Significant ($\alpha = 0.05$) or highly significant ($\alpha = 0.01$) multiple correlation coefficiants were obtained for all taxa during one or both sampling periods (Table 3). The lack of significant multiple correlation coefficients for Palpomyia sp. during Sampling Period II and for the Sphaeriidae during Sampling Period I was probably due to a decrease in the number of organisms collected in the respective sampling periods (Table 2). A significant multiple correlation coefficient was not indicated for the Hirudinea during Sampling Period II (Table 3). The reason for this finding is unknown. It may be concluded from the multiple correlation coefficients that the dominant macroinvertebrates found in Lake Pepin were significantly influenced by the interaction of the six physical factors tested.

SUMMARY AND CONCLUSIONS

A complete survey of the macroinvertebrate community found in Lake Pepin on the Upper Mississippi River was completed during the summer of 1977. Fifty four taxa, representing 38,874 individuals, were collected. As a result of the study, the following conclusions can be made:

1. The benthic macroinvertebrate community is dominated by the pollution-tolerant midge, Chironomus plumosus; the Hexagenia population has failed to return to its historically reported levels of abundance.
2. The prominence of the C. plumosus-Oligochaeta-Sphaeriidae-Hirudinea complex and the lack of Hexagenia representatives indicates that Lake Pepin is a eutrophic system.
3. Lake Pepin continues to receive a considerable silt load and high concentrations of nutrients in the form of sewage effluent and agricultural run-off; this organic material has a biochemical demand sufficient to produce severe oxygen deficiencies during periods of calm weather.
4. Nitrogen and phosphorus concentrations remain quite high despite the high flushing rate of Lake Pepin.
5. The low species diversity, dominant community complex, and the reported high nutrient levels are evidence that Lake Pepin is a severely stressed aquatic ecosystem.
6. The bottom sediments of the lake are rather homogenous and are composed primarily of a clay-silt mixture. Sand is confined mainly to shoreline sites and the vicinity of the Chippewa River delta.
7. Statistical analyses indicate that the environmental requirements of C. plumosus, and thus its distribution, change with age; older larvae are capable of tolerating more severe environmental conditions, therefore avoiding predation and competion.
8. The Oligochaeta and C. plumosus exhibit similar environmental

requirements. When conditions are suitable, both groups will reach high densities.

9. The distribution of the Hirudinea was influenced by the interaction of a physical factor (a hard sand substrate) and a biological factor (the presence of suitable prey items).

10. The distribution of *Palpomyia* sp. appeared to depend more on the distribution of potential prey items rather than on the physical factors examined.

11. Multiple correlation coefficient analyses indicated that the seven taxonomic groups studied were significantly influenced by the combined action of the six physical factors surveyed.

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