THE MACROBENTHOS OF A NEW RESERVOIR, LAKE ANNA, LOUISA COUNTY, VIRGINIA

by

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INTRODUCTION

Significance of Reservoirs

A reservoir is the body of water which results when any water-course is dammed. Very early in the history of the United States, small dams were built to provide water power for mills. As the technology of dam building advanced, dams were constructed on some of our largest streams. This has resulted in some very large impoundments, such as a few of the Tennessee Valley Authority reservoirs which exceed 300,000 acres. Neel (1963) light-heartedly attributes our excessive damming of streams to an inherited mammalian trait with its origins in the beaver. Whatever the motivation behind their creation, reservoirs are now a significant portion of the surface waters of the world. They are built for public water supply, irrigation reserves, flood control, recreation, navigation purposes, fish and wildlife protection, hydro-electric power, and more recently, to provide cooling water for power generating facilities, both fossil fuel and nuclear. In the United States, there are over 13 million acres of reservoirs. In the Soviet Union, where there are 37 million acres of reservoirs in various stages of construction, Zhadin and Gerd (1961) state that "V. I. Lenin, the great founder of the first socialist state in the world," recognized that "the growing material needs of a socialist society call for better exploitation of water bodies." Perhaps Neel's theories about the beaver should not be dismissed so lightly.

In recent years the construction of new reservoirs has come under heavy attack from many persons, whom I will collectively refer to as environmentalists. They view our wilderness areas and free-flowing rivers as parts of our heritage which should be passed on, unaltered, to future generations. On the other hand, engineers, supported by industry, state that more reservoirs are necessary to maintain our present standard of living, something no one wishes to sacrifice. A detailed discussion of these two viewpoints is beyond the scope of the present work. Briefly, it would seem folly to impound every stream, but in all likelihood more reservoirs will be constructed to meet the needs of our growing population. What is essential is that we, as limnologists, come to understand exactly what happens when a lotic ecosystem is suddenly transformed into a lentic ecosystem. This understanding will assure that the sites for future reservoirs will be well chosen, and that as reservoirs age they will remain the multi-purpose entities which most are designed to be.

Objectives

Pre- and post-impoundment studies, in general, have been rare, and there have been none in Virginia or its surrounding southeastern states. Macrobenthos has not received as much attention in new reservoirs as other limnological properties. When macrobenthos has been investigated it has usually been restricted to the deep-water, sediment-inhabiting types. This is because most studies have been in storage reservoirs, characterized by large fluctuations of water level which prevent the formation of permanent shallow-water benthic communities. However, in mainstream reservoirs, the water level is relatively constant, thus allowing a diverse benthic fauna to develop in shallow water, where, in the summer months, fish are restricted because of oxygen depletion in the hypolimnion. The benthos of shallow water is therefore an important part of the diet of most fish, and an important component in the flow of energy through the reservoir ecosystem.

The construction of Lake Anna by Virginia Electric and Power Company provided the opportunity to study the development of macrobenthic communities in a new reservoir. Lake Anna is a mainstream impoundment that was designed to provide cooling water for a large nuclear powered electrical generating facility, the North Anna Power Station. The first of four nuclear reactors was scheduled to begin operation in 1975, but because of construction delays none of the reactors has commenced operation. In order to comply with the present environmental legislation, Virginia Electric and Power Company has supported a broad environmental research project in Lake Anna, which included an investigation of the macrobenthos.

The objectives of this study were as follows: (1) to examine the initial macrobenthic colonization of a new lentic habitat; (2) to compare the composition of pre- and post-impoundment macrobenthic communities; (3) to determine structural and functional characteristics of early macrobenthos in Lake Anna, which may apply to other new reservoirs; (4) to analyze the horizontal, vertical, and temporal distribution of macrobenthos in Lake Anna; (5) to compare changes in benthic community structure during the first 3 years of a reservoir's existence with general trends expected in ecosystem development (Table 1); and (6) to compare the abundance of macrobenthos in a new reservoir during the first 3 years with a general model of productivity in new reservoirs. The accomplishment of these objectives would, therefore, provide a large base of pre-operational data that could later be used to assess the effects of the power plant operation.

Description of Study Area

Lake Anna is a mainstream impoundment of the North Anna River, located in Louisa, Spotsylvania, and Orange Counties, Virginia (Fig. 1). The reservoir began filling in January, 1972 and reached normal pool level in November, 1972. It filled much quicker than expected because of heavy floods brought about by a hurricane during the summer of 1972. Lake Anna is 24 km long and has an area of 5261 ha. The reservoir has a maximum depth of 25 m at the dam at the normal pool elevation of 75 m. The shoreline of Lake Anna is very irregular and totals 169 km.

Lake Anna was built by Virginia Electric and Power Company to provide cooling water for a 4 million kilowatt nuclear powered electrical generating facility, the North Anna Power Station. Several tributaries on the south side of the North Anna River (Sedges Creek, Elk Creek, Millpond Creek, and Coleman's Creek), were impounded separately from the main reservoir by earthen dikes, to act as waste heat treatment facilities, or cooling lagoons. The heated effluent which will be released into the first lagoon is supposed to return to near normal temperatures before it enters the main reservoir through an adjustable gate in the dike of the third lagoon. The waste heat treatment facilities (1456 ha) will not be open to the public, but the main reservoir (3804 ha) is intended for recreational use.

Lake Anna drains 88,837 ha. There are few municipalities or industries in the drainage basin and the land use is primarily agricultural. However, due to the recreational opportunities, many cottages, camp grounds, and marinas are being constructed on the shores of the reservoir, and the Commonwealth of Virginia also has plans to build a large state park at the western end of Lake Anna. Because of its proximity to the "urban corridor", heavy recreational pressures have been predicted for Lake Anna, and the reservoir could receive excess nutrients in the future.

Before impoundment the North Anna River was typical of Virginia's Piedmont region, possessing long stretches of slow moving water with sandy bottom, interspersed with riffles having rocky substrate. The tributaries of the river were small woodland streams with a dense forest canopy. Contrary Creek, one of the inundated tributaries of the North Anna River, was the site of extensive mining operations from 1882-1920. The tailings left on the stream bank resulted in acid mine drainage into Contrary Creek and the North Anna River for nearly 100 years. Simmons (1972a) reported that the acid mine drainage had a deleterious effect on the macrobenthos of the entire pre-impoundment basin below the confluence of Contrary Creek and the North Anna River. However, the areas of the North Anna River above Contrary Creek were quite "healthy" in regard to density and diversity. The dilution of acid mine drainage by the construction of a reservoir is another unique aspect of the present study.

According to the thermal classification of lakes presented by Hutchinson (1957), Lake Anna is a second-class, warm, monomictic lake. Warm monomictic lakes are those with the water temperature never appreciably below 4^{o} C at any level, freely circulating in the winter at or above 4^{o} C, and directly stratified in summer. In addition, Hutchinson further classifies warm, monomictic lakes in regard to completeness of thermal stratification and mean depth. Lake Anna is a second-class lake, because the bottom temperature is sufficiently above 4° C for the extrapolation of the summer temperature curve to involve a significant increase in the heat entering the lake. The thermal classification of Lake Anna should be interpreted with caution, since the classification scheme is intended for natural lakes, and Lake Anna is actually a man-made impoundment or reservoir. Reservoirs have unique properties, such as short retention times, but at present, there is no corresponding classification scheme specific to reservoirs.

Ecological Delimitation of Biota and Habitat

The classification of lacustrine biological communities used during my study followed that of Hutchinson (1967). He defined a biotope as any segment of the biosphere with convenient arbitrary upper and lower boundaries, which is horizontally homogenously diverse relative to the larger motile organisms present within it. An ecosystem is the entire contents of a biotope, and a biocoenosis is the totality of organisms living in a biotope, or the living part of an ecosystem. The benthos is defined as that part of the biocoenosis which consists of organisms associated with the solid-liquid interface. Benthos may either be phytobenthos or zoobenthos, but in this work it refers only to zoobenthos. The terms macrobenthos and microbenthos have been used to provide approximate size categories. Originally, macrobenthos referred to those organisms retained on a No. 30 U. S. Standard sieve (.600 mm opening). In addition, benthos is further categorized according to the relation to the substrate. Herpobenthos includes the organisms living in or on the sediment, while haptobenthos includes the organisms adnate to solid surfaces. When the term benthos is used without qualification, most authors are referring to herpobenthos. Organisms commonly encountered in the herpobenthos include Chironomidae, Oligochaeta, Pelecypoda, and some Ephemeroptera such as *Hexagenia* spp. Organisms commonly encountered in the haptobenthos include Ephemeroptera, Odonata, Trichoptera, and Gastropoda. The herpobenthos is the only component of the bottom fauna in deep water, but both herpobenthos and haptobenthos occur significantly in the shallow water biocoenosis. *In this work the term benthos includes both the herpobenthos and haptobenthos*. I feel this is justified according to the definition of benthos, which does not distinguish between a sediment-type, solid-liquid interface or a firm solid-liquid interface, such as a rock.

It is also necessary to delimit the zone of the reservoir bottom which was the object of the study because the traditional schemes of lake bottom zonation are not applicable to new reservoirs. Hutchinson (1967) included various subdivisions of a littoral zone, which all have some type of macroscopic vegetation, and a profundal zone, which consists of fine, bare mud. In a new reservoir, there has not been time for macroscopic vegetation to become established, therefore all of the bottom would be profundal according to Hutchinson's scheme. Odum (1971) defined the littoral zone as the shallow-water region with light penetration to the bottom, and the profundal zone as the deep-water area beyond the depth of effective light penetration. Reservoirs are usually very turbid, therefore almost all of the bottom would also be profundal according to Odum's scheme. I do not feel that either scheme is useful in a new reservoir because the shallow areas of a new reservoir, which are technically profundal, contain a benthic fauna typical of the littoral zone of natural lakes. The object of this study was to examine the benthos to the depth where oxygen depletion occurred in the summer (about 7 m). Rather than attempt to define this zone in precise ecological terms, it will merely be referred to as the shallow-water zone. The upper boundary of this zone is the edge of the water, and the lower boundary is the shallowest portion of the hypolimnion during summer stratification.

REVIEW OF LITERATURE

Investigations of the macrobenthos in new reservoirs of the southeastern United States have been infrequent, and, to date, there have been none in Virginia. However, if one considers other geographical areas, there have been a few such studies reported in the literature.

Nursall (1952) investigated the early development of bottom fauna in the Barrier reservoir in the Rocky Mountains of Alberta. This new power reservoir was originally eutrophic but soon became oligotrophic, as the rich leaf litter of the original bottom was covered by sediment. The bottom fauna consisted almost entirely of Chironomidae. It was observed that the dominant genus of Chironomidae changed from _Pentapedilum_ to _Chironomus_ to _Tanytarsus_ as the reservoir became oligotrophic.

O'Connell and Campbell (1953) conducted pre- and post-impoundment investigations of macrobenthos in the Black River and its subsequent impoundment, Clearwater Lake, in Missouri. They found that the lotic fauna quickly changed to a typical lentic fauna dominated by Oligochaeta, Chironomidae, and Chaoboridae. This change occurred quite rapidly, with the abundance of organisms being as high 3 months after impoundment as it was 3 years later. In addition to this work, Campbell and Funk (1953) conducted extensive pre-impoundment studies of the physical-chemical properties of the Black River basin.

The bottom fauna development of a small pond in Oklahoma was investigated by Burris (1954). Burris found that the peak population was reached 8 months after impoundment, and that the dominant organisms were _Chironomus_ sp. and _Chaoborus_ sp.

Hulsey (1956) investigated the physical, chemical, and biological features of a 170-acre impoundment in Arkansas during the first year of its existence, and included a brief discussion of macrobenthos. He found that Oligochaeta and Chironomidae were dominant at depths ranging from 0-6 m, and that Chaoboridae were dominant in deeper water where the oxygen was depleted. He also reported both winter and summer maxima for Oligochaeta and Chironomidae, but only a winter maximum for Chaoboridae.

Sublette (1957) made a detailed study of the ecology of the macroscopic bottom fauna of Lake Texoma, a reservoir located in Oklahoma and Texas. Lake Texoma was 7 years old at the time of this study, and there does not appear to have been any macrobenthic studies conducted during the early years of the reservoir. Sublette (1955) had previously presented preliminary results on the physical-chemical and biological features of Lake Texoma. In his detailed study of the macrobenthos, he found that horizontal distribution was largely dependent upon substrate-type, which, in turn, was dependent upon the nature of the original basin, and modifications by depth and wave action. His data also indicated the presence of an ecotone between the littoral and profundal zones. Lastly, the maximum standing crop was found to occur in late winter and early spring, while the minimum occurred in late summer.

Since 1926 there have been many large reservoirs constructed in the Soviet Union, primarily for hydroelectric purposes. Zhadin and Gerd (1961) included a chapter on artificial reservoirs in their book on the fauna and flora of freshwater in the USSR. They discuss many reservoirs but provide very little quantitative data. They state that impoundment produces a transformation from a rheophilic fauna to a limnophilic fauna, but indicate that the early macrobenthos of reservoirs consists of facultative organisms. Inundation of rich organic soil was observed to trigger a tremendous multiplication of midge larvae. In one instance it was reported that in the first year of a reservoir, swarming midges made navigation on the surface difficult. Zhadin and Gerd also reported that a much sparser fauna replaced the dense population of midge larvae as the original organic matter became depleted.

Macroinvertebrate colonization of a small reservoir in eastern Canada has been intensively investigated by Paterson and Fernando (1969a, 1969b, 1970). They found that the dominant organisms colonizing the reservoir were Chironomidae, and that colonization was essentially complete by the end of the first summer period. They also presented a model of colonization which indicated that obligate rheophilic organisms were soon lost, while facultative organisms dominated the fauna during the early stages, and a true limnophilic fauna developed later.

Summer benthos in newly flooded areas of Beaver reservoir, in Arkansas, was investigated in the second and third years of filling by Aggus (1971). He used multiple-plate artificial substrate samplers suspended 0.15 m above the bottom to sample macrobenthos. Aggus found that Chironomidae were the dominant organisms, and that the total density of all organisms increased in the third year. He also found that the highest benthic densities occurred in regions of recently flooded herbaceous vegetation, and that there was little benthic activity below the point of thermal stratification. Aggus and Warren (1965) published a pre-impoundment study of the bottom organisms in the Beaver reservoir basin, but unfortunately Aggus (1971) did not include data from the first year after impoundment, or make comparisons of the pre- and post-impoundment faunas.

Isom (1971) reported on the effects of storage and mainstream reservoirs on benthic macroinvertebrates in the Tennessee Valley. However, he only discussed downstream effects of mainstream reservoirs. It was shown that there was little benthic fauna in storage reservoirs due to fluctuating water levels. Other limiting factors of benthos in reservoirs included siltation, rheotactile deprivation, hypolimnetic oxygen deficiency, increased hydrostatic pressure, and light.

Gurvich, et al. (1972) reported on a study of the bottom associations in the Dnieper River reservoirs and their productivity. They found two distinct cenoses in these reservoirs: 1. cenoses of shallow waters (surface - 3.0 m), corresponding to the photic zone; 2. cenoses of deep water (3.0 m and deeper), with slight illumination. Formation of these cenoses required 3-4 years. The abundance of zoobenthos in the cenoses depended on the qualitative and quantitative composition of phytoplankton.

The benthic fauna of a tropical man-made lake (Volta Lake, Ghana) was investigated over the filling period (1965-1968) by Petr (1972). Quantitative and qualitative changes in the individual taxa of the bottom fauna were observed. These changes were due to changing environmental factors, such as oxygen concentration, substrate, degree of exposure to waves, and establishment of littoral aquatic macrophytes. During the early stages only marginal areas were colonized because of the absence of oxygen in deeper water. As the reservoir matured, there was better oxygenation in deeper water, and the bottom fauna of the profundal zone became more abundant. In shallow water, the diversity of invertebrates increased with the advent of macrophytes. Chironomidae were the dominant organisms in all areas of the reservoir.

Some of the oldest and also most continuous macrobenthic research in reservoirs has been conducted in Poland. The macrobenthos of the Goczalkowice reservoir has been sampled since impoundment occurred in 1955. Zacwilichowska (1965a, 1965b) reported on the benthos of the littoral zone from 1958-1960. Krzyzanek (1973) investigated the bottom fauna of the Goczalkowice reservoir 1965-1969, and also presented a summary of all previous results. He reported that the maximum development of macrobenthos occurred 4-7 years after impoundment. A minimum occurred 11-13 years after impoundment, but there was a slight increase 14-15 years after impoundment. Krzyzanek found Chironomidae to be the dominant organisms along with Oligochaeta. In the bank areas, large molluscs, such as Unio pictorum and Anodonta cygnea, were numerous. Less common organisms which he deemed worthy of note included Gastropoda, Hirudinea, Ephemeroptera, Trichoptera, and Ceratopogonidae. Another impoundment in Poland, the Tresna dam reservoir, was investigated in the first year of its existence by Krzyzanek (1971). In Tresna reservoir, Chironomidae and Oligochaeta predominated in almost the whole reservoir, with the Oligochaeta alone prevailing in deeper water. Krzyzanek pointed out that this trend was consistent in all new European reservoirs.

The preceding review of literature has indicated that very few studies of the early macrobenthos in reservoirs have included pre-impoundment surveys of the lotic habitat.

Fortunately, this was not the case for Lake Anna. Thomas and Simmons (1970) investigated the community structure of the macrobenthos in four tributaries of the North Anna River that were destined to become part of the cooling lagoons or waste heat treatment facilities. They reported a diverse fauna dominated by Gastropoda, Pelecypoda, Ephemeroptera, Odonata, and Trichoptera. Simmons and Winfield (1971) conducted a feasibility study using Conservation Webbing for macrobenthic studies in a tributary of Contrary Creek. In addition to evaluating the artificial substrate, they also published a list of organisms encountered. Simmons (1972a, 1972b) and Simmons and Reed (1973) conducted very thorough investigations of the macrobenthos in the North Anna River. The North Anna River had been suffering from acid mine drainage from Contrary Creek for almost 100 years. Above the entrance of Contrary Creek, the North Anna River possessed a "healthy" macrobenthic fauna including many Mollusca. Below Contrary Creek the macrobenthos was affected by acid mine drainage as far downstream as the beginning of the Pamunkey River. While the insect portion of the fauna recovered quickly, no molluscs were found until the confluence of the North and South Anna Rivers to form the Pamunkey. For this reason Simmons and Reed placed the biological recovery zone of the river at the beginning of the Pamunkey. In the section of the river to be included in the reservoir, the dominant organisms belonged to the orders of Trichoptera, Plecoptera, and Ephemeroptera. Above the entrance of Contrary Creek, Gastropoda were also abundant. Finally, the U. S. Atomic Energy Commission, Directorate of Licensing (1973) prepared a complete environmental statement related to the continuation of construction and the operation of the North Anna Power Station. This report summarized the previously mentioned macrobenthic studies in the North Anna River and also made predictions for the new reservoir. These predictions included a general model of expected changes in reservoir productivity. Thus, the wealth of pre-impoundment data from the North Anna River and tributaries provided an excellent opportunity to study the changes which occur when a lotic ecosystem is changed into a lentic ecosystem.

MATERIALS AND METHODS

Sampling Technique

It was difficult to choose an appropriate method for studying the development of macrobenthos in the shallow-water zone of Lake Anna, because I was equally interested in sampling the herpobenthos and haptobenthos. Herpobenthos inhabits soft sediment and can be effectively sampled with grab samplers, but haptobenthos inhabits firm substrates, such as rocks, sticks, and other debris, which lodges in the jaws of grab samplers and causes the loss of organisms. In addition, it was necessary that the sampling method be reasonably replicable, so that the data could later be compared with future years to reliably assess the effects of the thermal effluent. If a grab sampler fell in silt one year, and fell upon sand in a later year, there would be a completely different fauna in each sample. It would appear that some factor, such as a thermal effluent, may have produced a change, while in reality the only difference was substrate. A feasibility study, which compared artificial substrates with a Ponar grab, indicated that artificial substrates were the most suitable sampling technique for an investigation of the shallow-water macrobenthos in a new reservoir (Voshell and Simmons, in press). Artificial substrates were shown to more reliably estimate the abundance of haptobenthic organisms, while reflecting the natural dominance of herpobenthic organisms, and also to exhibit less variability, because they provide a constant substrate for colonization.

Study Design

In September, 1973 eight stations (A-H) were established in the reservoir and waste heat treatment facilities (Fig. 1). In order to collect reliable data, avoid any damage which might occur to suspended substrates, and also to avoid creating navigational hazards, I employed the SCUBA sampling technique which had been developed in the feasibility study (Voshell and Simmons, in press). Three rope transects were placed along the contour at the desired depths. These transects were held in place by numbered stakes, which also served as markers for the placement of the artificial substrates. There were twelve stakes, located 5 meters apart on each transect. The stakes held the transect lines approximately 0.5 m off the bottom, and both stakes and rope were underwater. The three transects were placed at depths of 2 meters, 4 meters, and 7 meters, respectively. All three transects were connected by a rope on one end.

The two artificial substrate samplers used were 3M Corporation's #200 conservation web and leaves. Two of the web samplers and three of the leaf samplers were placed on the bottom at each of eleven stakes on the transects. At all stations the samplers were placed in September of 1973 and 1974 and sampling began 6 weeks later in November. From November of each year through September of each succeeding year, one stake from each transect was randomly selected, and all of the samplers were removed. This provided two replications of the web samplers and three replications of the leaf samplers at each depth, at each station, in each month.

Description of Samplers

The artificial substrate materials used were 3M Corporation's #200 conservation web and leaves. The web was cut in 10.2 cm by 10.2 cm squares, and four squares were stacked in the bottom of the respective baskets. The leaves were raked from a stand of hardwoods near the shore of the reservoir and sifted over chicken wire to remove fine detritus and sticks. Baskets were then filled with the large leaves remaining on the chicken wire.

The baskets used to hold the artificial substrate materials were made in the laboratory from #2064, 2 quart, plastic food containers with lids, obtained from Mammoth Plastics, Inc., Wellsburg, West Virginia. These cylindrical baskets were 11.4 cm tall with a diameter of 16.0 cm at the top and 13.5 cm at the bottom. Twenty-two 3.8 cm holes were cut in the top, sides, and bottom.

The samplers were placed on the bottom in the vicinity of the transect stakes. They were arranged in a straight line, parallel to the transect rope, with the baskets approximately 30 cm apart. Each basket was held in place on the bottom by a wooden "T". The vertical shaft of the "T" was driven into the substrate until the horizontal arm rested firmly on the top of the basket.

Sample Collection and Treatment

To pick up the artificial substrates, divers swam from shore until they reached the 2 meter transect and then proceeded to the correct stake on each of the transects (Voshell and Simmons, in press). Usually there were three divers, each being responsible for one transect. Each diver pulled a buoy by a rope that had a large clip on the end. Upon reaching the correct stake, each diver gently pushed aside the wooden "T's", and quickly slipped the baskets individually into labelled cloth sacks. The cloth sacks, which were manufactured in the laboratory from fine mesh flour sacks, were large enough to hold one basket, and had a nylon draw string sewn around the opening. After the basket was placed in the bag, the opening was pulled shut, and the excess draw string was used to put a half-hitch around the top of the bag. All five of the bags from one stake were then clipped to the buoy rope, and each diver returned to shore, leaving the bags at the transect. When all of the divers had returned, assistants in the boat pulled the bags containing the artificial substrates from the water. All the bags from one station were placed into a 24-gallon metal trash can filled with water, and later transported to the laboratory. In the laboratory, the bags were opened, the artificial substrate materials removed from the baskets, and washed on a No. 35 U. S. Standard sieve (.500 mm opening). In addition, the baskets, interior surfaces of the bags, and any sediment contained in the bags were also washed on the sieve. The artificial substrate material and the material retained on the sieve from each sampler were then placed in containers filled with 5 percent formalin. In order to remove the organisms from each sample, the preserved material was thoroughly washed again over the same size sieve, and small amounts of the material placed into a white enamel tray. Enough water was added to the tray to disperse the material, and the organisms were removed with forceps. All of the organisms from each sampler were stored in individual vials filled with 80 percent isopropyl alcohol. Finally, the organisms were identified to the lowest taxonomic level and counted.

Statistical Treatment

All data were stored and analyzed by means of the Statistical Analysis System (Barr and Goodnight, 1972). Two basic parametric statistical tests were used to detect significant differences between means: Analysis of Variance and Duncan's Multiple Range Test. My work with artificial substrates indicated that the data met the assumptions of these tests, if transformed by LOG_{10} (X + 1). The analysis of variance used was the Model I, completely random design. All hypotheses were rejected at $P = 0.05$. In 1974-75 it was noticed that significant amounts of leaves were beginning to wash out of the baskets. This was attributed to unusually rough weather in this year. For this reason, the data from the leaf samplers were not used for statistical tests, but were included in such qualitative analyses as percentage composition.

RESULTS AND DISCUSSION

Density

The initial colonization of macroinvertebrates has been examined separately in the reservoir (Stations D, E, F, G, H) and lagoons (Stations A, B, C). The main reservoir was formed from a large river, while the lagoons were formed from small woodland streams. Since each habitat possessed a unique fauna (Thomas and Simmons, 1970; Simmons, 1972a, 1972b), it seemed likely that colonization and succession would proceed differently in each of the two new lentic habitats. In addition, the dikes separating the lagoons and main reservoir are almost a complete physical barrier for non-insect species. Direct passage from one side to the other is presently only possible beneath the gates of the dike in the third lagoon. The densities of the major macrobenthic groups occurring on the web samplers in each year are presented in Table 2. In the first year after impoundment, 1972-73, the most abundant organisms in the reservoir were Amphipoda (65.8 per sampler). These were followed in abundance by Chironomidae (29.2 per sampler) and Gastropoda (23.5 per sampler). It is significant to note that no Oligochaeta or Turbellaria were collected in the first year. In the second year after impoundment, 1973-74, there were major changes in the abundance of these organisms in the reservoir. The number of Amphipoda and Gastropoda declined sharply, while the number of Chironomidae tripled. In 1973-74, Oligochaeta became the second most abundant organisms (51.4 per sampler). In the third year after impoundment, 1974-75, Chironomidae continued to become more abundant (124.4 per sampler), while Oligochaeta declined slightly (33.9 per sampler). Trichoptera also became more numerous in the third year (11.6 per sampler). By the third year after impoundment Turbellaria had also increased to 6.8 per sampler. During the first 3 years following inundation the total number of organisms per sampler increased each year. Samples were not collected in the lagoons the first year after impoundment, 1972-73, but in the second and third years, the densities of the major macroinvertebrates were very similar to those observed in the main reservoir. The same trends in density, observed in the reservoir over the first three years, were also observed in the lagoons. In the second and third years, the total number of organisms per sampler was almost identical in both areas.

Although it would be difficult to compare the actual density of macroinvertebrates in Lake Anna with other new reservoirs because of different sampling techniques, a few qualitative comparisons can be made. The initial colonization of the bottom in Lake Anna occurred very rapidly. When the first samplers were removed in October, 1973 the reservoir had not reached capacity, yet there were 175.2 organisms per sampler. A review of the literature reveals that new lentic habitats are always colonized very rapidly. O'Connell and Campbell (1953) found that the macrobenthos of Clearwater Lake was as abundant 3 months after impoundment as it was 3 years later. Paterson and Fernando (1969a) also proposed that the processes of macroinvertebrate colonization of new lentic habitats are very rapid. They stated that these processes approach stability with regard to prevailing environmental conditions after one summer period.

Variety and Equitability

In order to examine the variety and equitability components of diversity, I analyzed the number of taxa and the percentage composition of these taxa. This information is presented for the major groups of macroinvertebrates in Tables 3 and 4, respectively. The pre-impoundment data in these tables, and similar following tables, were synthesized from Thomas and Simmons (1970) and Simmons (1972a, 1972b). Stations above and below Contrary Creek were included in this synthesis. Simmons (1972a) stated that the total diversity of macrobenthos in the river returned to upstream levels shortly below the entrance of Contrary Creek. However, the molluscan fauna, which was quite abundant above Contrary Creek, never became re-established in the area to be impounded. The post-impoundment values were calculated from both the web and leaf samplers at all depths. Combining the river and tributaries, 90 taxa were collected before impoundment. In the river before impoundment the dominant organisms were Trichoptera (33%), Gastropoda (21%), Ephemeroptera (14%), and Plecoptera (12%). In the tributaries before impoundment the dominant organisms were Ephemeroptera (19%), Trichoptera (15%), Odonata (14%), Gastropoda (11%), and Pelecypoda (Sphaeriidae) (11%). In the first year after impoundment, 1972-73, only 40 taxa were collected. This figure does not include the number of genera of Chironomidae, because the Chironomidae were not identified to the generic level during the pre-impoundment studies. The dominant organisms in the reservoir the first year were Amphipoda (49%), Chironomidae (31%), and Gastropoda (12%). The abundance of these three groups began immediately after inundation. The second year after impoundment, 1973-74, a total of 54 taxa were collected in the reservoir and lagoons. Amphipoda and Gastropoda decreased sharply, but the most striking change this second year was the sudden appearance of a large percentage of Oligochaeta. All of the oligochaetes encountered during the study were members of the family Naididae. Since the populations of Amphipoda and Gastropoda declined in 1973-74, the percentage of Chironomidae increased greatly. In the reservoir and lagoons the third year after impoundment, 1974-75, there were no major changes in community structure at the ordinal level. Oligochaeta and Chironomidae still dominated the macrobenthos. A total of 54 taxa were collected in this year also. Additional examination of the data from all three years reveals several subtle changes. Turbellaria increased from 0% to as much as 5%; Ephemeroptera decreased from 4% to less than 1%; Trichoptera increased from 2% to 6%. Trichoptera have not been reported to compose such a significant portion of the macrobenthos in any other reservoir. There were no samples collected in the lagoons the first year after impoundment, 1972-73, but by the second year after impoundment the community structure of the lagoons was approximately the same as the reservoir. In addition, there was no major change in community structure at the ordinal level between the second and third years in the lagoons.

Table 5 has been assembled to compare the percentage composition of the macrobenthos in Lake Anna with other new reservoirs. In every study of newly formed lentic habitats Chironomidae were immediately one of the major colonizers and remained dominant thereafter. In addition to the studies presented in Table 5, this same trend has been recorded in other parts of the world: Soviet Union (Zhadin and Gerd, 1961), Poland (Krzyzanek, 1971), and Ghana (Petr, 1972). One major difference in the colonization of Lake Anna and other new reservoirs was the number of Amphipoda and Gastropoda. These two groups accounted for 61% of the bottom fauna in Lake Anna the first year, but have not been reported as occurring significantly in other new reservoirs.

Zhadin and Gerd (1961) mentioned that some Amphipoda and Gastropoda were common in new reservoirs of the Soviet Union, but they did not provide quantitative data. A comparison of oligochaete colonization in Lake Anna with other new reservoirs reveals both similarities and differences. In Lake Anna there were no Oligochaeta the first year and large numbers the second. O'Connell and Campbell (1953), Hulsey (1956), and Paterson and Fernando (1969b) all reported large percentages of Oligochaeta the first year after impoundment. However, Nursall (1952) and Aggus (1971) reported insignificant percentages of Oligochaeta after inundation. Aggus (1971) also sampled the second year after impoundment and found a larger percentage of Oligochaeta (9%), but not nearly so large as the percentage composition of Oligochaeta in Lake Anna the second year (18-22%).

The preceding discussion has not proceeded further than the ordinal taxonomic level, as these are the only data presented in other studies. However, in order to obtain a significant understanding of the intricacies of macrobenthic community development, it is necessary to examine the results at the generic and specific level. Due to difficulties in taxonomy and the collection of such large numbers of organisms, many of which were early instars, it was not possible to quantitatively identify all Oligochaeta and Chironomidae. For these reasons, Gastropoda, Ephemeroptera, Odonata, and

Trichoptera were chosen to examine more detailed changes in community structure. A complete list of all organisms collected in Lake Anna, including the authors of scientific names, is presented in Table 52. Table 6 presents the percentage composition of each of the major Gastropoda for the first 3 years. The values in the table are the percentage composition of the total number of Gastropoda collected, not the total macrobenthos. This was done to eliminate the effect of large changes in other population densities, such as Amphipoda. Before impoundment the dominant snails were members of the subclass Prosobranchia. Prosobranchia are characterized by having gills and, thus, relying entirely on dissolved oxygen for respiration. In the river above Contrary Creek, the dominant snail was Goniobasis sp., while in the tributaries of the North Anna River it was Campeloma sp. Some Pulmonata were also present in both areas before impoundment (Physa sp. and Helisoma sp.). Pulmonata are the snails which have a mantle cavity modified into a lung, and are thus able to utilize atmospheric oxygen for respiration. In 1972-73, in the reservoir, the dominant snail was a member of the Pulmonata: Physa sp. (60%). In the second year, two different Pulmonata shared dominance: Ferrissia sp. (57%) and Helisoma sp. (41%). By the third year, in the reservoir, Helisoma sp. accounted for 89% of the snails, and the originally dominant gastropod, Physa sp., had declined to 1%. In

1973-74, in the lagoons, the situation was somewhat different; *Ferrissia* sp. and *Helisoma* sp. were dominant gastropods but their magnitude was reversed: *Helisoma* sp. (63%) and *Ferrissia* sp. (28%). By the third year, 1974-75, the reservoir and lagoons exhibited the same general composition with *Helisoma* sp. dominant, and the original dominant, *Physa* sp., drastically reduced. Impoundment did not significantly change the number of gastropod species collected (5 before impoundment and 4 each year after impoundment), however, the relative abundance of these species changed greatly.

Table 7 presents the percentage compositions of the Ephemeroptera. Before impoundment the dominant mayflies in the river were *Stenonema* sp., *Isonychia* sp., and *Centroptilum* sp. All of these species are typical of flowing water. In the tributaries before impoundment, a burrowing mayfly, *Ephemera* sp., and *Brachycercus* sp. were the most common. Immediately after impoundment, 1972-73, the mayfly fauna of the reservoir was entirely composed of one species, *Caenis amica*. *C. amica* was common during the first year, accounting for 4% of all macroinvertebrates. In the second year, *C. amica* declined in abundance and composed only 1% of the total fauna. In the third year, the total mayfly population continued to decrease, but a new mayfly, *Hexagenia munda*, became established. *H. munda* did not appear until late in the summer of 1975, yet still accounted for 71% of the mayflies as compared to 25% for *Caenis amica*. The same trends were observed in the lagoons the second and third years, although *H. munda* was less abundant in 1974-75. Impoundment produced a drastic change in the number of species of Ephemeroptera. There were 14 species collected in the river and tributaries, but only 3-4 collected in the reservoir and lagoons.

Table 8 presents the percentage composition of the major Odonata collected each year. Before impoundment, *Progomphus obscurus* and *Macromia* sp. were most abundant in the river, while *Calopteryx* sp. and *Argia* spp. were most common in the tributaries. Again, in the first year after impoundment, one member of the group was clearly dominant; damselflies of the genus *Enallagma* accounted for 95% of the Odonata. In 1973-74, in the reservoir, several additional Odonata became abundant with the dragonfly *Perithemis tenera* being dominant (40%) and *Enallagma* spp. declining to 29%. In 1974-75, *Perithemis tenera* declined sharply and there were three dominant groups: the damselflies *Argia* spp. (38%) and *Enallagma* spp. (30%), and the dragonfly *Epicordulia princeps* (22%). The composition of Odonata in the lagoons was somewhat different, both in the second and third years after impoundment; members of the genus *Argia* were the dominant Odonata (37% and 50%), followed by *Perithemis tenera* (31% and 24%). The number of species of Odonata was reduced from 16 before impoundment to 6 after impoundment, but increased to 9 species in each of the second and third years after impoundment.

Table 9 presents the major Trichoptera which have been collected in Lake Anna. Before impoundment the dominant caddisflies were typical riverine forms, all members of the family Hydropsychidae: *Cheumatopsyche* sp., *Hydropsyche* sp. and *Macronemum* sp. Trichoptera data were not available from the tributaries. Immediately after impoundment *Oecetis cinerascens* and *O. inconspicua* comprised almost all of the caddisflies (87%). These two species have been grouped together because the early instars, which abandoned their cases when preserved, were difficult to distinguish, and both species appear to have the same distribution in Lake Anna. Both species are also ecologically similar, being predators. In the second year after impoundment the composition was more evenly distributed. *Oecetis* spp. were 34%, *Orthotrichia* sp. 25% and two species not previously encountered, *Cyrnellus fraternus* and *Polycentropus* sp. were 26% and 12%, respectively, of all Trichoptera. In the third year, major changes in the fauna continued to occur. *Polycentropus* sp. increased in number to become the most abundant (63%), *Cyrnellus fraternus* remained about the same (28%), and *Oecetis* spp. declined sharply (4%). In the lagoons the second year, there was one major difference in the fauna; a localized population of *Nyctiophylax affinis* composed 21% of the caddisflies. By 1974-75 the composition of lagoons and reservoir had become almost identical.

The Trichoptera, in contrast to most of the orders in Lake Anna, have increased in percentage composition as the reservoir has matured. In 1974-75 they composed 6% of the total fauna, a much higher percentage than other workers have found in reservoirs. In the late summer months at 2 meters, the Trichoptera were approximately 50% of the total fauna, and were thus one of the major food items available for forage fish. There have also been interesting changes in the number of species of caddisflies, since prior to inundation there were 17 species in the lotic ecosystem, but the first year after impoundment there were only 6 species. By the second year after impoundment there were again 17 species, however, examination of the composition of the fauna reveals that different species were dominant.

Factors Determining Community Composition

From the preceeding results it should be apparent that impoundment produces an immediate and drastic change in the macrobenthic community. The initial changes include the complete loss of abundant groups such as Plecoptera, Hemiptera, Megaloptera, and Pelecypoda, and great reduction of other groups such as Trichoptera, Ephemeroptera, and Coleoptera. These losses and reductions, however, are accompanied by initial increases of other groups such as Amphipoda and Chironomidae. In the major groups which occurred in both the lotic and lentic ecosystems, there were immediate changes in composition at the generic and specific level. This information is consistent with the observations of O'Connell and Campbell (1953). In addition, the fact that this situation existed by the fall of the first year after impoundment, is in agreement with Paterson and Fernando (1969a), who stated that new reservoirs reach an equilibrium with existing environmental conditions after one summer period.

It appears that new reservoirs are initially colonized by species from the lotic habitat which are facultative to lotic and lentic conditions. The immediate appearance of large numbers of chironomids is to be expected for several reasons. The family Chironomidae is a large, diverse group, and some members of the family are found in almost any aquatic situation (Oliver, 1971). They generally reproduce in large numbers and some species have several generations per year. In addition, both the adults and larvae may be rapidly dispersed. The adults are moderately strong fliers, and are also small enough to be dispersed by wind. In addition, there is evidence that the larvae exhibit periodic drift patterns similar to those of invertebrates in streams (Mozley, 1975). Since several species of chironomids occurred in the North Anna River and its tributaries, it is, therefore, not surprising that this group quickly colonized Lake Anna.

The initial abundance of Gastropoda in Lake Anna is probably also due to facultative pre-impoundment species.

Before impoundment pulmonate snails, including Physa sp., occurred in the North Anna River above Contrary Creek, and the tributaries of the river. They did not occur in the pre-impoundment basin below the entrance of Contrary Creek, due to acid mine drainage. Impoundment produced a dilution of the effects of Contrary Creek, and thus allowed the large population of gastropods to disperse into a new habitat. This dispersal occurred rapidly because Lake Anna filled almost instantly from floods in the summer of 1972. The only study of a new reservoir in Table 5 for which pre-impoundment data is also available is that of O'Connell and Campbell (1953). They reported very few gastropods in the new reservoir (1%), but there had also been very few in the river (1%). Gastropoda accounted for 21% of the total fauna in the North Anna River and 10% of the total fauna in its tributaries before impoundment, and therefore, accounted for 12% of the total macrobenthos in Lake Anna the first year after impoundment.

The most abundant organisms in Lake Anna the first year, Amphipoda, were not abundant in the river or its tributaries. However, several farm ponds were flooded by the impoundment, and these would be likely sources for large populations of amphipods. It is also possible that amphipods came from outside sources by passive transport on the legs of birds, but the inundated farm ponds seem a more likely source for the immediate abundance observed in Lake Anna.

The dominant mayfly in the reservoir the first year, *Caenis amica*, was also present in the river and tributaries before impoundment. It is interesting to note that members of a closely related genus, *Brachycercus*, were also present in large numbers in the tributaries before impoundment, but did not become established in the reservoir. Roback (1974) reported that members of the genus *Caenis* were more tolerant of the reduced oxygen concentrations, which would be found in a new reservoir, than members of the genus *Brachycercus*.

The dominant Odonata in Lake Anna the first year, *Enallagma* spp. were found in the river, and thus it was not surprising that they were also found in the reservoir. The dominant Trichoptera the first year, *Oecetis cinerascens* and *O. inconspicua*, were not collected in any of the pre-impoundment surveys. These two species probably arrived in Lake Anna the first summer by active transport, which Paterson and Fernando (1969b) defined as the flight by adults to a new lentic habitat for oviposition.

While the initial colonization of reservoirs appears to be largely dependent on the pre-impoundment fauna, other factors are also involved. Oligochaeta were fairly abundant in the North Anna River and its tributaries, yet were not found in the reservoir the first year. Oligochaeta are capable of rapid reproduction, and are certainly as easily dispersed as the Gastropoda which quickly colonized the reservoir. In most studies of new reservoirs (Table 5), Oligochaeta were very abundant the first year. O'Connell and Campbell (1953) found very few in the river, yet reported that Oligochaeta were 17% of the macrobenthos in the reservoir the first year. Two of the most obvious factors which would affect the success of macrobenthic organisms in a new lentic habitat are available food and substrate. The substrate of a new reservoir has very little fine silt and contains a great deal of terrestrial organic matter. Oligochaeta burrow through the substrate and feed by ingesting quantities of the substrate, the organic component being digested as it passes through the alimentary canal (Pennak, 1953). Brinkhurst (1974) states that the total amount of organic matter in the sediment is not as important to sediment feeders as the quality of organic matter, or the amount of "useful food". He emphasizes the importance of the microflora growing on the organic material in the substrate, particularly the microflora of faeces. Apparently, the terrestrial organic matter in the sediment of Lake Anna the first year was not "useful food" for the type of Oligochaeta (Naididae) which were available for colonization. During the first year of impoundment, this organic matter was ingested and egested by other invertebrates, while the descent of dead planktonic organisms also altered the quality of organic matter in the sediment. Both events resulted in the sediment becoming "useful food" for the Oligochaeta, and thus they became quite abundant the second year.

The Chironomidae of lentic habitats are primarily filter feeders, which construct tubes with nets across the openings, and draw water through the nets by undulating their bodies. They consume food trapped on the nets, primarily seston (Oliver, 1971). Chironomidae, therefore, in contrast to Oligochaeta, rely on food in the water rather than in the substrate. Since seston has been plentiful in the reservoir since impoundment (Armitage and Simmons, 1975), Chironomidae have not been affected by the quality of available food.

In the second and third years after impoundment, some of the other initially dominant organisms declined, probably because of changes in available food and substrate. Hyalella azteca is a sediment feeding amphipod which digests algae and bacterial cells from ingested sediment material (Hargrave, 1970). In addition, amphipods have been reported as being most abundant in vegetation (Pennak, 1953). Apparently the first year after impoundment Lake Anna was an ideal environment for Hyalella azteca. The inundated organic matter must have been suitable for its nutritional requirements, and the terrestrial vegetation which was flooded provided a preferred habitat. As in all reservoirs, the original organic matter in the sediment and the terrestrial vegetation decomposed by the second year. Thus, with the abundant food supply and habitat eliminated, the number of Hyalella azteca declined sharply the second year. Similar trends were observed for the Gastropoda. Freshwater snails are either grazers, feeding on periphyton, or scavengers. It has been well documented that certain species have definite substrate preferences (Harman, 1972). Therefore, I attribute the initial abundance of snails to the inundated organic matter and terrestrial vegetation, and the subsequent decline in numbers to the decomposition of these materials. In addition, there has been a change in the dominance hierarchy. *Physa* sp., originally the most abundant, probably required a firm substrate such as inundated vegetation while *Helisoma* sp., presently most abundant, does well on more silty substrate.

Some important changes have also been observed among the Ephemeroptera of Lake Anna. *Caenis amica* is an omnivore feeding chiefly on plant material. It is commonly found on rooted vegetation, leaf debris, and trash (Berner, 1959). The explanation of the population trends of *Caenis amica* is, therefore, probably the same as the gastropods and amphipods. *Hexagenia munda*, presently the most abundant mayfly in Lake Anna, probably did not become established in the reservoir the first two years because of the physical characteristics of the substrate. Members of this genus require silty bottoms in which to burrow and feed (Eriksen, 1966). Silt was not present in appreciable amounts immediately after impoundment, but has been slowly deposited since. The occurrence of *Hexagenia munda* in Lake Anna is very important. Members of this genus have been reported as one of the major components of the benthic community in other reservoirs, especially in terms of biomass. It has also been shown to be a major source of food for certain fish. Finally, the continuous burrowing in the sediment, and ingestion and egestion of organic material, is very important in the trophic dynamics of a lentic ecosystem. Their faeces and the constituent microflora make new organic material available to other organisms.

The changes which occurred in the composition of the Odonata and Trichoptera are not as easily explained. All of the species involved here are predators, and there has been an abundance of prey species, such as chironomids, throughout the study. In addition, all species are typically haptobenthic. Since the only type of substrate which has increased during the first three years is soft sediment, substrate does not seem to explain the changes. Therefore, it is possible some species are dominant in the early macrobenthic communities of new reservoirs primarily because they arrive before their competitors. Examples of these species are *Oecetis cinerascens*, *O. inconspicua* (Trichoptera), and *Enallagma* spp. (Odonata). By arriving first, these species are able to exploit the resources of the new environment and maintain large populations. As other species arrive, such as *Cyrnellus fraternus*, *Polycentropus* sp. (Trichoptera), and *Perithemis tenera*, *Epicordulia princeps*, *Argia* spp. (Odonata), there is competition for the resources and shifts in the dominance hierarchy occur. If this is true, then most of these latter species could have been equally successful the first year as the original colonizers. Some species such as Enallagma spp. probably arrived in newly flooded areas because they were abundant in similar areas of the river, while other species such as Oecetis spp. may have existed in nearby ponds, some of which were inundated.

A comparison of the development of macrobenthos in the main reservoir and lagoons, reveals that these areas are becoming more similar with time. In the second year after impoundment, 1973-74, there were subtle differences in the fauna of the two areas. This is to be expected since the pre-impoundment fauna is largely responsible for colonizing the new habitat. In addition, new species which arrive by active transport, probably begin as localized population in certain areas. However, by the third year after impoundment the reservoir and lagoons developed similar substrates and the original and introduced species dispersed into both areas. Examination of Tables 4, 6, 7, 8, and 9 indicates that the reservoir and lagoons were most similar in the third year after impoundment.

Classification of Early Macrobenthos

New reservoirs are quickly colonized by macroinvertebrates. The composition of the benthic communities of new reservoirs is drastically different from pre-impoundment communities, but the originally dominant organisms in the reservoir are usually present in the pre-impoundment basin in low numbers. Impoundment produces a reduction of the number of species but this increases with time. The composition of the benthic community the first year after impoundment is unique when compared to following years because during the first year a few species are completely dominant, but during the following years additional species become more evenly dominant. Thus, the macrobenthos of new reservoirs can be classified into three major groups which are presented in Table 10. The first colonizers are those organisms which are most successful in the conditions offered immediately following inundation. They are capable of utilizing the submerged terrestrial organic matter for food, and prefer the flooded vegetation for substrate. In Lake Anna these organisms included Hyalella azteca (Amphipoda); Physa sp. (Gastropoda); Caenis amica (Ephemeropters); Enallagma sp. (Odonata); Oecetis cinerascens, and O. inconspicua (Trichoptera). There is a possibility that some of the predatory organisms such as the Odonata and Trichoptera mentioned above are abundant because of lack of competition rather than an ecological preference for the original benthic habitat. Second, there are the omnipresent or consistently abundant organisms, such as Chironomidae. They also quickly colonize the new lentic habitat because of wide ecological tolerance and the abundance of useful food in the water column rather than the substrate. The feeding activities of both groups probably modifies the nature of the substrate. The original organic matter is ingested and egested, producing changes in the organic matter itself, and also its constituent microflora. Besides these changes brought about by the original biota, mineral nutrients and organic materials are leached from the soil, while the submerged terrestrial vegetation decomposes and disappears. Finally, the descent of dead planktonic organisms and the deposition of silt carried by the river further change the nature of the bottom. All of these changes result in the first colonizers becoming less successful and the second colonizers becoming dominant. At the same time the omnipresent Chironomidae remain a dominant group. In Lake Anna the second colonizers included: Turbellaria; Oligochaeta; *Helisoma* sp. (Gastropoda); *Asellus* sp. (Isopoda); *Hexagenia munda* (Ephemeroptera); *Argia* spp., *Perithemis tenera*, *Epicordulia princeps* (Odonata); *Cyrnellus fraternus*, *Polycentropus* sp. (Trichoptera). Again, it is possible that some of the organisms are second colonizers because of their delayed arrival rather than a preference for the modified substrate. However, this certainly does not appear to be the case for organisms such as Oligochaeta, *Helisoma* sp., and *Hexagenia munda*. Whatever the reason for their secondary arrival, the effect is the same. The increased number of similar species results in increased competition for resources, thus several species become more evenly abundant.

In order for this classification of the early macrobenthos to be meaningful in other new reservoirs it is necessary to examine the functional significance of these organisms. Table 11 presents such a functional classification of the early macrobenthos based upon Cummins (1974). Food habits were not examined during this project but could be obtained from the literature (Pennak, 1953; Berner, 1959; Hargrave, 1970; Oliver, 1971; Winterbourn, 1971; Cummins, 1973, 1974). Only four functional categories were encountered in Lake Anna. The micro- and macropredators categories should not need explanation, but it would probably be beneficial to distinguish between collector-microgatherers and collector-microfilterers. Collector-microgatherers are those organisms which feed upon medium particulate organic matter (>0.25 mm, < 1 mm) or small particulate organic matter (>0.075 mm, < 0.25 mm) which occurs in sediment. This material includes plant and animal fragments and faeces of invertebrates. Collector-microfilterers are those organisms which feed upon small particulate organic matter or very small particulate organic matter (>0.0005 mm, < 0.075 mm) which occurs suspended in the water. This material consists of very small detrital fragments, faeces of small invertebrates and free microorganisms, such as phytoplankton. The gastropods have been included in the collector group rather than the scraper group, as in streams, because the species encountered in new reservoirs are probably omnivorous scavengers. It is significant to note that the functional categorization of early lentic macrobenthos is much simpler than that shown by Cummins (1974) for small streams. Even though there is considerable course particulate organic matter present the first year after impoundment, there are no macrobenthic organisms feeding directly on this material. All of the most abundant macrobenthos in the reservoir feed upon fine particulate organic matter, either suspended or in the sediment. The course particulate organic matter which is inundated becomes available to these organisms as it is broken down to fine particulate organic matter by the action of the water and microbes. It is likely that the fine particulate organic matter already existing in the soil before inundation is the most important early source of food for these organisms.

There are generally few species of the first colonizers present in each of the functional categories. In Lake Anna there were three species of first colonizers present in the collector-microgatherers category but Hyalella azteca far outnumbered the other species. It is likely that there may be more than one species present in this latter category due to the large amount of fine particulate organic matter in new reservoirs. The omnipresent group, Chironomidae, are the only organisms belonging to the collector-microfilterers category. The arrival of the second colonizers brings about the co-existence of several species in each of the first three functional groups.

The following model summarizes early macrobenthic colonization in new reservoirs. The reservoir is first colonized by a few dominant species, with each dominant species belonging to a different functional category. Since there is little competition between different functional categories, each species is able to fully exploit the resources of the new habitat and become totally dominant. As the reservoir matures, other species belonging to the same functional category are introduced, and competition for resources ensues. This results in shifts of the dominance hierarchy and several species tend to share dominance within the functional categories. Although different species may occur in other reservoirs, I feel that the same functional trends will occur in new reservoirs of the southeastern United States.

Statistical Analysis of Distribution

It was necessary to statistically examine the distribution of macrobenthos during the pre-operational phase of the project so that these data could be compared with that obtained during the post-operational phase. Thus, any effects of the thermal effluent on the macrobenthos could be determined in the future when the power plant begins operation. In order to analyze the pre-operational data a three-way analysis of variance, Model I, completely random design, was employed. The sources of variation which were analyzed were stations, depths, time, and all possible interactions. The parameters examined were the total number of organisms and total number of different taxa. These parameters were selected because they summarized a considerable amount of data, and because earlier work indicated that these parameters met the assumptions of the ANOVA when transformed by LOG_{10} (X + 1). Four such ANOVA's were performed, one for each parameter in both years which the entire reservoir-lagoon complex was sampled (1973-74 and 1974-75). The results of these ANOVA's are presented in Tables 12-15. In every case, there were very significant differences (P = .001) for every source of variation including the interactions. This indicates that the distribution of macrobenthos in Lake Anna is very complex and heterogeneous. Since the significant differences among the interactions made the three-way ANOVA difficult to interpret, it was decided that more meaningful results could be obtained from a series of one-way analyses of variance. The sources of variation were analyzed as follows. First, the differences among stations were analyzed for each depth, at each of four selected months. The four months chosen were November, February, May and August. These were selected because they represented "shock periods" such as the period immediately following turnover (November), and the period of maximum stratification (August). These ANOVA's were again performed for total organisms and total taxa in both 1973-74 and 1974-75 (48 total ANOVA's). In order to analyze depth as a source of variation, one-way ANOVA's were performed for each station (32 total ANOVA's). In order to analyze time as a source of variation, one-way ANOVA's were performed at each depth (12 total ANOVA's). Again, there were significant differences among the means for every source of variation ($P = .05$). In an attempt to determine where these significant differences were, all of the prededing ANOVA's were followed with Duncan's multiple range test (92 total Duncan's). Since there were so many multiple range tests it would be impossible to discuss each one, and, therefore, a summary is presented.

In regard to stations, A, D, and E tended to have the lowest number of total organisms. This was especially noticeable for A at 7 meters, while stations D and E tended to be low at all depths. These trends seemed to be consistent at all seasons. Of the remaining stations, B, C, F, G, and H, none seemed to consistently have more organisms than any other. In regard to total taxa, the stations were found to be more similar. Stations B and C tended to have more taxa at 2 meters but all the stations were very similar at 4 meters and 7 meters.

Analysis of the variation due to depth produced only one clear trend. There were always significantly fewer organisms and taxa at 7 meters. This is understandable because this depth is within the hypolimnion during summer, and is subject to very low oxygen concentrations. Tables 16-18 present a summary of the basic physical-chemical parameters during the first 3 years after impoundment. The situation at 2 meters and 4 meters is more complex. At some stations (B, C, D, E) there were significantly more organisms or taxa at 2 meters, but at some stations (A, F, G, H) there was no significant difference between these two depths. There were never significantly more organisms or taxa at 4 meters.

Analysis of the variation due to time did not produce any clear trends of significant difference as one might expect. It would seem that there would be significantly less organisms and taxa during the summer months when insect species emerge. The total number of organisms was generally lower in summer, but usually not significantly different from some months of other seasons. This applied to all depths. The total number of taxa was significantly lower in August at 2 meters, and in August and September at 7 meters. However, at 4 meters there was no clear significant difference among the months. Various species have population fluctuations at different times of the year, but these are offset by the simultaneous fluctuations of other species, so that the total number of organisms does not exhibit a clear pattern of variation with respect to time.

In order to provide data for post-operational comparisons, I performed a series of one-way ANOVA's between the second and third years after impoundment. The first year was not compared because samples were collected at only one station during the first year, and this station was at a different location from the stations established in the second and third years (Fig. 1). The second and third years were compared at two stations (B and F), at each depth, in each of the four months discussed earlier. The total number of organisms and the total taxa were again selected as parameters. This required a total of 48 ANOVA's. Stations B and F were chosen because they were located in the middle of the lagoons and reservoir, respectively, and neither had appeared significantly different in any of the previous statistical tests. There were no significant differences between the two years, either for total number of organisms or total taxa. This is probably the most important information to come from all the statistical tests. By the second and third years after impoundments, the total number of organisms and total number of taxa have apparently become consistent. When the power plant begins operation, the data from these same stations, depths, and months can be compared with the pre-operational data, and thus it will be possible to determine the effects of the thermal effluent on the macrobenthos with statistical confidence.

In summary, statistical analysis of the variation in the distribution of the macrobenthos (horizontal, vertical, and temporal) indicates that there are significant differences, but there is no clear pattern as to where these differences lie. This is because there are complex interactions between the stations, depths, and times which complicate the interpretation. These complex interactions, while difficult to interpret individually, are meaningful when considered together. They indicate that Lake Anna is developing into a complex ecosystem. Unique microhabitats are developing in various areas of the reservoir because of differences in factors such as wind exposure, wave action, light penetration, and oxygen depletion. The development of unique microhabitats is apparent, even though the differences brought about by variability in natural substrate have been reduced by the use of artificial substrates. Brinkhurst (1974) has shown that even the profundal zone of lakes is not homogeneous. Neighboring profundal communities are often distinctly different from one another due to subtle differences in available food and biotic interactions between species. Apparently, this situation has also begun to develop in the shallow-water areas of Lake Anna. Thus, the most meaningful assessment of the effects of the thermal effluent will be made by comparing a given station, depth, time combination with the same spatial and temporal combination of other years.

Biological Analysis of Distribution

While the rigorous statistical analysis revealed significant differences in the distribution of macrobenthos in Lake Anna, it did not determine where these differences existed. Therefore, it was necessary to take a non-statistical approach to this problem. In order to understand the development of macrobenthic community structure in a new ecosystem it was imperative to determine the trends in horizontal and vertical distribution. In ecosystem development, one expects to find the spatial heterogeneity and stratification becoming better organized (Table 1). In addition, one would expect the temporal distribution to exhibit similar trends. The approach was the same as that taken for number of species and percentage composition. The distribution of the major orders were examined first and then the distribution of the species of Gastropoda, Ephemeroptera, Odonata, and Trichoptera. Table 19 presents the horizontal distribution of the major groups at the eight stations in 1973-74 and Table 20 does the same for 1974-75. All of the distributional tables were derived only from web samplers. Both density per sampler and percentage of a particular taxon collected at each station are expressed. For example, in 1973-74 at station A, there were 0.9 Turbellaria per sampler and of all Turbellaria collected in this year, 4% occurred at this station. In addition, Figures 2-17 are histograms of the community composition at each station in both 1973-74 and 1974-75. There are separate histograms for web and leaf samplers. Examination of the data in Tables 19 and 20 reveals that almost all of the taxa are very heterogenously distributed, but each taxon has a unique distribution. If a particular taxon was homogeneously distributed among the stations, one would expect to find 12.5% at each station. In the following summary I have considered a taxon to be abundant at a station if approximately 20% of that group occurred there (expected percent + 7.5%), and scarce if approximately 5% of that group occurred there (expected percent -7.5%).

Turbellaria were most abundant at stations E, in 1973-74, but most abundant at stations A and E in 1974-75. They were least abundant at stations B and C in 1973-74 and became even less abundant at these stations in 1974-75, while also becoming scarce at stations D and G. Oligochaeta were especially numerous only at station G in both years. They occurred in conspicuously low numbers at stations D and E in 1973-74 and stations B, D, and E in 1974-75. Gastropoda were very numerous at station A and very sparse at stations D, E, F, G, H, in 1973-74. In 1974-75 they were numerous only at station G, while scarce at stations D, F, and H. Isopoda were only abundant at station E in both years. They were most notably scarce from stations A, B, D, F, and G in both years. Amphipoda were most abundant at station F and least abundant at station C and D in both years. Ephemeroptera were most abundant at station A in 1973-74 and most abundant at stations B and C in 1974-75. They were least abundant at stations E and H in 1973-74 and least abundant at stations E, F, G, and H in 1974-75. Odonata occurred more often at stations B, C and H in 1973-74, and B and C in 1974-75. They were least encountered at station E in 1973-74, and E and F in 1974-75. Trichoptera were the most homogeneously distributed order, never occurring more than 17% or less than 9% at any station. Chironomidae were also very evenly distributed. In 1973-74 they were equally abundant at all stations except E, and in 1974-75 they were especially abundant at station G, while again being sparse at E. Chaoborus sp. was most abundant at station B and G in 1973-74 and most abundant at station B in 1974-75. It was least abundant at station E in both years. In regard to the total number of organisms, station G consistently had the highest density while stations D and E had conspicuously lower densities.

This review of the horizontal distribution of the major groups seems to indicate that each organism has become distributed in areas where it can be most successful. This success can probably be explained by the availability of useful food and biotic interactions between organisms, since the samplers that were employed provided a uniform substrate for colonization. These biotic interactions could be negative interactions, such as predation, or positive interactions, such as the feeding habits of one species making useful food available to other species. This latter type of interaction is suggested at station G where there were the highest numbers of Oligochaeta, Gastropoda, and Chironomidae. Chironomidae were classified as collector-microfilterers in Table 11. Large numbers of Chironomidae, ingesting suspended organic matter and egesting faeces, would probably provide abundant useful food for collector-microgatherers, such as Oligochaeta and Gastropoda.

The vertical distribution or stratification of the major groups of macrobenthos is presented in Table 21 for 1973-74 and Table 22 for 1974-75. In addition, Figures 18 through 29 are histograms of macrobenthic community structure at various groups of stations, considering the depth distribution. These figures include data from web and leaf samplers, respectively. In reviewing these data one finds that certain groups are more successful at different depths. Turbellaria, Amphipoda, Ephemeroptera, Odonata, and Trichoptera are more abundant at 2 meters. Oligochaeta, Gastropoda (1974-75), and Chironomidae are most abundant at 4 meters. Only Chaoborus sp. is most abundant at 7 meters. While the factors mentioned in the discussion of horizontal distribution are also at work here, dissolved oxygen is another factor affecting vertical distribution.

A summary of basic physical-chemical properties is presented in Tables 16-18. Due to thermal stratification, dissolved oxygen levels are very low at 7 meters in the summer months. Only a few aquatic organisms can tolerate prolonged periods of stagnation. In Lake Anna, Chaoborus sp. is the only organism clearly most abundant at 7 meters. One member of the Chironomidae, Chironomus sp., also seems most abundant at 7 meters. The Oligochaeta collected thus far in Lake Anna (Naididae) are definitely not as abundant at 7 meters as other depths, especially in the summer months. At 4 meters the oxygen concentrations are somewhat lower than 2 meters, but not appreciably so. The difference between the fauna of these two depths is probably more the result of biotic interactions and available useful food. It is important to note that the three groups of organisms thought to be most abundant at station G because of favorable feeding interactions (Oligochaeta, Gastropoda, and Chironomidae), are also most abundant at the same depth (4 meters), especially in 1974-75. This would seem to support the idea that Oligochaeta and Gastropoda are most successful where the faeces of Chironomidae provide abundant useful food.

More trends in the horizontal and vertical distribution of macrobenthos can be observed by examination of particular species within some of the major groups. The horizontal distributions of the Gastropoda in 1973-74 and 1974-75, are presented in Tables 23 and 24, respectively, while the vertical distributions in these same years are presented in Tables 25 and 26. In 1973-74, all three snails, Helisoma sp. Physa sp. and Ferrissia sp., were fairly abundant. In addition, all three snails were most abundant at station A. However, examination of Table 25 reveals that these species tended to segregate themselves vertically. The dominant snail, Helisoma sp., was most abundant at 4 meters, while the other two were most abundant at 2 meters. In 1974-75, Helisoma sp., was again distributed heterogeneously, but was most abundant at a different station, G. It was also most abundant at 4 meters in this year. By 1974-75, the other two snails had decreased sharply in numbers. Physa sp. continued to exhibit its maximum abundance at station A, while Ferrissia sp. was most abundant at station B. Thus, in 1974-75, we see that each of the three snails was most successful at different horizontal locations of Lake Anna.

Horizontal and vertical distributions of the Ephemeroptera are presented in Tables 27 and 28, and Tables 29 and 30, respectively. In 1973-74 there was only one abundant species in Lake Anna, Caenis amica. It was most abundant at station A. In 1974-75 there were two common species, Caenis amica and Hexagenia munda. C. amica was most abundant at stations B and C, while H. munda was most abundant at stations B, C, and D. Both species were most successful at 2 meters. Neither species occurs significantly in Lake Anna at present. The expected significance of H. munda has already been discussed. It is interesting to note that *H. munda* is one of the few organisms in Lake Anna which occurs most abundantly at station D.

Horizontal and vertical distributions of the Odonata are presented in Tables 31 and 32, and Tables 33 and 34, respectively. The densities of Odonata are rather low but they are significant because they are the largest invertebrate predators. In many cases they are probably secondary carnivores, and are thus important in the flow of energy through the ecosystem. In 1973-74 there was considerable overlap in the stations where the species were most successful. By 1974-75 the species tended to exhibit more distinct patterns of horizontal heterogeneity. *Perithemis tenera* was most abundant at stations A and C. *Argia* spp. were clearly most abundant at station B, but also abundant at C. *Enallagma* spp. were most abundant at station D, while *Epicordulia princeps* was more evenly distributed at stations C, D, G, and H. Thus, we see a significant overlap of abundance only at station C between *Argia* spp. and *Perithemis tenera*. Examination of the vertical distribution reveals that these species tend to be most abundant at different depths. *Argia* spp. tend to be most numerous at 2 meters, while *Perithemis tenera* tends to be most numerous at 4 meters.

Horizontal distributions of the Trichoptera in 1973-74 and 1974-75 are presented in Tables 35 and 36, respectively, while vertical distributions in the same years are presented in Tables 37 and 38. In 1973-74 there were very few caddisflies in Lake Anna, averaging only about 2 per sampler. Since there were so few caddisflies, there was probably little interaction between species, and thus, the horizontal distribution of the dominant species was rather homogenous. One exception to this was Nyctiophylax affinis which was only collected at stations B and C. It was quite abundant at those stations, comprising 21% of all Trichoptera collected in the lagoons. This is probably an example of the introduction of new species as a localized population in a small area. By 1974-75, N. affinis occurred at more stations, but was still most abundant at station C. All species were most abundant at 2 meters in 1973-74, again indicating little interaction between species. By 1974-75 there were really only 2 significant Trichoptera: Cyrnellus fraternus and Polycentropus sp. These two species accounted for approximately 90% of all Trichoptera. Also, in 1974-75 the density of both species increased greatly so that there were an average of 12 Trichoptera per sampler, considering the entire year at all depths. In the summer months at 2 meters, as many as 249 caddisflies were collected on one sampler. One would expect this increase in density to bring about competition between these similar species. Both species are micro-predators which reside in silk nets and attack small prey near the opening of their refugium (J. B. Wallace, personal communication). Thus, it would seem likely that there would be competition both for food, and space to construct their nets. The distribution of these species indicates that this assumption is probably true. Proceeding horizontally one finds that usually only one species was abundant at a station. At stations A, C, D, E, and H, *Polycentropus* sp. far outnumbered *Cyrnellus fraternus*. At station B the situation was reversed. Only at stations F and G did the two species occur in similar densities. Examination of the vertical distribution revealed that in 1974-75, *Cyrnellus fraternus* occurred more often at 4 meters than it had in 1973-74. At station F in 1974-75, where the 2 species exhibited near-identical densities, *Polycentropus* sp. outnumbered *Cyrnellus fraternus* by 18.3 to 12.0 per sampler at 2 meters, while *C. fraternus* outnumbered *Polycentropus* sp. by 10.2 to 3.2 per sampler at 4 meters. This clearly indicates that similar species, which must compete for the same resources, are tending to become separated, both horizontally and vertically.

Since trends in spatial heterogeneity and stratification were shown to exist in Lake Anna, it seemed likely that trends in temporal distribution of macrobenthos would also exist. Tables 39 and 40 present the temporal distribution of the major groups in 1973-74 and 1974-75, respectively. Tables 41-48 present the temporal distribution of the species of Gastropoda, Ephemeroptera, Odonata, and Trichoptera in 1973-74 and 1974-75. In addition, Figures 30-38 are graphs of the temporal distribution of the total number of organisms, Oligochaeta, and Chironomidae at each depth and group of stations. The graphs for 2 meters and 4 meters indicate that Chironomidae and Oligochaeta usually had their lowest densities in the summer months. In 1974-75 both Chironomidae and Oligochaeta had a distinct increase in population during July. It is understandable that Chironomidae would have their lowest density in the summer, as they are holometabolous insects and emerge as adults during this period. The peak in July would indicate two emergence periods. Very little is known about the biology of Naididae, however, so I cannot offer an explanation for this phenomenon. It is possible that they also reproduce prolifically in the summer, and the immatures are not collected because of their small size. Other organisms common at 2 and 4 meters, which had their lowest densities in the summer were: Turbellaria, Amphipoda, Ephemeroptera, and Odonata. However, there were several groups which became most abundant in the summer. The most significant of these were the Trichoptera. Both dominant species had their highest densities in August and September. Another group which became most abundant in the summer were the Gastropoda. Helisoma sp. exhibited maximum density in July. It is important to note that the maximum density of the Gastropoda was coincident with the interim summer maxima of Chironomidae and Oligochaeta. This supports the possibility of positive interaction between these three groups.

At 7 meters there were very significant changes in the populations of Chironomidae and Oligochaeta with time. These two groups became very scarce in the summer, probably due to oxygen depletion in the hypolimnion. However, the graphs of total organisms at 7 meters do not change appreciably in the summer months. This is because Chaoborus sp. became most abundant at this time and offset the decrease of other groups. Members of this genus have been shown to be able to withstand prolonged periods of oxygen depletion. In addition, they possess the capability of migrating upward at night to areas where aerobic conditions exist. Thus, it appears that temporal heterogeneity also exists among the dominant macrobenthos of Lake Anna. Most organisms have their lowest density in summer, especially June and August, while a few organisms have their maximum density during this season.

The preceding biological discussion of horizontal, vertical, and temporal distribution has shown the major trends of the differences detected by statistical analysis. However, it should be noted that the ANOVA's and Duncan Multiple Range Tests indicated significant and complex interactions between these variables. Unfortunately, these statistical tests were not practical, as no clear pattern of distribution emerged. The non-statistical treatment of the data has provided a basic understanding of the distributional trends which will be useful in distinguishing between successional changes in macrobenthic community structure and changes due to the thermal effluent.

A concise tabular summary of the distributional trends is presented in Tables 49-51. Table 49 is a summary of the horizontal distribution, listing the species which exhibit their greatest densities at each station. Greatest emphasis was placed on the results from the last year of the study, 1974-75. It should be noted that this list is mostly concerned with organisms other than Oligochaeta and Chironomidae. Oligochaeta and Chironomidae were generally the most abundant organisms at all stations, and their unusual abundance is only listed at one station, G. Table 50 is a summary of the vertical distribution of macrobenthos. It should be noted here that Chironomidae and Oligochaeta were also abundant at 2 meters, but are only listed at 4 meters where they exhibited greatest density. Table 51 is a summary of temporal distribution. Even though Chironomidae and Oligochaeta showed an additional peak in July, I felt that in comparison to the rest of the year, they were still least abundant in the summer.

Successional Dynamics

The almost instantaneous transformation of a lotic habitat to a lentic habitat provided an excellent opportunity to study succession. As stated earlier, one of the objectives of this study was to compare the development of macrobenthic community structure in Lake Anna with the general trends expected in ecosystem development. There were both academic and practical reasons for this interest in succession. From an academic standpoint, a new reservoir provides a natural laboratory in which to study aquatic succession, similar to the opportunity the Lake Michigan dunes provide to study terrestrial succession. From a practical standpoint, it was necessary to understand the successional changes occurring in Lake Anna, so that these changes could be distinguished from any changes produced by the thermal effluent.

Odum (1971) defines ecosystem development, or ecological succession, in terms of three parameters: "(1) It is an orderly process of community development that involves changes in species structure and community processes with time; it is reasonably directional and, therefore, predictable. (2) It results from modification of the physical environment by the community; that is succession is community-controlled even though the physical environment determines the pattern, the rate of change, and often sets the limits as to how far development can go. (3) It culminates in a stabilized ecosystem in which maximum biomass (or high information content) and symbiotic function between organisms are maintained per unit of available energy flow." In addition, he presented a table of 24 trends to be expected in the development of ecosystems. Table 1 contains four of these trends expected in regard to community structure. The species diversity-variety component will be considered first. Immediately after impoundment there was a drastic reduction in the number of species (90 to 40). However, in the succeeding years this number increased significantly (54). Therefore, it appears this component of diversity has proceeded from low to somewhat higher. In regard to species diversity-equitability component, the first year after impoundment there were just a few dominant species. There were four functional categorizations of macrobenthos in Lake Anna. The first year after impoundment, each category contained one dominant organism. By the second year after impoundment, there were several dominant organisms in most of the functional categories and these organisms tended to be more evenly dominant. Thus, it appears that this aspect of diversity has also gone from low to somewhat higher. Considering the spatial heterogeneity (horizontal distribution), it appears that each organism is becoming distributed so that it will attain optimum success. In the case of species which compete for the same resources, such as the micropredator caddisflies, they tend not to occur at the same locations. Species which benefit from each other's presence, such as snails and oligochaetes which possibly feed upon faeces of chironomids, occur at the same locations. This seems to indicate that Lake Anna has become better organized in regard to spatial heterogeneity. Finally, the stratification (vertical distribution) of Lake Anna has also become better organized. Again, species which compete for the same resources (Gastropoda, Odonata, Trichoptera) occur at different depths, while those species which benefit from each other's presence (Oligochaeta, Gastropoda, and Chironomidae) tend to occur at the same depth. In addition to these attributes listed by Odum, it seems likely that the organizational stage of temporal heterogeneity would also be a trend in ecosystem development. In Lake Anna the benthic community has become better organized temporally, with some species being most abundant when other species exhibit their minimum.

In summary, the benthic communities of Lake Anna appear to be following the general trends expected in ecosystem development. The greatest change occurred between the first and second years; however, Lake Anna has not become a stable ecosystem by any means. As one example, the burrowing mayflies (Hexagenia) have just become established in Lake Anna. As they become more abundant, their extensive burrowing, ingestion, and egestion of the sediment will modify the quality of useful food for other organisms. In addition, the physical environment, which sets the limits for succession, may be modified by increased silt deposition. The change in quality of organic matter and increased silt deposition may lead to the success of more typical herpobenthic forms, such as Tubificidae and Spaeriidae. Large mussels are also becoming established in the main reservoir, probably from the upper reaches of the North Anna River. Finally, succession may be influenced by the establishment of significant areas of macrophytes. It appeared that Potamogeton sp. was becoming established the second year, but it was not very successful in the third year. Abundant aquatic macrophytes would certainly favor the success of additional haptobenthic forms. Therefore, the first and second colonizers I have listed may be followed by third and even fourth colonizers. This could result in the loss or addition of trophic functional categories. Future attempts to determine the effects of the thermal effluent on the macrobenthos should consider that this study indicates changes due to ecological succession are also to be expected.

Overall Reservoir Productivity and Macrobenthos

It has been observed that reservoirs, in contrast to natural lakes, begin their existence with high productivity, but tend to suffer productivity declines with the passage of time (Neel, 1963). Figure 39 is a hypothetical model of productivity changes expected in new reservoirs (U. S. Atomic Energy Commission, Directorate of Licensing, 1973). There is an initial period of increasing productivity followed by a longer period of productivity decline. Inundation of fertile topsoils and the subsequent leaching of mineral nutrients and organic materials is responsible for the early period of high productivity. When these original mineral nutrients and organic materials have been thoroughly leached from the substrate, reservoirs become less productive. Factors affecting this process include stratification, density currents, rapidity of water replacement, level of most frequent withdrawal, and prevalent operation practices (Neel, 1963). Eventually there is a recovery of productivity, followed by equilibrium with the prevailing conditions of the basin, but reservoirs never regain their original level of productivity.

In order that this study of early macrobenthos would have predictive value, the data from Lake Anna were compared to the expected trends of productivity in new reservoirs. In addition, macrobenthic studies in older reservoirs were reviewed for this same purpose. Since secondary production, per se, was not estimated in Lake Anna and very little secondary production data are available in the literature, it was necessary to use standing crop as the parameter. This should make little difference in a general model. The oldest reservoir for which continuous annual macrobenthic data is available is the Goczalkowice dam reservoir in Poland. It was created in 1955, and macrobenthos has been investigated each year since impoundment. Much of the early literature on this reservoir was published in government bulletins written in Polish, but Krzyzanek (1973) discussed the bottom fauna from 1965-69 and also presented a summary of all previous findings. Maximum macrobenthic densities occurred in Goczalkowice reservoir 4-7 years after impoundment.

In succeeding years, densities declined until a minimum was reached 11-13 years after impoundment. There were increased densities 14-15 years after impoundment, but not nearly as high as in the early years of the reservoir. Thus far, the density trends in Lake Anna are consistent with those of Goczalkowice reservoir. In each of the first 3 years following impoundment, the density of macrobenthos has increased. Therefore, it appears that macrobenthos also follows the general trends predicted in Figure 39. Figure 40 presents the general trends to be expected in macrobenthic standing crop over the first 15 years of a newly impounded reservoir. Thus, in Lake Anna, one would expect the density of macrobenthos to increase for several more years before declining. It is interesting to note that, in Lake Anna, phytoplankton density and volume have also increased in each of the first 3 years after impoundment (G. B. Hall, personal communication), indicating a possible direct relationship between phytoplankton abundance and macrobenthos abundance.

CONCLUSIONS

The following conclusions have been reached regarding the macrobenthos of Lake Anna, a new mainstream reservoir located in central Virginia. These conclusions are probably true for all mainstream reservoirs of the southeastern United States. This is not to imply that they are not valid in other geographical areas, but due to extreme differences in climate and the geology of pre-impoundment basins, it would be necessary to collect data from other areas before extending these conclusions.

1. New reservoirs are quickly colonized by benthic invertebrates, probably after the first summer period. The density of benthic organisms continues to increase, at least for the first 3 years, and possibly for as long as 7 years.

2. The benthic fauna of a new reservoir is completely different in composition from the pre-impoundment fauna. Most early dominant species in the reservoir are probably minor facultative species from the previous lotic habitat. Later dominant species probably arrive by active transport.

3. The composition of the benthic community at different areas of the reservoir is much more similar than different areas of the previous lotic habitat. While polluted and unpolluted stretches of a river possess a different macrobenthic fauna, these areas become very similar following impoundment. The same is true for the fauna of small woodland streams and large rivers after inundation.

4. There are very few trophic functional categories in new reservoirs. Even though initially there is a considerable amount of submerged terrestrial vegetation, there are no benthic organisms which feed directly upon this material, such as the detritus shredders found in streams. The collector-microfilterers and collector-microgatherers of new reservoirs rely on fine particulate organic matter for food. Thus, the course organic matter only becomes available food after it is broken down by microbes and the physical action of the water. The collector-microfilterers and collector-microgatherers, in turn, are prey for micro- and macropredators.

5. The early macrobenthos of new reservoirs can be classified into three groups: first colonizers, omnipresent, and second colonizers. The first colonizers have one completely dominant species in each of three functional categories. The second colonizers have several species more evenly dominant in each of the same functional categories. The omnipresent group consists of Chironomidae, which are continuously dominant in the fourth functional category, collector-microfilterers.

6. The new lentic ecosystem is very complex in regard to the horizontal, vertical, and temporal distribution of benthic organisms, but it is possible to distinguish certain trends. In general, benthic organisms of new reservoirs become distributed so that those which compete are separated

in space or time, while those organisms which benefit from each other's presence, occur together.

7. During the first 3 years, benthic community structure follows the general trends expected in ecosystem development. While the greatest changes occur between the first and second years, the ecosystem is not stable after the third year, and further changes are to be expected.

8. A comparison of the density of macrobenthos in new reservoirs with the expected changes in productivity, indicates that the general model of productivity is probably also true for macrobenthos. The time period from impoundment to the second increase in abundance of macrobenthos is about 15 years. The abundance of macrobenthos may be directly related to the abundance of phytoplankton.

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APPENDIX A

Table 1. Community structure trends expected in ecosystem development (Odum, 1971).

Ecosystem Attributes	Developmental Stages	Mature Stages
Species diversity-variety component	Low	High
Species diversity-equitability component	Low	High
Spatial heterogeneity	Poorly organized	Well organized
Stratification	Poorly organized	Well organized

Table 2. Density of dominant macrobenthos in Lake Anna for the first three years after impoundment. Density is expressed as number of organisms per sampler. These values were calculated only from web samplers. Values from the larger web samplers used in 1972-73 were corrected by an appropriate volume factor (0.1975).

Taxa	Reservoir			Lagoons		
	1972-73	1973-74	1974-75	1972-73	1973-74	1974-75
Turbellaria		4.4	6.8		0.8	4.4
Oligochaeta		51.4	33.9		49.3	27.9
Gastropoda	23.5	1.5	4.5		9.5	6.7
Amphipoda	65.8	15.2	12.8		8.8	4.3
Isopoda	1.4	0.9	1.4		0.1	0.3
Ephemeroptera	3.8	1.2	0.1		1.5	0.8
Odonata	0.8	0.9	0.9		1.4	2.0
Trichoptera	3.0	3.8	11.6		3.2	12.2
Chironomidae	29.2	88.0	124.4		95.6	135.3
Chaoborus	0.2	5.5	5.7		6.7	9.9
Total Organisms	127.8	173.1	201.7		176.9	204.6

Table 3. Number of taxa collected in dominant macrobenthic groups before impoundment and in each of the first three years after impoundment.

Taxonomic Group	Pre-impoundment	1972-73	1973-74	1974-75
Gastropoda	5	4	4	4
Ephemeroptera	14	3	4	3
Odonata	16	6	9	9
Trichoptera	17	6	17	14
Total Macrobenthos	90	40	54	54

Table 4. Percentage composition of dominant macrobenthos before impoundment and in each of the first three years after impoundment. The reservoir and lagoons have been treated separately. The values were calculated from both web and leaf samplers. An asterisk (*) denotes less than 1 %.

Taxa	Reservoir				Lagoons			
	River	1972-73	1973-74	1974-75	Tribs.	1972-73	1973-74	1974-75
Turbellaria			3	5			*	3
Oligochaeta	1		22	18	1		18	15
Gastropoda	21	12	1	3	10		7	5
Pelecypoda	3		*	*	10			*
Amphipoda	*	49	8	5	1		3	2
Isopoda		1	1	1	2		*	*
Decapoda	1	*	*		4			*
Ephemeroptera	14	4	1	*	18		1	*
Plecoptera	12				1			
Odonata	2	1	*	*	13		1	1
Hemiptera	7				2			

Table 4. (continued).

Taxa	Reservoir				Lagoons			
	River	1972-73	1973-74	1974-75	Tribs.	1972-73	1973-74	1974-75
Trichoptera	33	2	3	6	14		2	6
Megaloptera	1		*	*	7		*	*
Coleoptera	4	*	*	*	9		*	*
Chironomidae	1	31	57	58	4		62	63
Chaoborus		*	4	2			5	5

Table 5. Percentage composition of dominant macrobenthos in first years of other reservoirs. These percentages were calculated from the original published data. An asterisk (*) denotes less than 1 %. References: 1. (Nursall, 1952); 2. (O'Connell and Campbell, 1953); 3. (Hulsey, 1956); 4. (Paterson and Fernando, 1969b); 5. (Aggus, 1971).

Ref.	Taxa	Year 1	Year 2	Year 3
1	Chironomidae	91		
	Oligochaeta and <u>Gammarus</u>	?		
2	Oligochaeta	17	21	10
	Gastropoda	*		*
	Ephemeroptera	1	8	*
	Odonata	*		*
	Trichoptera	*		
	Chironomidae	27	60	32
	Chaoboridae	53	9	56
3	Oligochaeta	64		
	Chironomidae	32		
	Chaoboridae	1		
4	Oligochaeta	35		
	Gastropoda	1		
	Chironomidae	59		

Table 5. (continued).

Ref.	Taxa	Year 1	Year 2	Year 3
5	Oligochaeta	1	9	
	Crustacea (cladocerans)	2	30	
	Ephemeroptera	*	2	
	Odonata	*	1	
	Trichoptera	2	5	
	Chironomidae	94	53	

Table 6. Percentage composition of dominant Gastropoda before impoundment and in each of the first three years after impoundment. The numbers are percent of total Gastropoda, not total macrobenthos. The reservoir and lagoons have been treated separately. The values were calculated from both web and leaf samplers. An asterisk (*) denotes less than 1 %.

Taxa	Reservoir				Lagoons			
	River	1972-73	1973-74	1974-75	Tribs.	1972-73	1973-74	1974-75
(Pulmonata)								
Ferrissia sp.		25	57	10			28	20
Helisoma sp.	14	15	41	89	8		63	76
Lymnaea sp.	*	*	*	*			*	
Physa sp.	3	60	2	1			9	4
(Prosobranchia)								
Campeloma sp.	8				92			
Goniobasis sp.	74							

Table 7. Percentage composition of dominant Ephemeroptera before impoundment and in each of the first three years after impoundment. The numbers are percent of total Ephemeroptera, not total macrobenthos. The reservoir and lagoons have been treated separately. The values were calculated from both web and leaf samplers. An asterisk (*) denotes less than 1 %.

Taxa	Reservoir				Lagoons			
	River	1972-73	1973-74	1974-75	Tribs.	1972-73	1973-74	1974-75
(Ephemeridae)								
<u>Ephemera</u> sp.					53			
<u>Hexagenia</u> <u>munda</u>				71				31
(Caenidae)								
<u>Brachycercus</u> sp.					27			
<u>Caenis</u> <u>amica</u>	2	100	99	25	4		99	66
(Baetidae)								
<u>Centroptilum</u> sp.	17							
(Siphlonuridae)								
<u>Isonychia</u> sp.	29	*	*				*	

Table 7. (continued).

Taxa	Reservoir				Lagoons			
	River	1972-73	1973-74	1974-75	Tribs.	1972-73	1973-74	1974-75
(Heptageniidae)								
Cinygmula sp.					12			
Stenonema sp.	49		*	1			1	*

Table 8. Percentage composition of dominant Odonata before impoundment and in each of the first three years after impoundment. The numbers are percent of total Odonata, not total macrobenthos. The reservoir and lagoons have been treated separately. The values were calculated from both web and leaf samplers. An asterisk (*) denotes less than 1 %.

Taxa	Reservoir				Lagoons			
	River	1972-73	1973-74	1974-75	Tribs.	1972-73	1973-74	1974-75
(Gomphidae)								
Progomphus obscurus	56							
(Aeschnidae)								
Aeschna sp.	5				10			
(Libellulidae)								
Epicordulia princeps		*	13	22			12	11
Perithemis tenera	1	1	40	7	3		31	24
(Macromiidae)								
Macromia sp.	19		2	1	1		1	1

Table 8. (continued).

Taxa	Reservoir				Lagoons			
	River	1972-73	1973-74	1974-75	Tribs.	1972-73	1973-74	1974-75
(Calopterygidae)								
Calopteryx sp.					41			
(Coenagrionidae)								
Argia spp.	1		13	38	37		37	50
Enallagma spp.	5	95	29	30			17	12

Table 9. Percentage composition of dominant Trichoptera before impoundment and in each of the first three years after impoundment. The numbers are percent of total Trichoptera, not total macrobenthos. The reservoir and lagoons have been treated separately. The values were calculated from both web and leaf samplers. An asterisk (*) denotes less than 1 %.

Taxa	Reservoir				Lagoons			
	River	1972-73	1973-74	1974-75	Tribs.	1972-73	1973-74	1974-75
(Hydropsychidae)								
Cheumatopsyche sp.	44		1				*	*
Hydropsyche sp.	34	*						
Macronemum sp.	12		*	*				
(Hydroptilidae)								
Orthotrichia sp.		11	25	*			13	*
(Polycentropodidae)								
Cyrnellus fraternus			26	28			24	30
Nyctiophylax affinis				2			21	2
Polycentropus sp.			12	63			21	60

Table 9. (continued).

Taxa	Reservoir				Lagoons			
	River	1972-73	1973-74	1974-75	Tribs.	1972-73	1973-74	1974-75
(Leptoceridae)								
Oecetis spp.		87	34	4			18	4

Table 10. Taxonomic classification of early macrobenthos.

First Colonizers	Omnipresent	Second Colonizers
Gastropoda	Chironomidae	Turbellaria
Physa sp.	*Glyptotendipes* sp.	Oligochaeta
Amphipoda	*Chironomus* sp.	Gastropoda
Hyalella azteca		*Helisoma* sp.
Ephemeroptera		Isopoda
Caenis amica		*Asellus* sp.
Odonata		Ephemeroptera
Enallagma spp.		*Hexagenia munda*
Trichoptera		Odonata
Oecetis		*Epicordulia princeps*
		Perithemis tenera
		Argia spp.
		Trichoptera
		Cyrnellus fraternus
		Polycentropus sp.

Table 11. Functional classification of early macrobenthos. The functional groups are those of Cummins (1974).

Functional Groups	First Colonizers	Omnipresent	Second Colonizers
Micropredators	*Oecetis* spp		*Cyrnellus fraternus*
			Nyctiophylax affinis
			Polycentropus sp.
Macropredators	*Enallagma* spp.		*Epicordulia princeps*
			Perithemis tenera
			Argia spp.
Collector-microgatherers	*Hyalella azteca*		Oligochaeta
	Physa sp		*Helisoma* sp.
	Caenis amica		Turbellaria
			Asellus sp.
			Hexagenia munda
Collector-microfilterers		Chironomidae	

Table 12. Analysis of variance table for total organisms in 1973-74. All data were transformed by $LOG_{10}(X+1)$.

Source of Variation	df	SS	MS	F	Prob > F
Station	7	6.83	0.98	25.51	.0001
Month	10	11.09	1.11	29.00	.0001
Transect	2	10.56	5.28	137.98	.0001
Station X Transect	14	4.10	0.29	7.65	.0001
Station X Month	70	8.56	0.12	3.20	.0001
Month X Transect	20	1.65	0.08	2.16	.0032
Residual	394	15.07	0.04		
Total	517	57.86	0.11		

Table 13. Analysis of variance table for total organisms in 1974-75. All data were transformed by $LOG_{10}(X+1)$.

Source of Variation	df	SS	MS	F	Prob > F
Station	7	11.05	1.58	38.52	.0001
Month	10	6.37	0.64	15.53	.0001
Transect	2	21.21	10.61	258.75	.0001
Station X Transect	14	6.38	0.46	11.12	.0001
Station X Month	70	8.54	0.12	2.98	.0001
Month X Transect	20	2.43	0.12	2.96	.0001
Residual	385	15.78	0.04		
Total	508	71.77	0.14		

Table 14. Analysis of variance table for total taxa in 1973-74. All data were transformed by $LOG_{10}(X+1)$.

Source of Variation	df	SS	MS	F	Prob > F
Station	7	0.32	0.05	5.75	.0001
Month	10	0.49	0.05	6.10	.0001
Transect	2	11.49	5.74	719.19	.0001
Station X Transect	14	0.97	0.07	8.64	.0001
Station X Month	70	1.02	0.01	1.82	.0004
Month X Transect	20	0.95	0.05	5.93	.0001
Residual	394	3.15	0.01		
Total	517	18.37	0.04		

Table 15. Analysis of variance table for total taxa in 1974-75. All data were transformed by $LOG_{10}(X+1)$.

Source of Variation	df	SS	MS	F	Prob > F
Station	7	0.71	0.10	12.5	.0001
Month	10	0.84	0.08	10.35	.0001
Transect	2	12.14	6.07	750.20	.0001
Station X Transect	14	0.57	0.04	5.01	.0001
Station X Month	70	1.27	0.02	2.25	.0001
Month X Transect	20	0.62	0.03	3.81	.0001
Residual	386	3.12	0.01		
Total	509	19.26	0.04		

Table 16. Summary of basic physical-chemical parameters from October, 1972 to September, 1973. The numbers are the minimum and maximum, respectively, for each parameter at a given depth.

Parameters	Reservoir			Lagoons		
	2 Meters	4 Meters	7 Meters	2 Meters	4 Meters	7 Meters
Temperature	2.6-27.5	2.6-27.0	3.2-20.0	5.0-28.0	5.0-26.0	5.0-18.0
Oxygen	6.8-12.5	3.0-12.5	0.2-12.6	6.3-11.3	3.4-11.3	0.2-11.3
Alkalinity	13 -21	11 -18	12 -18	22 -27	22 -27	22 -31
pH	6.6- 7.3	6.4- 7.1	6.4- 7.0	6.6- 7.5	6.4- 7.2	6.6- 6.9

Table 17. Summary of basic physical-chemical parameters from October, 1973 to September, 1974. The numbers are the minimum and maximum, respectively, for each parameter at a given depth.

Parameters	Reservoir			Lagoons		
	2 Meters	4 Meters	7 Meters	2 Meters	4 Meters	7 Meters
Temperature	6.0-27.0	6.0-25.0	6.0-20.5	6.5-27.0	6.5-24.5	6.0-20.0
Oxygen	6.0-13.0	7.6-11.7	0.7-11.3	7.2-11.9	7.0-11.8	0.0-10.1
Alkalinity	12 -24	11 -24	16 -26	14 -33	26 -33	23 -36
pH	6.4- 7.7	6.5- 7.2	6.2- 7.0	6.2- 7.3	6.8- 7.3	6.5- 7.6

Table 18. Summary of basic physical-chemical parameters from October, 1974 to September, 1975. The numbers are the minimum and maximum, respectively, for each parameter at a given depth.

Parameter	Reservoir			Lagoons		
	2 Meters	4 Meters	7 Meters	2 Meters	4 Meters	7 Meters
Temperature	2.5-29.0	1.0-29.0	1.0-21.0	5.0-29.0	4.5-27.0	4.0-20.0
Oxygen	5.9-14.4	5.2-13.1	0.5-12.8	6.6-14.2	5.5-13.0	0.4-12.7
Alkalinity	14 -27	12 -25	9 -24	25 -31	23 -32	24 -31
pH	6.5- 7.5	6.4- 7.2	6.6- 6.9	6.7- 7.0	6.5- 7.4	6.3- 7.0

Table 19. Horizontal distribution of dominant macrobenthos in 1973-74. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each station. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms per sampler or less than 1 %.

Taxa	Lagoon Stations			Reservoir Stations				
	A	B	C	D	E	F	G	H
Turbellaria								
Density	0.9	1.3	0.3	2.1	9.2	3.8	2.8	3.9
Percent	4	5	1	8	37	16	12	16
Oligochaeta								
Density	42.9	50.1	54.9	12.1	22.2	57.4	101.2	59.6
Percent	11	12	14	3	5	14	25	15
Gastropoda								
Density	16.5	6.1	5.8	0.3	1.6	2.2	1.7	1.9
Percent	46	17	16	1	4	6	5	5

Table 19. (continued).

Taxa	Lagoon Stations			Reservoir Stations				
	A	B	C	D	E	F	G	H
Isopoda								
Density		*	0.4		3.7		*	0.6
Percent		*	8		78		1	13
Amphipoda								
Density	6.9	19.7	0.2	1.0	18.8	30.3	14.0	10.6
Percent	7	19	*	1	18	30	14	11
Ephemeroptera								
Density	2.1	1.4	1.0	2.0	0.6	1.7	1.5	0.5
Percent	20	13	10	17	5	16	14	5
Odonata								
Density	0.8	1.7	1.7	0.6	0.4	0.6	0.9	1.8
Percent	10	20	20	6	4	7	11	22

Table 19. (continued).

Taxa	Lagoon Stations			Reservoir Stations				
	A	B	C	D	E	F	G	H
Trichoptera								
Density	1.8	3.5	4.2	3.8	3.1	4.2	3.7	3.9
Percent	7	12	15	12	11	15	13	14
Chironomidae								
Density	67.4	90.4	128.6	79.8	38.9	88.0	125.4	105.5
Percent	9	12	18	10	5	12	18	15
Chaoborus								
Density	4.5	10.2	5.6	3.1	1.3	6.6	10.2	5.9
Percent	10	21	12	6	3	14	22	13
Total Organisms								
Density	143.7	184.6	202.7	105.0	99.8	195.4	261.9	195.0
Percent	10	13	15	7	7	14	19	14

Table 20. Horizontal distribution of dominant macrobenthos in 1974-75. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each station. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms per sampler or less than 1 %.

Taxa	Lagoon Stations			Reservoir Stations				
	A	B	C	D	E	F	G	H
Turbellaria								
Density	12.5	0.3	0.1	1.6	17.5	5.7	2.2	7.1
Percent	27	*	*	3	36	12	5	15
Oligochaeta								
Density	24.9	13.8	44.7	12.5	15.4	36.9	61.0	43.1
Percent	10	5	18	5	6	14	24	17
Gastropoda								
Density	7.5	6.7	5.8	1.3	5.2	1.9	10.6	3.5
Percent	18	15	14	3	12	4	25	8

Table 20. (continued).

Taxa	Lagoon Stations			Reservoir Stations				
	A	B	C	D	E	F	G	H
Isopoda								
Density	*		1.0		5.9	*		1.3
Percent	*		12		71	1		15
Amphipoda								
Density	7.0	5.5	0.3	0.9	7.3	31.0	12.5	12.7
Percent	9	7	*	1	9	40	16	17
Ephemeroptera								
Density	0.2	1.3	1.1	0.3	0.2	*		*
Percent	6	41	35	10	5	1		2
Odonata								
Density	0.7	3.1	2.3	1.2	0.4	0.3	1.0	1.3
Percent	7	29	22	12	4	3	10	13

Table 20. (continued).

Taxa	Lagoon Stations			Reservoir Stations				
	A	B	C	D	E	F	G	H
Trichoptera								
Density	10.7	10.2	15.7	8.4	14.7	15.1	10.2	9.6
Percent	12	10	17	9	15	16	11	10
Chironomidae								
Density	79.5	184.1	145.5	109.1	23.3	116.3	207.6	163.6
Percent	8	17	14	11	2	11	20	16
<u>Chaoborus</u>								
Density	5.4	21.7	3.2	6.7	2.5	4.1	8.0	4.2
Percent	10	38	6	12	2	7	14	8
Total Organisms								
Density	148.9	247.8	220.3	142.3	96.8	213.8	305.9	247.6
Percent	9	15	14	9	6	13	19	16

Table 21. Vertical distribution of dominant macrobenthos in 1973-74. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each depth. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms or less than 1 %.

Taxa	2 Meters	4 Meters	7 Meters
Turbellaria			
Density	5.7	3.0	0.4
Percent	62	33	4
Oligochaeta			
Density	51.2	70.3	29.5
Percent	34	47	19
Gastropoda			
Density	7.8	5.6	0.1
Percent	57	42	1
Amphipoda			
Density	32.9	4.4	0.9
Percent	86	12	2
Isopoda			
Density	0.5	1.2	*
Percent	28	69	3

Table 21. (continued).

Taxa	2 Meters	4 Meters	7 Meters
Ephemeroptera			
Density	3.1	0.8	0.2
Percent	77	19	4
Odonata			
Density	2.0	1.1	0.1
Percent	63	35	2
Trichoptera			
Density	8.3	1.9	0.1
Percent	80	19	1
Chironomidae			
Density	92.8	124.5	53.8
Percent	34	47	19
<u>Chaoborus</u>			
Density	0.2	0.8	17.3
Percent	1	4	94
Total Organisms			
Density	205.1	214.1	102.1
Percent	39	42	19

Table 22. Vertical distribution of dominant macrobenthos in 1974-75. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each depth. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms or less than 1 %.

Taxa	2 Meters	4 Meters	7 Meters
Turbellaria			
Density	11.8	5.5	0.3
Percent	68	31	2
Oligochaeta			
Density	33.3	43.0	18.3
Percent	36	45	19
Gastropoda			
Density	5.2	10.4	0.2
Percent	33	65	1
Amphipoda			
Density	24.7	3.3	0.4
Percent	87	12	1
Isopoda			
Density	1.6	1.2	0.2
Percent	54	39	8

Table 22. (continued).

Taxa	2 Meters	4 Meters	7 Meters
Ephemeroptera			
Density	0.9	0.2	*
Percent	83	15	3
Odonata			
Density	2.5	1.1	0.1
Percent	68	30	1
Trichoptera			
Density	25.2	8.3	0.7
Percent	74	24	2
Chironomidae			
Density	153.6	180.2	50.2
Percent	40	47	13
Chaoborus			
Density	0.2	0.6	20.1
Percent	1	3	96
Total Organisms			
Density	257.9	256.1	92.2
Percent	43	42	15

Table 23. Horizontal distribution of dominant Gastropoda in 1973-74. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each station. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms per sampler or less than 1 %.

Taxa	Lagoon Stations			Reservoir Stations				
	A	B	C	D	E	F	G	H
(Pulmonata)								
Ferrissia sp.								
Density	4.8	1.2	0.5	*	0.2	1.8	0.6	1.2
Percent	47	11	5	*	1	17	6	12
Helisoma sp.								
Density	9.9	4.3	4.8	0.2	1.4	0.4	1.1	0.7
Percent	44	18	21	1	6	17	5	3
Physa sp.								
Density	1.7	0.7	0.5		0.1			
Percent	59	22	16		2			

Table 24. Horizontal distribution of dominant Gastropoda in 1974-75. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each station. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms per sampler or less than 1 %.

Taxa	Lagoon Stations			Reservoir Stations				
	A	B	C	D	E	F	G	H
(Pulmonata)								
<u>Ferrissia</u> sp.								
Density	0.4	1.4	0.2	0.1	*	0.4	1.0	0.1
Percent	12	39	6	3	*	11	27	3
<u>Helisoma</u> sp.								
Density	5.8	5.1	5.6	1.0	5.1	1.5	9.6	3.4
Percent	16	13	15	3	14	4	26	9
<u>Physa</u> sp.								
Density	1.3	0.1	*	0.2	0.1	*	*	*
Percent	72	6	2	11	6	1	2	1

Table 25. Vertical distribution of dominant Gastropoda in 1973-74. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each depth. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms or less than 1 %.

Taxa	2 Meters	4 Meters	7 Meters
(Pulmonata)			
Ferrissia sp.			
Density	3.2	0.6	*
Percent	82	17	1
Helisoma sp.			
Density	3.6	4.9	*
Percent	42	58	1
Physa sp.			
Density	1.0	0.1	*
Percent	92	7	1

Table 26. Vertical distribution of dominant Gastropoda in 1974-75. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each depth. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms or less than 1 %.

Taxa	2 Meters	4 Meters	7 Meters
(Pulmonata)			
Ferrissia sp.			
Density	0.8	0.5	*
Percent	63	36	1
Helisoma sp.			
Density	4.2	9.5	0.2
Percent	31	68	1
Physa sp.			
Density	0.2	0.5	*
Percent	33	66	1

Table 27. Horizontal distribution of dominant Ephemeroptera in 1973-74. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each station. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms per sampler or less than 1 %.

Taxa	Lagoon Stations			Reservoir Stations				
	A	B	C	D	E	F	G	H
(Caenidae)								
<u>Caenis</u> <u>amica</u>								
Density	2.1	1.4	1.0	2.0	0.6	1.7	1.5	0.5
Percent	20	13	10	17	5	16	14	4

Table 28. Horizontal distribution of dominant Ephemeroptera in 1974-75. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each station. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms per sampler or less than 1 %.

Taxa	Lagoon Stations			Reservoir Stations				
	A	B	C	D	E	F	G	H
(Ephemeridae)								
<u>Hexagenia munda</u>								
Density	*	0.5	0.3	0.3	0.2			
Percent	1	41	22	22	14			
(Caenidae)								
<u>Caenis amica</u>								
Density	0.2	0.8	0.8	*		*		*
Percent	9	42	44	3		1		3

Table 29. Vertical distribution of dominant Ephemeroptera in 1973-74. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each depth. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms or less than 1 %.

Taxa	2 Meters	4 Meters	7 Meters
(Caenidae)			
<u>Caenis</u> <u>amica</u>			
Density	3.1	0.8	0.2
Percent	77	19	4

Table 30. Vertical distribution of dominant Ephemeroptera in 1974-75. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each depth. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms or less than 1 %.

Taxa	2 Meters	4 Meters	7 Meters
(Ephemeridae)			
<u>Hexagenia munda</u>			
Density	0.4	0.1	
Percent	88	12	
(Caenidae)			
<u>Caenis amica</u>			
Density	0.5	0.1	*
Percent	79	16	4

Table 31. Horizontal distribution of dominant Odonata in 1973-74. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each station. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms per sampler or less than 1 %.

Taxa	Lagoon Stations			Reservoir Stations				
	A	B	C	D	E	F	G	H
(Libellulidae)								
<u>Epicordulia</u> <u>princeps</u>								
Density	0.1	0.2	0.2	0.1	0.1	0.2	0.1	0.1
Percent	6	19	21	8	10	18	10	8
<u>Perithemis</u> <u>tenera</u>								
Density	0.6	0.3	0.4	0.1	*	0.1	0.5	1.0
Percent	21	10	13	2	1	5	16	32

Table 31. (continued).

Taxa	Lagoon Stations			Reservoir Stations				
	A	B	C	D	E	F	G	H
(Coenagrionidae)								
<u>Argia</u> spp.								
Density	*	0.7	1.0	0.2	0.1	0.1	0.1	0.2
Percent	2	29	44	6	5	4	3	7
<u>Enallagma</u> spp.								
Density	0.1	0.5	0.1	0.3	0.1	0.2	0.3	0.6
Percent	4	22	5	11	5	10	14	28

Table 32. Horizontal distribution of dominant Odonata in 1974-75. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each station. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms per sampler or less than 1 %.

Taxa	Lagoon Stations			Reservoir Stations				
	A	B	C	D	E	F	G	H
(Libellulidae)								
<u>Epicordulia</u> <u>princeps</u>								
Density	0.1	*	0.3	0.3	*	0.1	0.3	0.3
Percent	5	2	23	22	1	6	21	21
<u>Perithemis</u> <u>tenera</u>								
Density	0.3	0.1	0.9	*		*	*	0.2
Percent	22	8	57	2		1	1	10

Table 32. (continued).

Taxa	Lagoon Stations			Reservoir Stations				
	A	B	C	D	E	F	G	H
(Coenagrionidae)								
Argia spp.								
Density	0.1	2.4	0.7	0.3	0.3	0.1	0.3	0.6
Percent	2	49	15	7	5	3	6	13
Enallagma spp.								
Density	0.2	0.4	0.2	0.5	0.1	0.1	0.4	0.3
Percent	8	19	9	24	5	4	18	13

Table 33. Vertical distribution of dominant Odonata in 1973-74. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each depth. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms or less than 1 %.

Taxa	2 Meters	4 Meters	7 Meters
(Libellulidae)			
Epicordulia princeps			
Density	0.2	0.1	*
Percent	69	26	5
Perithemis tenera			
Density	0.4	0.7	*
Percent	33	66	1
(Coenagrionidae)			
Argia spp.			
Density	0.7	0.2	*
Percent	80	18	2
Enallagma spp.			
Density	0.7	0.1	*
Percent	83	16	1

Table 34 . Vertical distribution of dominant Odonata in 1974-75. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each depth. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms or less than 1 %.

Taxa	2 Meters	4 Meters	7 Meters
(Libellulidae)			
Epicordulia princeps			
Density	0.3	0.2	*
Percent	62	38	*
Perithemis tenera			
Density	0.2	0.4	*
Percent	31	66	3
(Coenagrionidae)			
Argia spp.			
Density	1.4	0.4	*
Percent	79	20	1
Enallagma spp.			
Density	0.6	0.2	*
Percent	77	21	2

Table 35. Horizontal distribution of dominant Trichoptera in 1973-74. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each station. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms per sampler or less than 1 %.

Taxa	Lagoon Stations			Reservoir Stations				
	A	B	C	D	E	F	G	H
(Hydroptilidae)								
<u>Orthotrichia</u> sp.								
Density	0.2	0.9	0.7	0.8	1.1	1.5	1.2	1.5
Percent	3	11	10	9	14	19	15	19
(Polycentropodidae)								
<u>Cyrnellus</u> <u>fraternus</u>								
Density	0.6	0.5	1.0	1.0	0.3	1.2	0.9	0.4
Percent	10	8	18	16	6	20	16	6

Table 35. (continued).

Taxa	Lagoon Stations			Reservoir Stations				
	A	B	C	D	E	F	G	H
Nyctiophylax affinis								
Density		0.6	1.0					
Percent		37	63					
Polycentropus sp.								
Density	0.3	0.5	0.9	0.5	0.2	0.5	0.6	0.8
Percent	7	12	21	10	4	13	14	20
(Leptoceridae)								
Oecetis spp.								
Density	0.6	0.8	0.4	1.4	1.4	1.0	1.0	1.2
Percent	8	10	5	17	18	13	13	16

Table 36. Horizontal distribution of dominant Trichoptera in 1974-75. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each station. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms per sampler or less than 1 %.

Taxa	Lagoon Stations			Reservoir Stations				
	A	B	C	D	E	F	G	H
(Hydroptilidae)								
<u>Orthotrichia</u> sp.								
Density	*	*	*		*	*	*	
Percent	13	13	13		25	25	13	
(Polycentropodidae)								
<u>Cyrnellus</u> <u>fraternus</u>								
Density	0.7	7.5	3.7	0.7	3.6	7.2	3.9	2.8
Percent	2	24	12	2	12	24	13	10

Table 36. (continued).

Taxa	Lagoon Stations			Reservoir Stations				
	A	B	C	D	E	F	G	H
<u>Nyctiophylax</u> <u>affinis</u>								
Density	*	0.1	0.6		0.5	*		*
Percent	3	8	43		39	3		3
<u>Polycentropus</u> sp.								
Density	9.5	2.0	10.8	7.4	10.1	7.2	5.5	6.2
Percent	17	3	18	13	17	12	9	11
(Leptoceridae)								
<u>Oecetis</u> spp.								
Density	0.3	0.3	*	0.3	0.1	0.4	0.4	0.4
Percent	16	14	2	13	3	16	18	18

Table 37 . Vertical distribution of dominant Trichoptera in 1973-74. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occuring at each depth. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms or less than 1 %.

Taxa	2 Meters	4 Meters	7 Meters
(Hydroptilidae)			
Orthotrichia sp.			
Density	2.7	0.2	*
Percent	91	8	1
(Polycentropodidae)			
Cyrnellus fraternus			
Density	2.5	0.4	*
Percent	85	15	1
Polycentropus sp.			
Density	1.4	0.2	*
Percent	89	10	1
(Leptoceridae)			
Oecetis spp.			
Density	1.7	1.1	0.1
Percent	60	38	2

Table 38 . Vertical distribution of dominant Trichoptera in 1974-75. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each depth. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms or less than 1 %.

Taxa	2 Meters	4 Meters	7 Meters
(Hydroptilidae)			
<u>Orthotrichia</u> sp.			
Density	*	*	
Percent	88	12	
(Polycentropodidae)			
<u>Cyrnellus</u> <u>fraternus</u>			
Density	6.1	5.3	0.2
Percent	53	45	2
<u>Polycentropus</u> sp.			
Density	18.5	2.8	0.4
Percent	85	13	2
(Leptoceridae)			
<u>Oecetis</u> spp.			
Density	0.5	0.3	*
Percent	64	32	5

Table 39 . Temporal distribution of dominant macrobenthos in 1973-74. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each month. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms per sampler or less than 1%.

Taxa	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Turbellaria											
Density	4.9	7.3	4.2	4.1	2.4	3.5	2.6	0.7	0.6	0.5	2.6
Percent	15	22	12	12	7	11	8	2	2	1	8
Oligochaeta											
Density	92.1	131.1	82.5	82.0	52.5	42.6	31.5	16.5	3.9	9.6	12.2
Percent	17	24	15	14	9	8	6	3	1	2	2
Gastropoda											
Density	7.2	7.7	4.5	5.5	4.9	6.1	2.9	2.1	4.4	3.5	1.4
Percent	15	15	9	11	9	12	6	4	8	7	3

Table 39 . (continued).

Taxa	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Amphipoda											
Density	11.6	19.6	8.0	15.6	11.3	10.9	8.0	8.7	22.1	8.1	17.3
Percent	8	14	6	11	8	8	6	6	15	6	13
Isopoda											
Density	0.1	0.2	0.4	0.7	0.3	0.5	0.6	0.6	1.8	0.2	1.0
Percent	2	3	6	10	5	9	9	9	27	4	16
Ephemeroptera											
Density	1.8	1.7	1.0	1.0	1.5	2.3	3.5	0.8	0.3	0.4	*
Percent	13	12	7	7	10	16	24	6	2	3	*
Odonata											
Density	1.0	1.2	1.3	1.3	1.3	1.4	1.4	0.8	0.3	0.4	1.5
Percent	9	10	10	11	11	12	12	7	2	3	12
Trichoptera											
Density	0.3	0.5	0.4	0.4	1.3	3.0	8.6	3.2	3.4	5.5	12.0
Percent	1	1	1	1	3	8	23	8	8	14	31

Table 39 . (continued).

Taxa	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Chironomidae											
Density	69.8	109.8	102.1	109.6	107.4	107.2	104.6	66.0	47.2	84.7	89.5
Percent	7	11	10	10	10	11	11	7	5	9	9
Chaoborus											
Density	3.3	1.3	0.6	0.4	0.3	0.6	1.2	2.1	8.5	23.9	22.8
Percent	5	2	1	1	1	1	2	3	12	37	35
Total Organisms											
Density	192.3	280.6	204.8	220.9	183.4	178.3	165.2	102.1	92.3	137.8	160.8
Percent	10	14	11	11	9	9	9	5	5	7	9

Table 40 . Temporal distribution of dominant macrobenthos in 1974-75. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each month. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms per sampler or less than 1%.

Taxa	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Turbellaria											
Density	6.0	5.1	7.0	7.9	9.2	9.3	8.9	4.8	5.0	0.8	0.5
Percent	10	8	11	13	15	14	13	7	7	1	1
Oligochaeta											
Density	57.2	34.8	36.5	35.8	38.2	24.6	16.5	15.0	35.3	5.1	44.4
Percent	17	10	11	11	11	7	5	4	10	1	13
Gastropoda											
Density	2.0	4.9	4.5	4.4	4.6	9.1	5.9	4.4	16.5	0.8	1.8
Percent	4	9	8	8	8	15	10	7	27	1	3

Table 40 . (continued).

Taxa	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Amphipoda											
Density	15.2	11.9	10.5	10.0	11.4	19.9	14.2	5.4	5.8	0.5	0.1
Percent	15	12	10	10	11	19	13	5	5	*	*
Isopoda											
Density	0.1	0.1	0.1	0.3	4.0	0.4	0.7	1.9	2.0	1.1	0.8
Percent	1	1	1	2	36	4	6	16	17	9	7
Ephemeroptera											
Density	0.3	0.3	0.2	*	0.2	0.5	0.3	0.3	0.3	0.2	1.4
Percent	8	7	6	1	5	13	7	7	7	4	36
Odonata											
Density	1.6	1.4	1.6	1.4	1.5	1.8	1.7	0.7	0.6	0.3	1.5
Percent	19	10	12	10	11	12	12	5	4	2	11
Trichoptera											
Density	6.1	3.9	5.0	4.1	3.8	4.3	6.1	6.5	17.1	26.0	48.4
Percent	5	3	4	3	3	3	5	5	13	19	38

Table 40 . (continued).

Taxa	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Chironomidae											
Density	133.0	161.3	162.7	147.2	149.2	148.9	126.7	71.4	124.0	57.3	121.4
Percent	10	12	12	11	11	10	9	5	8	4	9
Chaoborus											
Density	3.9	0.2	0.2	0.2	0.3	0.2	0.3	0.2	9.0	18.8	43.9
Percent	5	*	*	*	*	*	*	*	11	23	58
Total Organisms											
Density	226.2	224.5	229.8	201.2	222.9	219.9	182.1	111.6	219.2	113.0	267.3
Percent	10	10	11	9	10	10	8	5	10	5	12

Table 41. Temporal distribution of dominant Gastropoda in 1973-74. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each month. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms per sampler or less than 1%.

Taxa	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
(Pulmonata)											
Ferrissia sp.											
Density	3.5	2.8	1.0	2.9	1.2	1.7	0.5	0.4	0.1	*	0.2
Percent	25	20	7	20	8	12	4	3	1	*	1
Helisoma sp.											
Density	3.4	4.8	2.9	2.5	2.4	3.9	2.2	1.6	4.2	2.9	0.9
Percent	11	15	9	8	8	12	7	5	13	9	3
Physa sp.											
Density	0.3	0.1	0.6	0.1	1.3	0.5	0.2	0.1	0.1	0.5	0.3
Percent	8	3	16	2	31	13	4	3	3	13	6

Table 42. Temporal distribution of dominant Gastropoda in 1974-75. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each month. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms per sampler or less than 1%.

Taxa	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
(Pulmonata)											
Ferrissia sp.											
Density	0.3	0.8	0.4	0.6	0.4	1.8	0.2	0.1	0.3		
Percent	6	16	9	13	8	38	4	1	6		
Helisoma sp.											
Density	1.7	4.0	4.0	3.5	4.1	6.9	5.3	4.1	14.7	0.7	1.7
Percent	3	8	8	7	8	14	11	8	28	1	3
Physa sp.											
Density	*	0.1	0.1	0.3	0.2	*	*	0.2	1.5	0.1	*
Percent	2	3	3	11	7	1	2	8	58	3	2

Table 43. Temporal distribution of dominant Ephemeroptera in 1973-74. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each month. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms per sampler or less than 1%.

Taxa	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
(Caenidae)											
Caenis amica											
Density	1.8	1.7	1.0	1.0	1.5	2.3	3.5	0.8	0.3	0.4	*
Percent	13	12	7	7	10	16	24	6	2	3	*

Table 44. Temporal distribution of dominant Ephemeroptera in 1974-75. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each month. These values were calculated only from web samplers. An asterisk (*) denotes less then 0.1 organisms per sampler or less than 1%.

Taxa	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
(Ephemeridae)											
Hexagenia munda											
Density			*	*						*	1.4
Percent			1	1						8	89
(Caenidae)											
Caenis amica											
Density	0.3	0.3	0.2	*	0.2	0.5	0.3	0.3	0.3	*	0.1
Percent	14	13	10	1	9	24	13	13	13	2	3

Table 45. Temporal distribution of dominant Odonata in 1973-74. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each month. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms per sampler or less than 1 %.

Taxa	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
(Libellulidae)											
<u>Epicordulia</u> <u>princeps</u>											
Density	0.1	0.1	0.2	0.1	0.1	0.2	0.3	0.1	*	*	0.1
Percent	2	3	7	4	2	8	9	4	1	1	4
<u>Perithemis</u> <u>tenera</u>											
Density	0.5	0.8	0.7	0.5	0.5	0.4	0.3	0.2		0.1	0.3
Percent	13	18	17	11	10	10	7	4		3	6
(Coenagrionidae)											
<u>Argia</u> spp.											
Density	0.3	0.1	0.1	0.2	0.2	0.3	0.3	0.4	0.2	0.1	1.0
Percent	8	5	4	7	7	7	9	12	6	5	31

Table 45. (continued)

Taxa	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Enallagma spp.											
Density	0.2	0.2	0.2	0.5	0.5	0.5	0.6	0.1	0.1	0.1	*
Percent	6	7	7	17	17	19	20	3	2	2	1

Table 46. Temporal distribution of dominant Odonata in 1974-75. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each month. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms per sampler or less than 1 %.

Taxa	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
(Libellulidae)											
<u>Epicordulia</u> <u>princeps</u>											
Density	0.2	0.3	0.3	0.1	0.4	0.2	0.1	*	0.2	0.1	*
Percent	9	18	15	5	21	8	7	2	9	5	1
<u>Perithemis</u> <u>tenera</u>											
Density	0.5	0.2	0.3	0.5	0.1	0.2	0.2	*	0.1	*	0.1
Percent	23	10	13	21	6	7	7	1	4	2	7
(Coenagrionidae)											
<u>Argia</u> spp.											
Density	0.5	0.5	0.6	0.5	0.5	1.0	0.8	0.4	0.1	*	1.3
Percent	8	8	10	8	8	16	12	7	2	1	19

Table 46. (continued).

Taxa	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Enallagma spp.											
Density	0.4	0.2	0.5	0.3	0.4	0.3	0.5	0.2	0.1		*
Percent	14	7	16	10	13	12	18	6	4		1

Table 47. Temporal distribution of dominant Trichoptera in 1973-74. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each month. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms per sampler or less than 1 %.

Taxa	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
(Hydroptilidae)											
<u>Orthotrichia</u> sp.											
Density	0.1	0.2	0.1	0.2	0.7	1.9	5.9	1.4	0.2	0.1	
Percent	1	2	1	2	7	18	55	13	2	1	
(Polycentropodidae)											
<u>Cyrnellus</u> <u>fraternus</u>											
Density	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.6	2.1	7.1
Percent	1	1	1	1	1	1	1	1	5	20	68
<u>Polycentropus</u> sp.											
Density									0.3	1.0	4.5
Percent									5	17	78

Table 47. (continued).

Taxa	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
(Leptoceridae)											
Oecetis spp.											
Density	0.1	0.1	0.1	0.1	0.3	0.9	2.6	1.4	2.2	2.4	0.3
Percent	1	1	1	1	2	9	25	13	20	23	3

Table 48. Temporal distribution of dominant Trichoptera in 1974-75. Density is expressed as number of organisms per sampler. Percent is the percentage of the total number of that particular taxon occurring at each month. These values were calculated only from web samplers. An asterisk (*) denotes less than 0.1 organisms per sampler or less than 1 %.

Taxa	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
(Hydroptilidae)											
<u>Orthotrichia</u> sp.											
Density							*	*			
Percent							88	12			
(Polycentropodidae)											
<u>Cyrnellus</u> <u>fraternus</u>											
Density	2.1	1.5	1.3	1.2	1.2	1.4	1.4	2.7	4.9	9.7	15.9
Percent	5	4	3	3	3	3	3	6	11	21	38
<u>Polycentropus</u> sp.											
Density	3.6	2.3	3.5	2.6	2.0	2.4	3.5	2.7	11.6	15.6	32.1
Percent	5	3	4	3	3	3	4	3	14	18	40

Table 48. (continued).

Taxa	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
(Leptoceridae)											
Oecetis spp.											
Density	0.1	0.1	0.1	*	0.4	0.1	0.9	0.6	0.4	0.1	0.2
Percent	5	4	4	1	14	3	28	18	11	4	6

Table 49. Summary of horizontal distribution. The organisms listed at each station are those for which the density or percentage occurrence at that station, in 1973-74 or 1974-75, was considerably higher than expected if homogenously distributed.

Station A	Station B	Station C	Station D
Turbellaria	(Gastropoda)	(Ephemeroptera)	(Ephemeroptera)
(Gastropoda)	*Ferrissia* sp.	*Hexagenia munda*	*Hexagenia munda*
Physa sp.	(Ephemeroptera)	*Caenis amica*	(Odonata)
(Odonata)	*Hexagenia munda*	(Odonata)	*Epicordulia princeps*
Perithemis tenera	*Caenis amica*	*Epicordulia princeps*	*Enallagma* spp.
(Trichoptera)	(Odonata)	*Perithemis tenera*	
Polycentropus sp.	*Argia* spp.	*Argia* spp.	
	(Trichoptera)	(Trichoptera)	
	Cyrnellus fraternus	*Polycentropus* sp.	
	(Diptera)		
	Chaoborus sp.		

Table 49. (continued).

Station E	Station F	Station G	Station H
Turbellaria	Amphipoda	Oligochaeta	(Odonata)
(Isopoda)	(Trichoptera)	(Gastropoda)	*Epicordulia princeps*
Asellus sp.	*Cyrnellus fraternus*	*Ferrissia* sp.	
(Odonata)	*Polycentropus* sp.	*Helisoma* sp.	
Epicordulia princeps		(Odonata)	
(Trichoptera)		*Epicordulia princeps*	
Polycentropus sp.		(Diptera)	
		Chironomidae	
		Total Organisms	

Table 50. Summary of vertical distribution. The organisms listed at each depth are those for which the density or percentage occurrence at that depth, in 1973-74 or 1974-75, was considerably higher than expected if homogenously distributed.

2 Meters	4 Meters	7 Meters
Turbellaria	Oligochaeta	(Chironomidae)
(Gastropoda)	(Gastropoda)	*Chironomus* sp.
Ferrissia sp.	*Helisoma* sp.	(Chaoboridae)
Physa sp.	(Isopoda)	*Chaoborus* sp.
(Amphipoda)	*Asellus* sp.	
Hyalella azteca	(Odonata)	
(Ephemeroptera)	*Perithemis tenera*	
Caenis amica	(Trichoptera)	
(Odonata)	*Cyrnellus fraternus*	
Epicordulia princeps	(Chironomidae)	
Argia spp.	*Glyptotendipes* sp.	
Enallagma spp.		
(Trichoptera)		
Polycentropus sp.		

Table 51. Summary of temporal distribution. The organisms listed for each time period are those for which the density or percentage occurrence during that time period, in 1973-74 or 1974-75, was considerably higher than expected if homogenously distributed.

Fall, Winter, Spring	Summer
Oligochaeta	Gastropoda
Turbellaria	Isopoda
Amphipoda	Trichoptera
Ephemroptera	<u>Chaoborus</u>
Odonata	
Chironomidae	

Table 52. Taxonomic list of all macrobenthic organisms collected in Lake Anna from October, 1972 to September, 1975.

- PHYLUM: Coelenterata
- PHYLUM: Platyhelminthes
  - CLASS: Turbellaria
- PHYLUM: Annelida
  - CLASS: Hirudinea
  - CLASS: Oligochaeta
    - ORDER: Plesiopora
      - Naididae
- PHYLUM: Mollusca
  - CLASS: Gastropoda
    - ORDER: Pulmonata
      - Physidae
        - *Physa* sp.
      - Lymnaeidae
        - *Lymnaea* sp.
      - Planorbidae
        - *Helisoma* sp.
      - Ancylidae
        - *Ferrissia* sp.
  - CLASS: Pelecypoda
    - ORDER: Heterodonta
      - Sphaeriidae

Table 52. (continued).

- PHYLUM: Arthropoda
  - CLASS: Arachnida
    - ORDER: Acarina
      - SUBORDER: Trombidiformes (Hydracarina)
  - CLASS: Crustacea
    - ORDER: Isopoda
      - Asellidae
        - *Asellus* sp.
        - *Lirceus* sp.
    - ORDER: Amphipoda
      - Talitridae
        - *Hyalella azteca* (Saussure)
      - Gammaridae
        - *Crangonyx* sp.
    - ORDER: Decapoda
      - Palaemonidae
        - *Palaemonetes* sp.
      - Astacidae
        - *Orconectes limosus* (Rafinesque)
  - CLASS: Insecta
    - ORDER: Ephemeroptera
      - Ephemeridae
        - *Hexagenia munda* Eaton

Table 52. (continued).

Caenidae
    Caenis amica Hagen
Ephemerellidae
    Ephemerella sp.
Leptophlebiidae
    Leptophlebia sp.
Baetidae
    Neocloeon sp.
Siphlonuridae
    Isonychia sp.
Heptageniidae
    Stenonema sp.

ORDER: Odonata
  SUBORDER: Anisoptera
    Gomphidae
        Dromogomphus spinosus Selys
        Hagenius brevistylus Selys
    Aeschnidae
        Boyeria vinosa Say
    Libellulidae
        Epicordulia princeps Hagen
        Tetragoneuria cynosura Say
        Erythemis simplicicollis Burmeister

Table 52. (continued).

Pachydiplax longipennis Burmeister
Perithemis tenera Say
Plathemis sp.
Macromiidae
Macromia sp.
SUBORDER: Zygoptera
Coenagrionidae
Argia apicalis (Say)
Argia translata Hagen
Enallagma basidens Calvert
Enallagma sp.
Ischnura sp.
ORDER: Plecoptera
Nemouridae
Brachyptera sp.
Leuctra sp.
Nemoura sp.
Perlidae
Acroneuria sp.
ORDER: Megaloptera
Sialidae
Sialis sp.

Table 52. (continued).

ORDER: Coleoptera

  Gyrinidae

    Dineutus sp.

  Dytiscidae

    Agabus sp.

    Bidessus sp.

    Hydroporus/Hygrotus sp.

    Laccophilus sp.

    Oreodytes/Deronectes sp.

  Hydraenidae

  Hydrophilidae

    Berosus sp.

    Helochares sp.

  Helodidae

    Scirtes sp.

  Psephenidae

    Psephenus herricki (DeKay)

  Dryopidae

    Helichus sp.

  Elmidae

  Staphylinidae

ORDER: Trichoptera

  Philopotamidae

Table 52. (continued).

- *Chimarra feria* Ross
- *Chimarra obscura* (Walker)
- *Chimarra socia* Hagen

Polycentropodidae

- *Cyrnellus fraternus* (Banks)
- *Nyctiophylax affinis* (Banks)
- *Polycentropus* sp.
- *Phylocentropus placidus* (Banks)

Hydropsychidae

- *Cheumatopsyche* sp.
- *Hydropsyche* sp.
- *Macronemum* sp.

Hydroptilidae

- *Hydroptila* sp.
- *Orthotrichia* sp.
- *Oxyethira* sp.

Phryganeidae

- *Agrypnia vestita* (Walker)
- *Phryganea sayi* Milne
- *Ptilostomis ocellifera* (Walker)

Limnephilidae

- *Drusinus* sp.

Leptoceridae

- *Leptocella* sp.

Table 52. (continued).

- *Oecetis cinerascens* (Hagen)
- *Oecetis inconspicua* (Walker)

Brachycentridae
- *Brachycentrus* sp.

ORDER: Diptera
- SUBORDER: Nematocera
  - Blepharoceridae
    - *Blepharocera* sp.
  - Tipulidae
    - *Limnophila* sp.
    - *Limonia* sp.
    - *Tipula* sp.
  - Chaoboridae
    - *Chaoborus* sp.
  - Sciaridae
    - *Sciara* sp.
  - Psychodidae
  - Ceratopogonidae
  - Chironomidae
    - Diamesinae
      - *Diamesa* sp.
    - Tanypodinae
      - *Ablabesmyia* sp.

Table 52. (continued).

- *Labrundinia* sp.
- *Procladius* sp.
- Chironominae
  - Tanytarsini
    - *Paratanytarsus* sp.
    - *Tanytarsus* sp.
  - Chironomini
    - *Chironomus* sp.
    - *Cryptochironomus* sp.
    - *Dicrotendipes* sp.
    - *Einfeldia* sp.
    - *Endochironomus* sp.
    - *Kiefferulus* sp.
    - *Glyptotendipes* sp.
    - *Microtendipes* sp.
    - *Parachironomus* sp.
    - *Polypedilum* sp.
    - *Stenochironomus* sp.
    - *Tribelos* sp.
- Orthocladiinae
  - *Cricotopus* sp.
  - *Eukiefferiella* sp.
  - *Heterotrissocladius* sp.

Table 52. (continued).

Orthocladius sp.

Psectrocladius sp.

Smittia sp.

SUBORDER: Brachycera

Tabanidae

Rhagionidae

Atherix sp.

Dolichopodidae

APPENDIX B

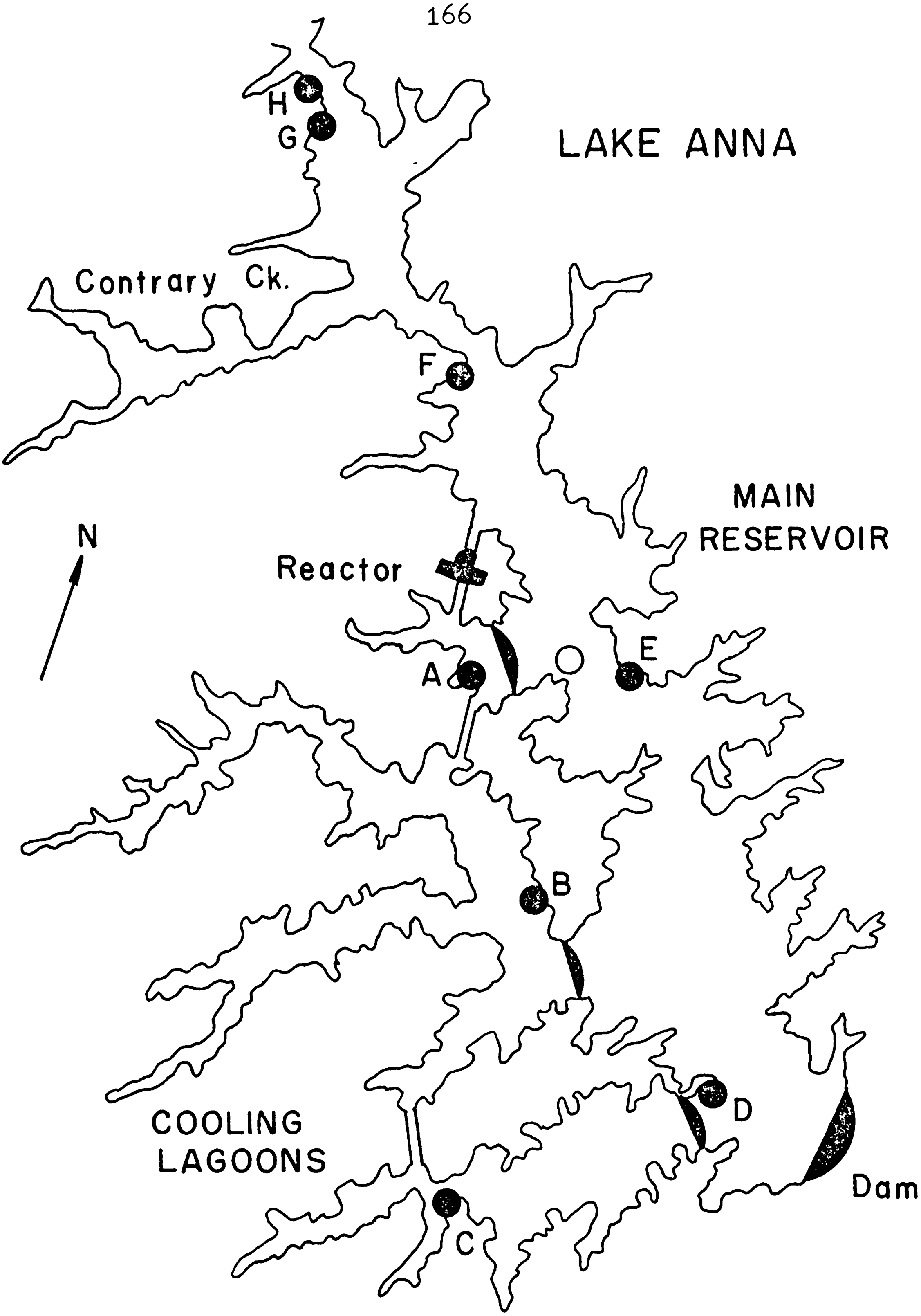

Fig. 1. Map of Lake Anna illustrating macrobenthic sampling stations. The open circle denotes the site of the 1972-73 feasibility study.

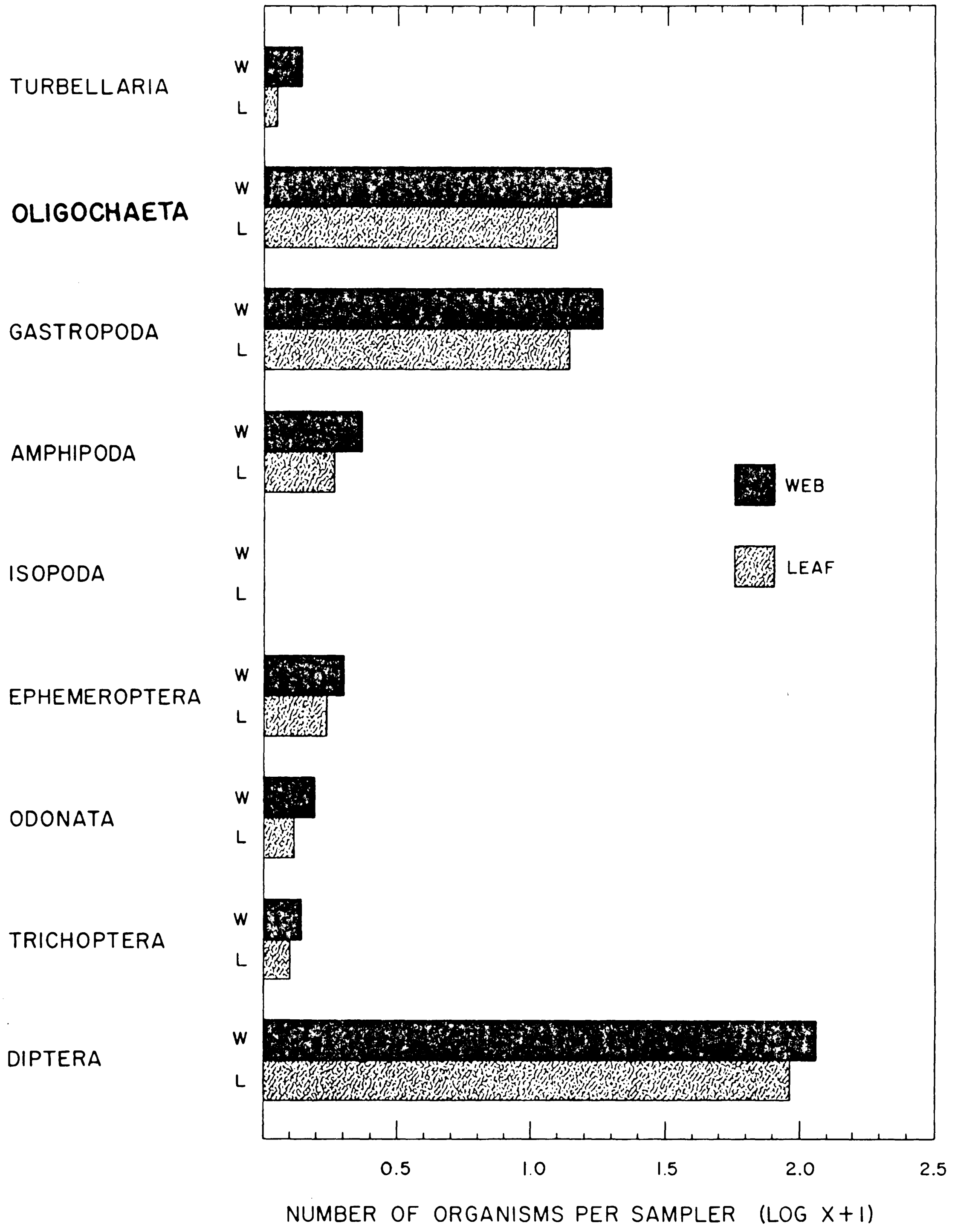

Fig. 2. Composition of macrobenthic community at Station A in 1973-74. These values are the mean of all depths.

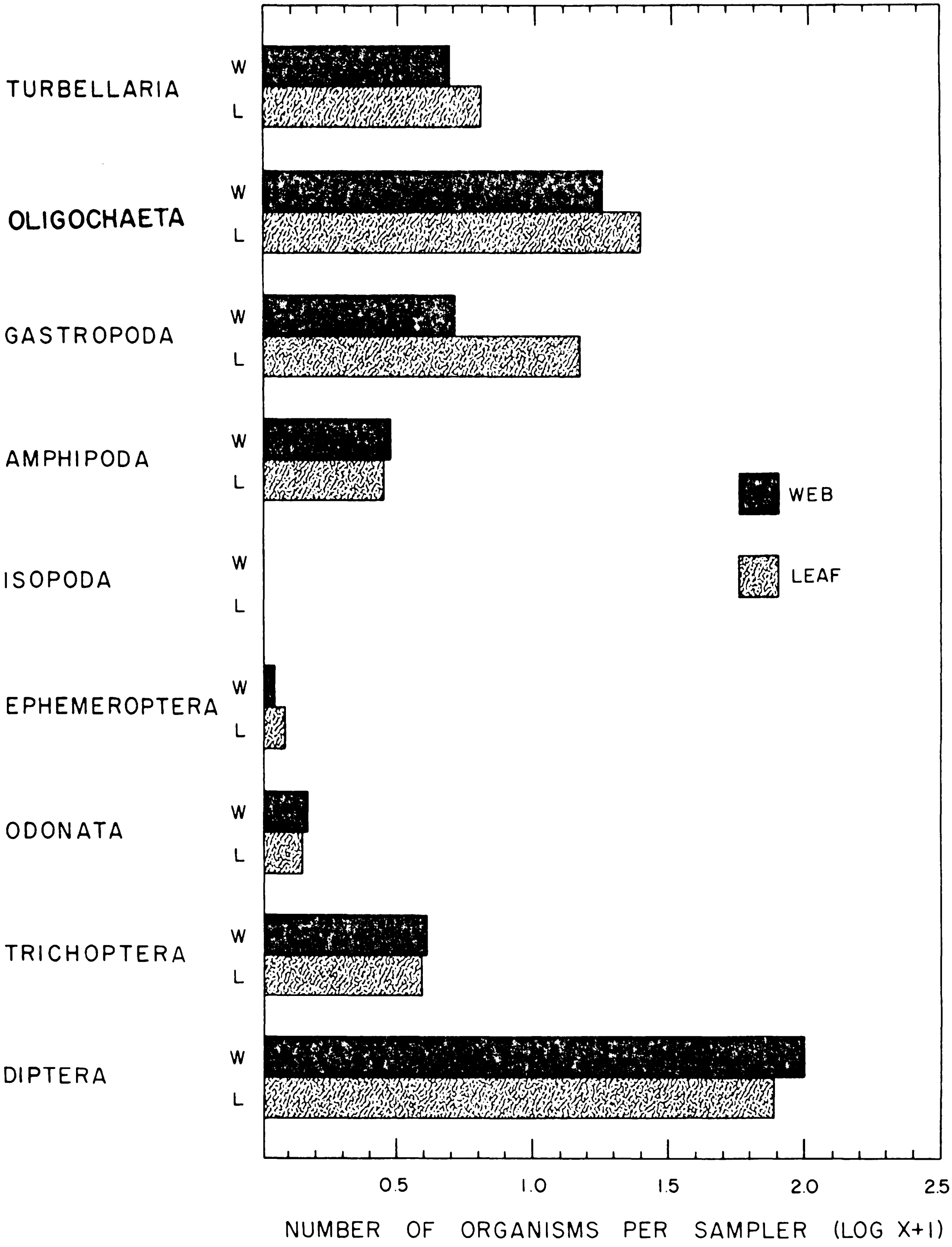

Fig. 3. Composition of macrobenthic community at Station A in 1974-75. These values are the mean of all depths.

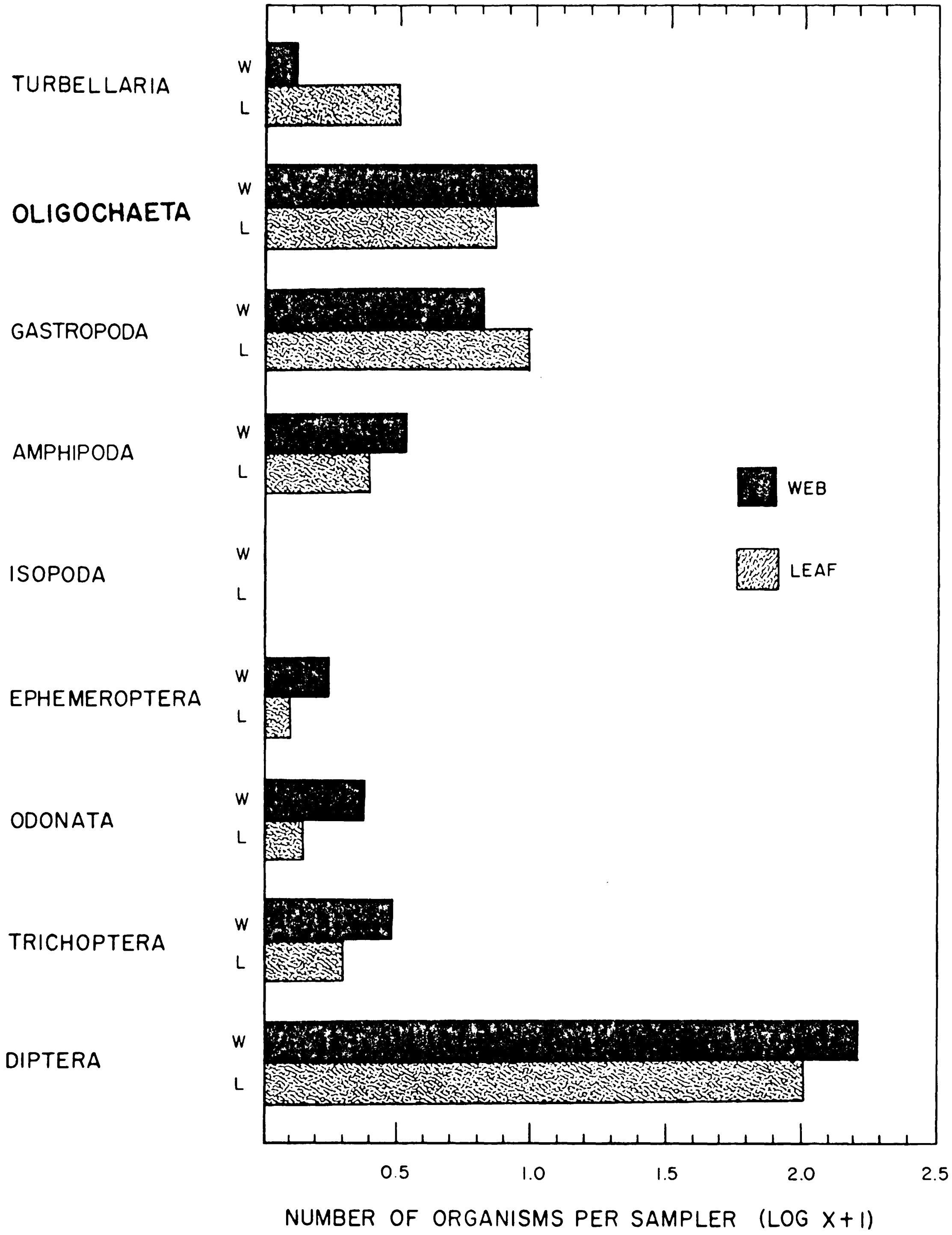

Fig. 4. Composition of macrobenthic community at Station B in 1973-74. These values are the mean of all depths.

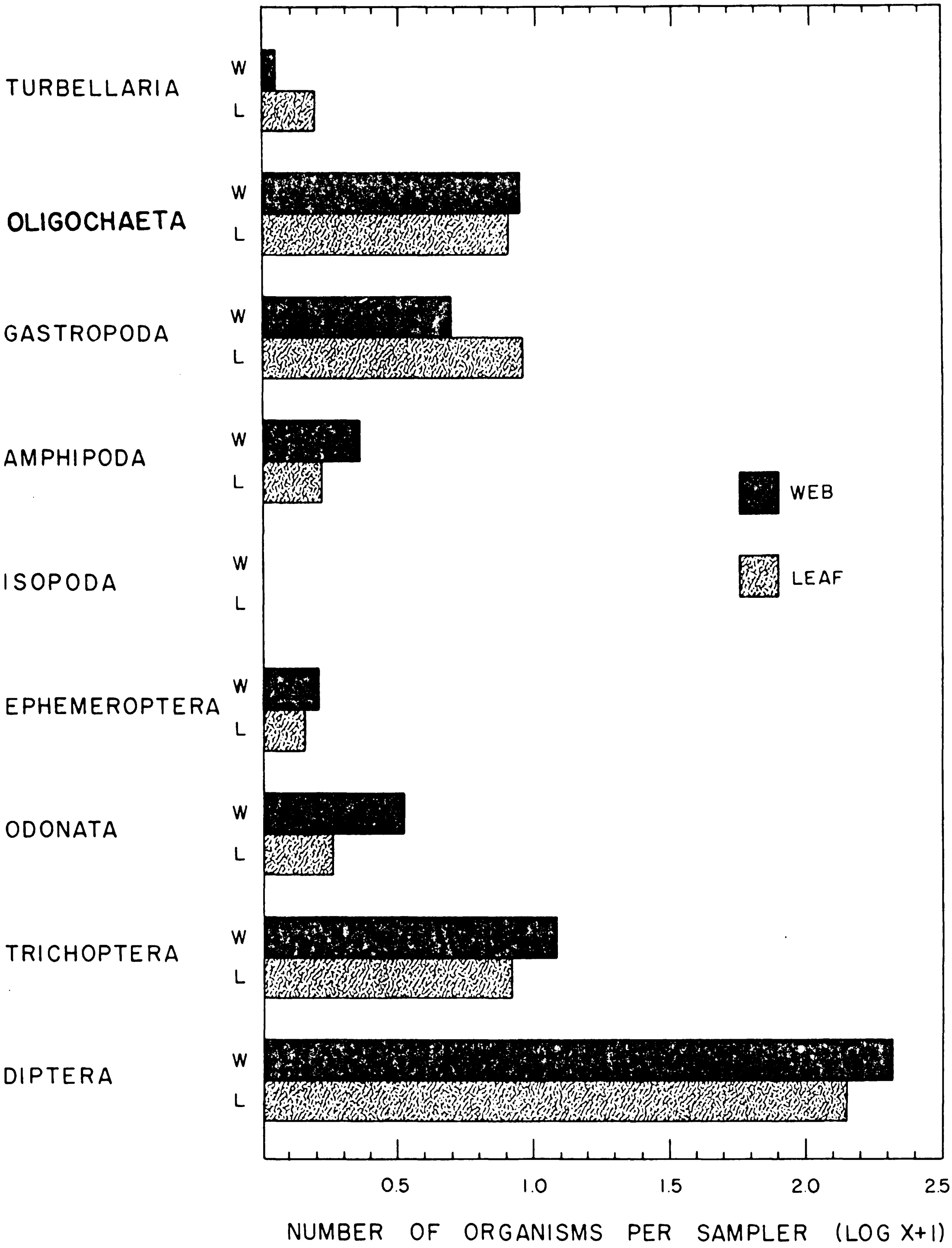

Fig. 5. Composition of macrobenthic community at Station B in 1974-75. These values are the mean of all depths.

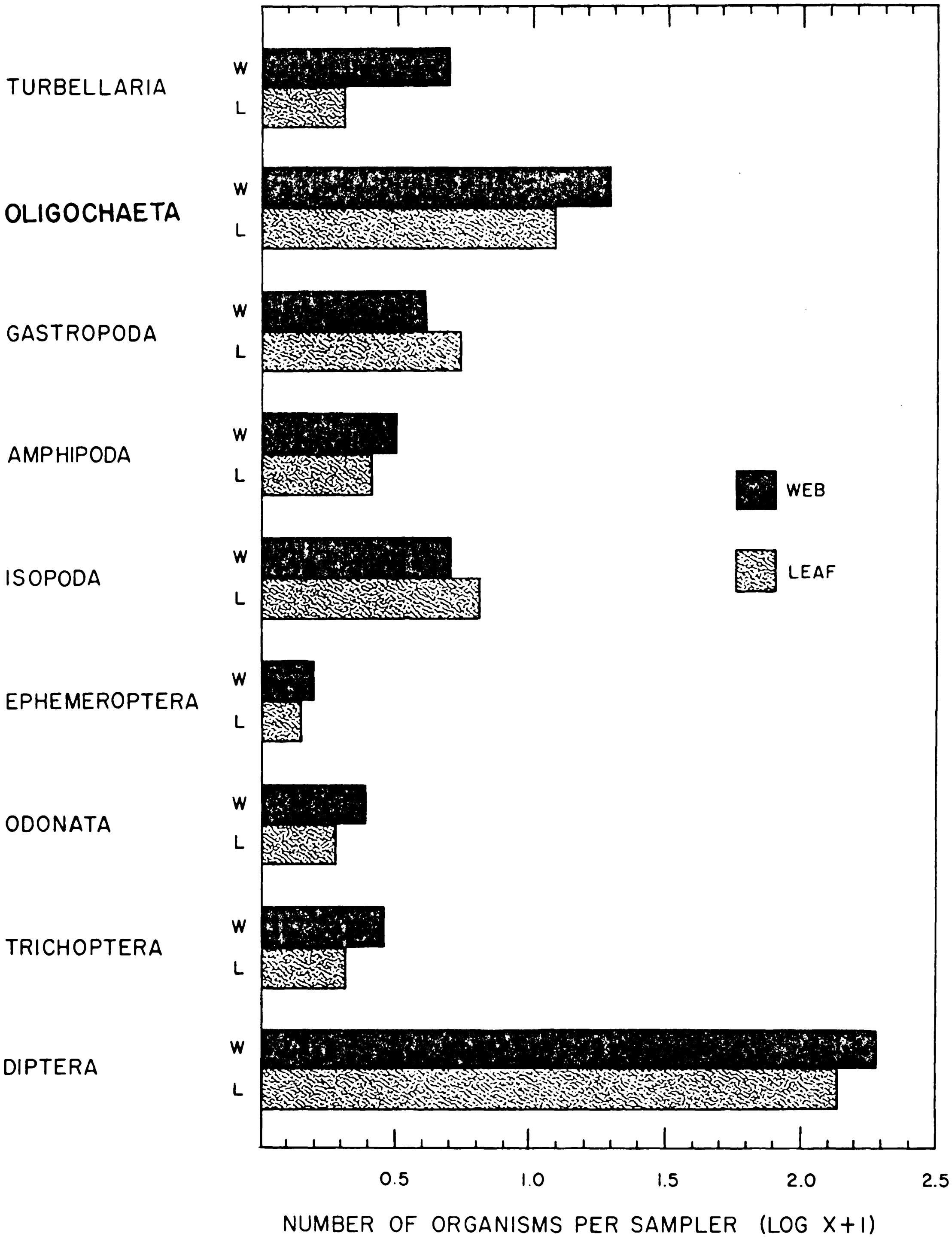

Fig. 6. Composition of macrobenthic community at Station C in 1973-74. These values are the mean of all depths.

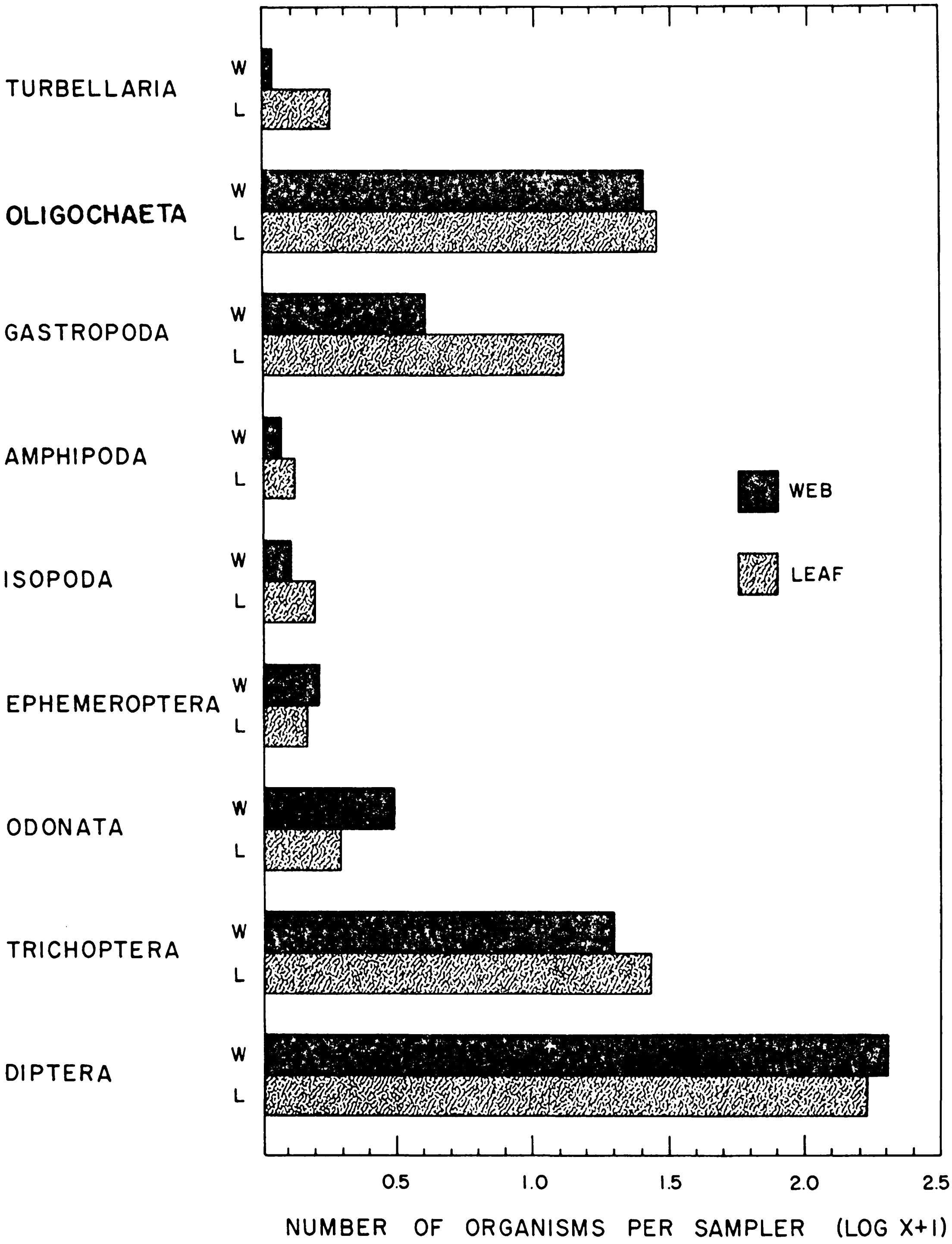

Fig. 7. Composition of macrobenthic community at Station C in 1974-75. These values are the mean of all depths.

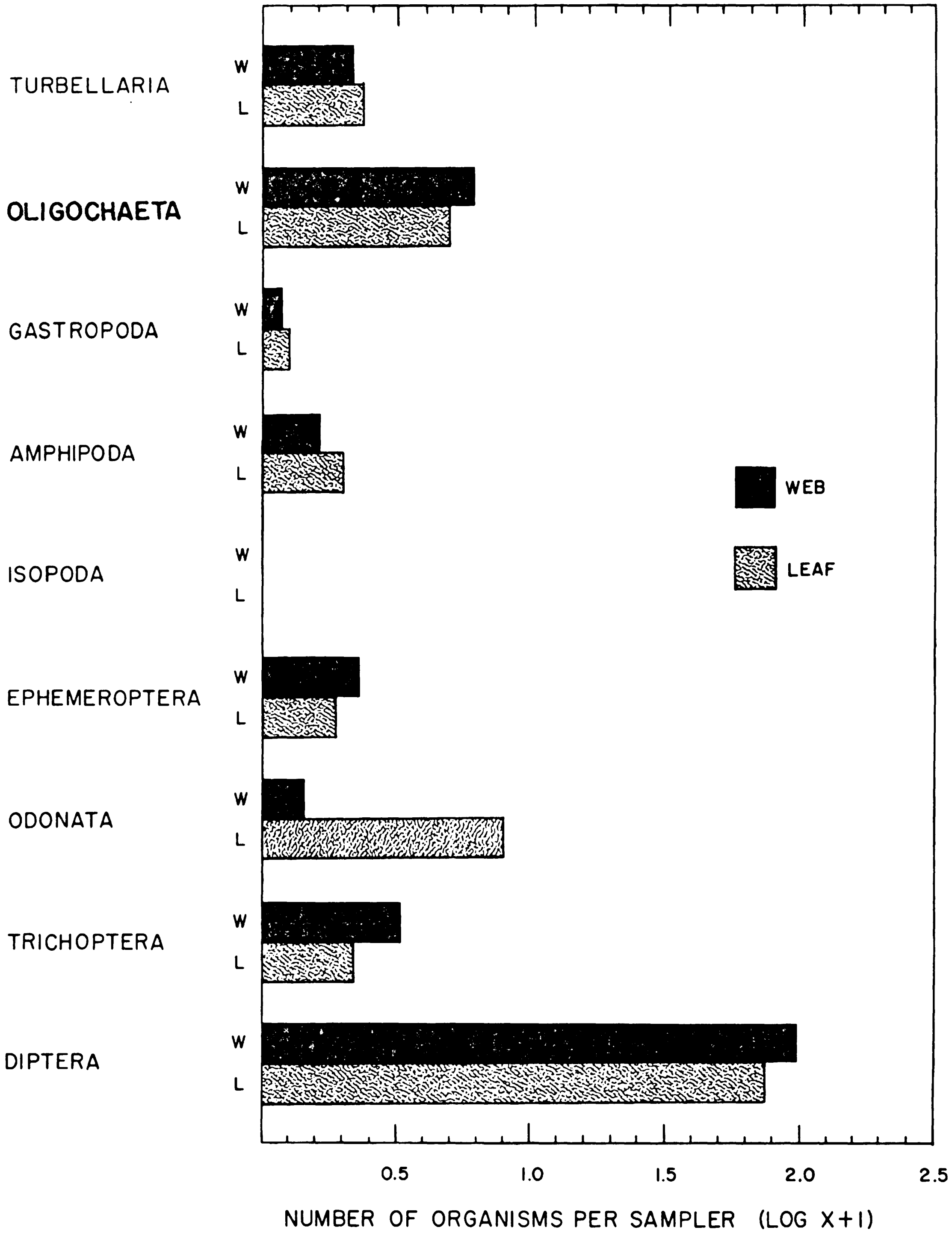

Fig. 8. Composition of macrobenthic community at Station D in 1973-74. These values are the mean of all depths.

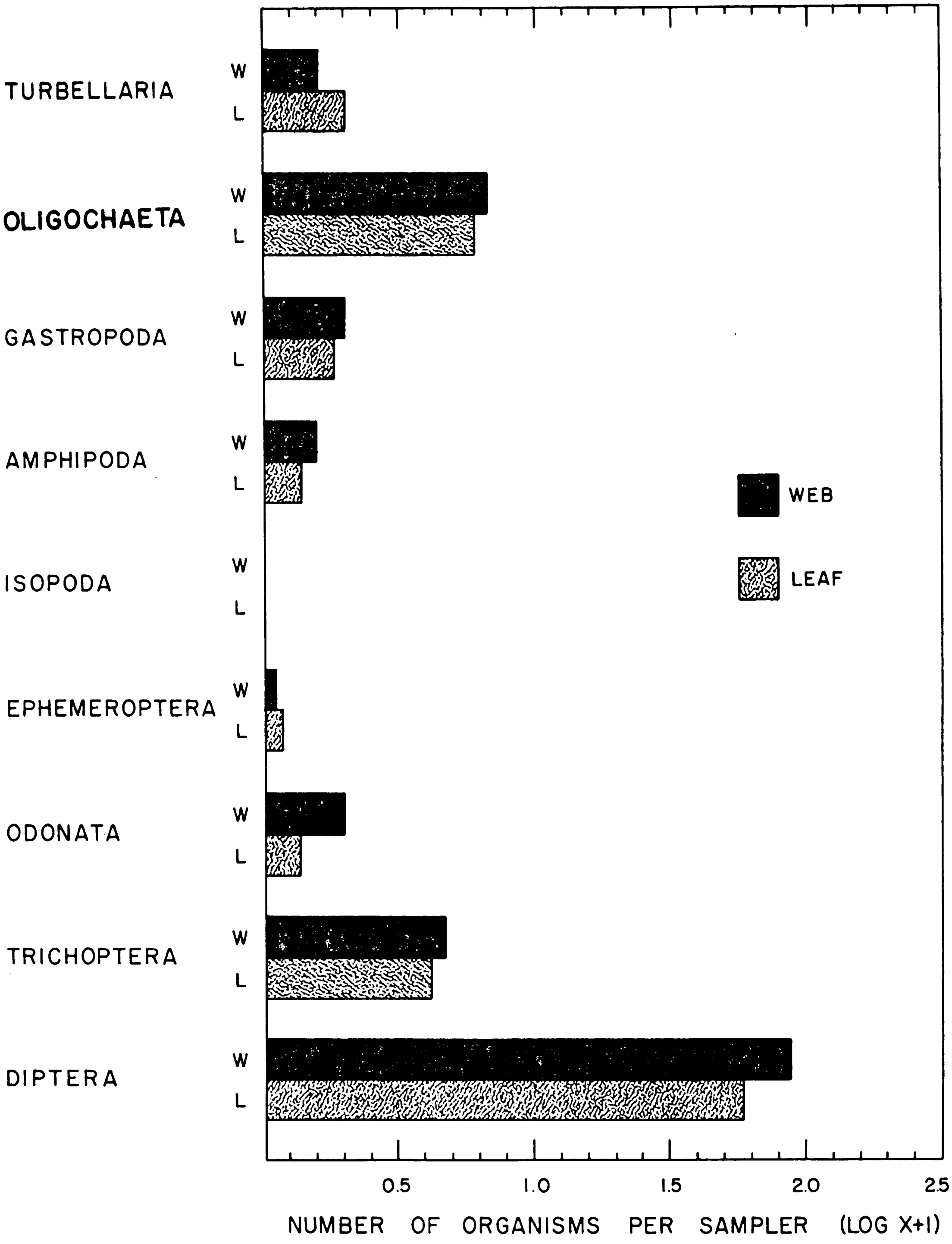

Fig. 9. Composition of macrobenthic community at Station D in 1974-75. These values are the mean of all depths.

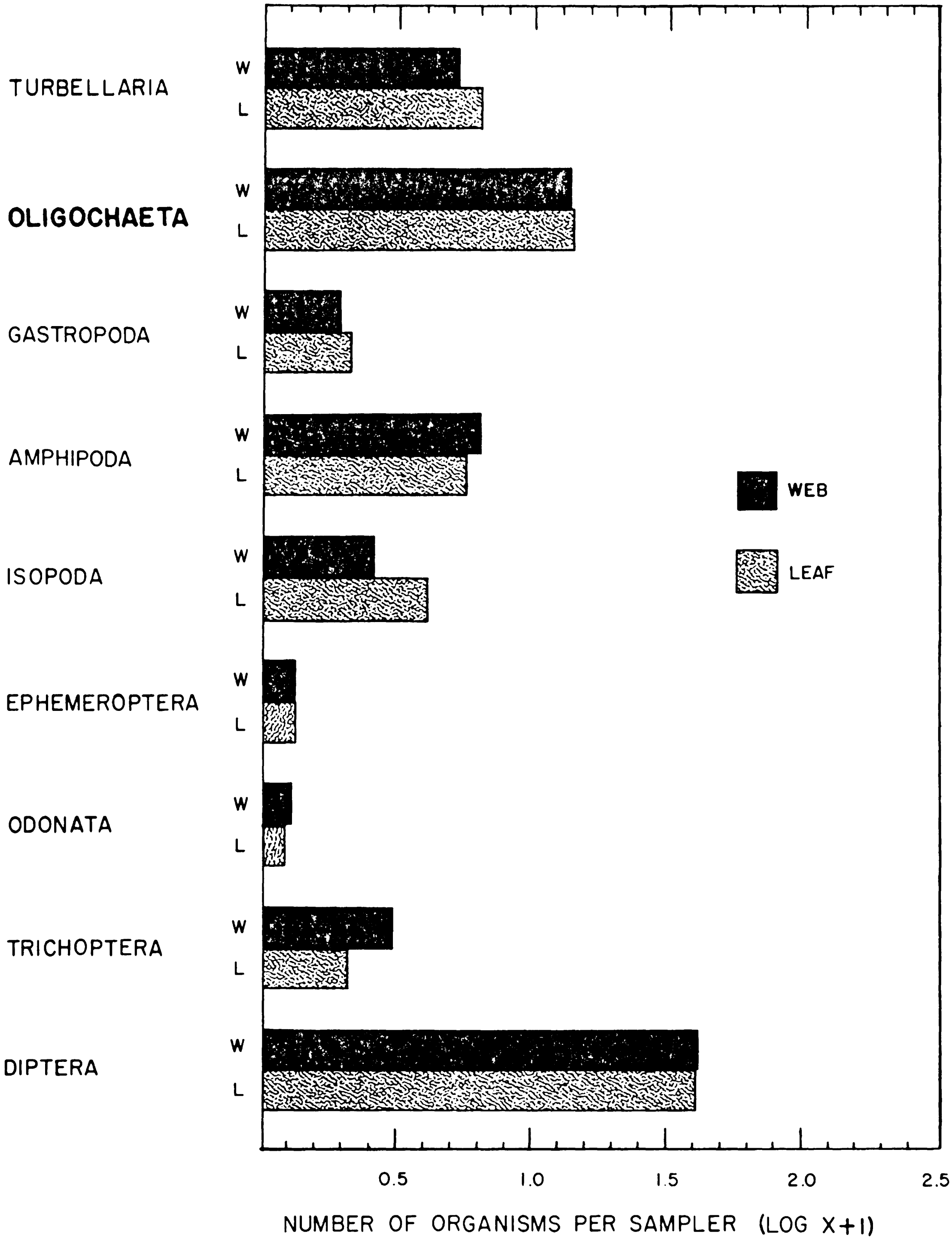

Fig. 10. Composition of macrobenthic community at Station E in 1973-74. These values are the mean of all depths.

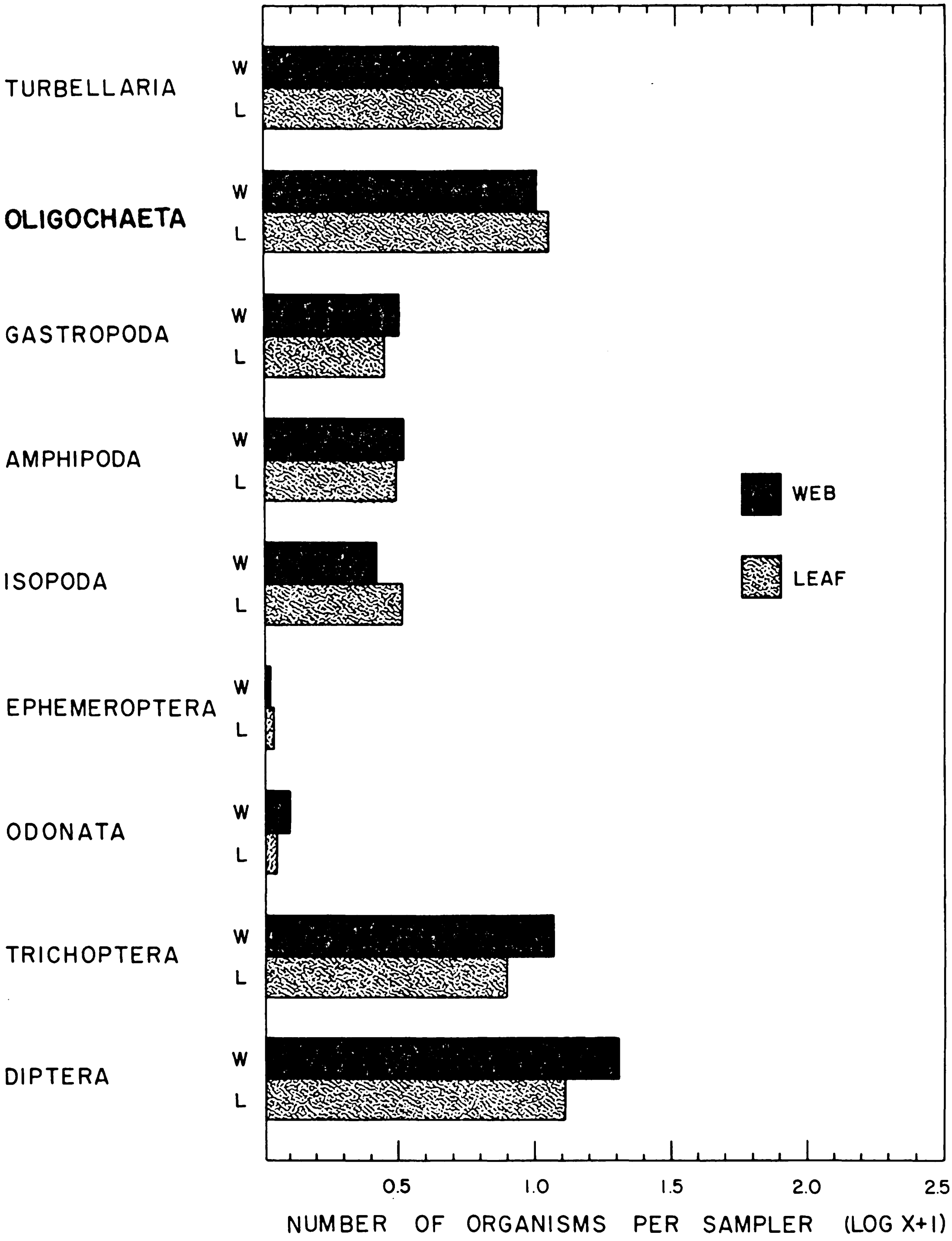

Fig. 11. Composition of macrobenthic community at Station E in 1974-75. These values are the mean of all depths.

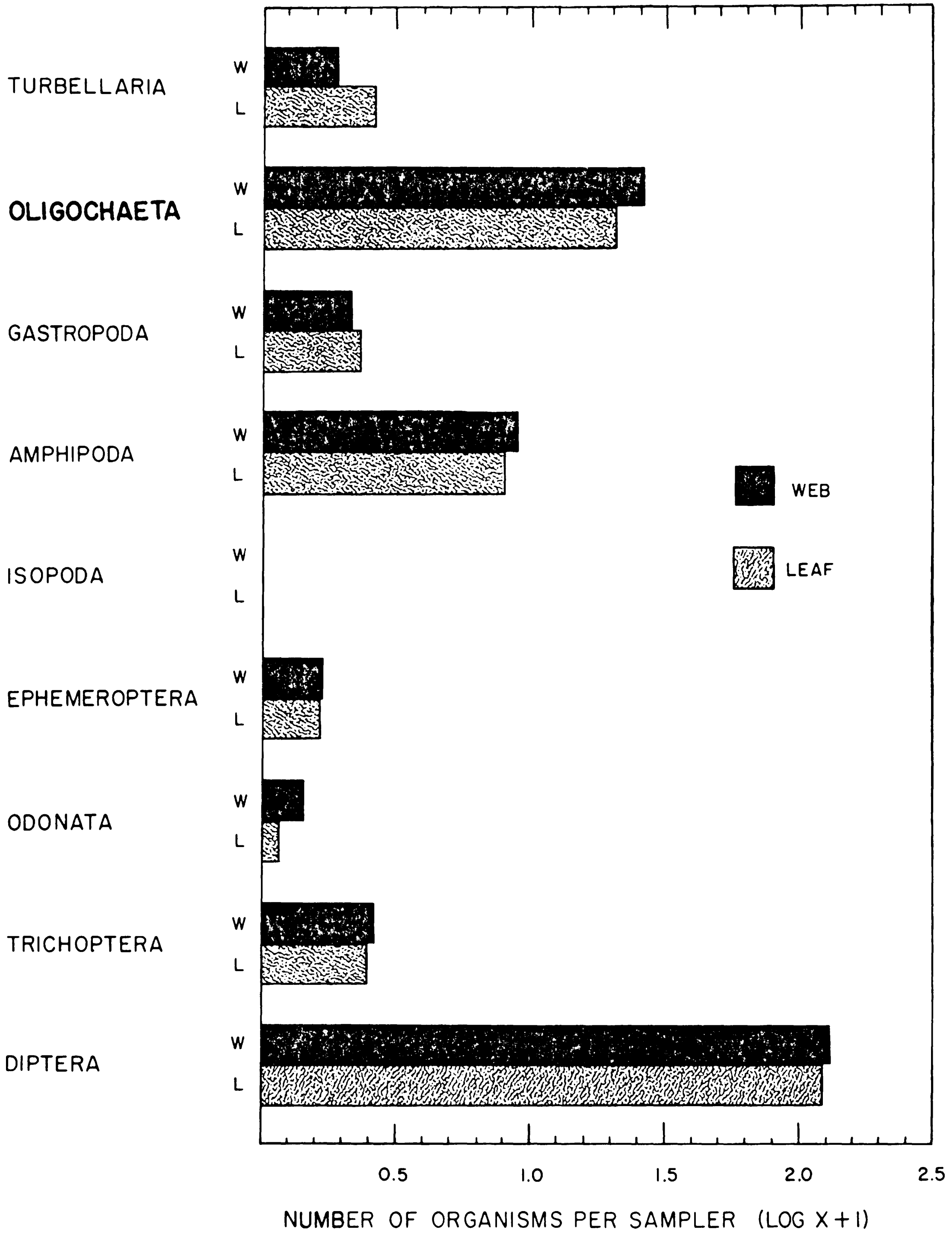

Fig. 12. Composition of macrobenthic community at Station F in 1973-74. These values are the mean of all depths.

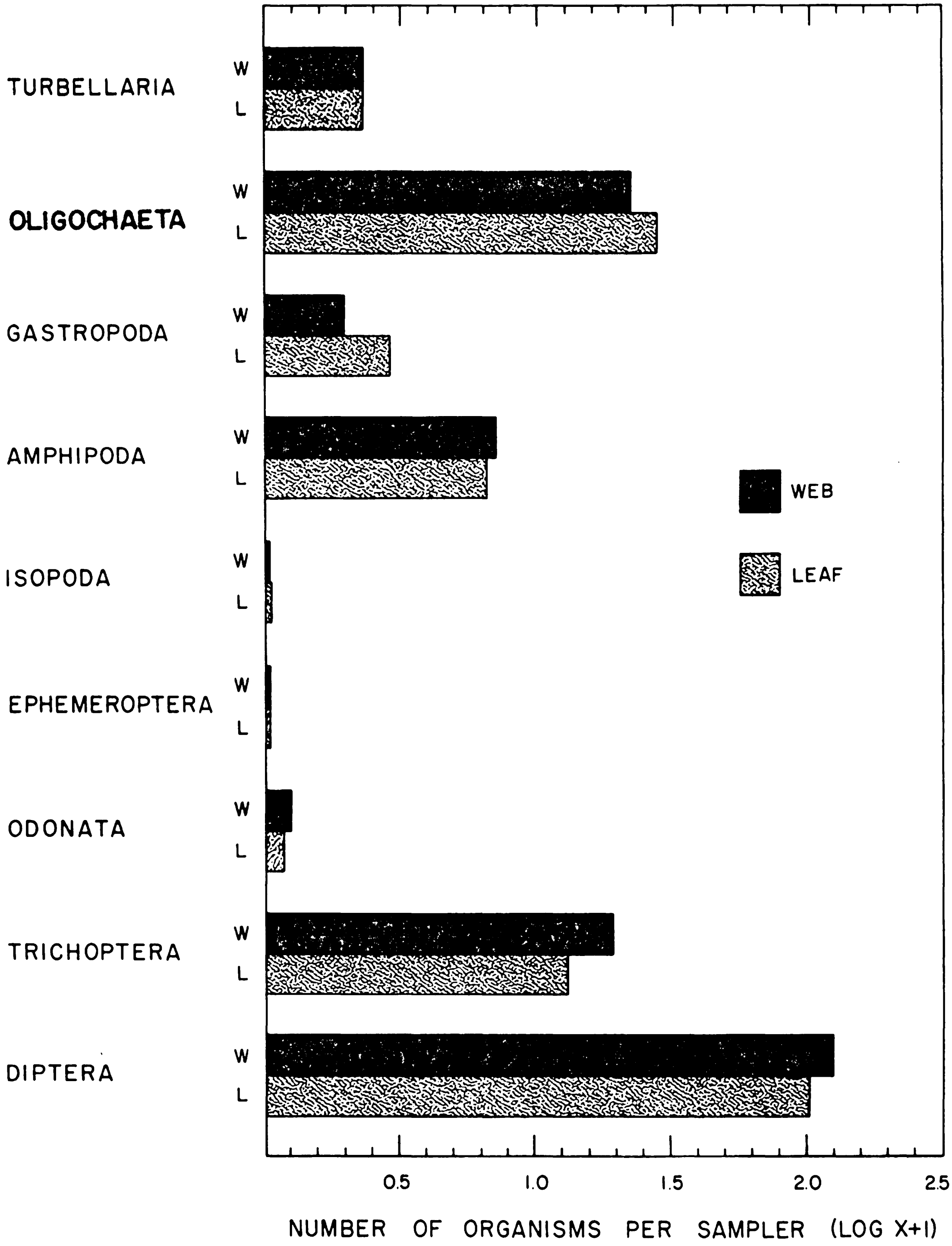

Fig. 13. Composition of macrobenthic community at Station F in 1974-75. These values are the mean of all depths.

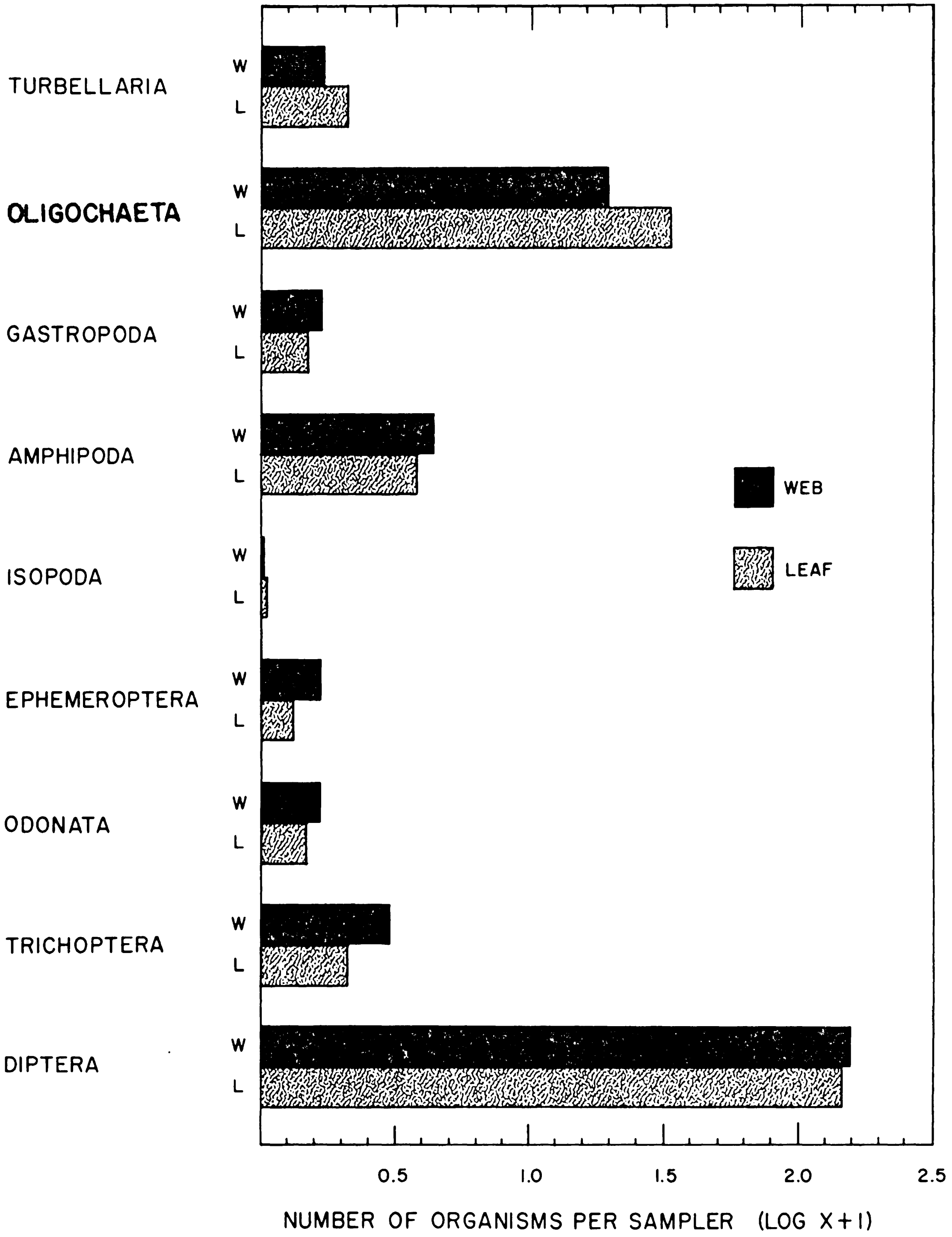

Fig. 14. Composition of macrobenthic community at Station G in 1973-74. These values are the mean of all depths.

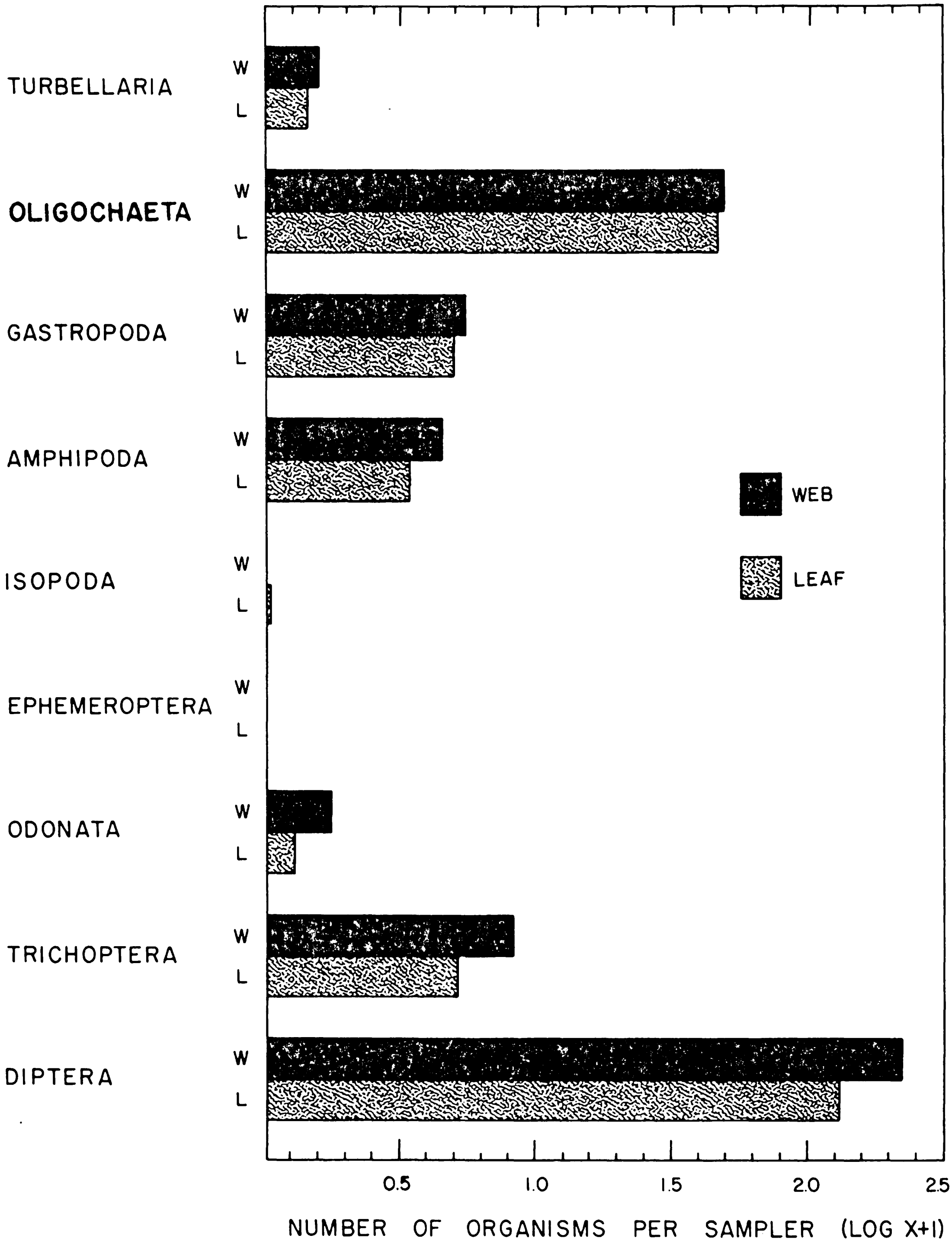

Fig. 15. Composition of macrobenthic community at Station G in 1974-75. These values are the mean of all depths.

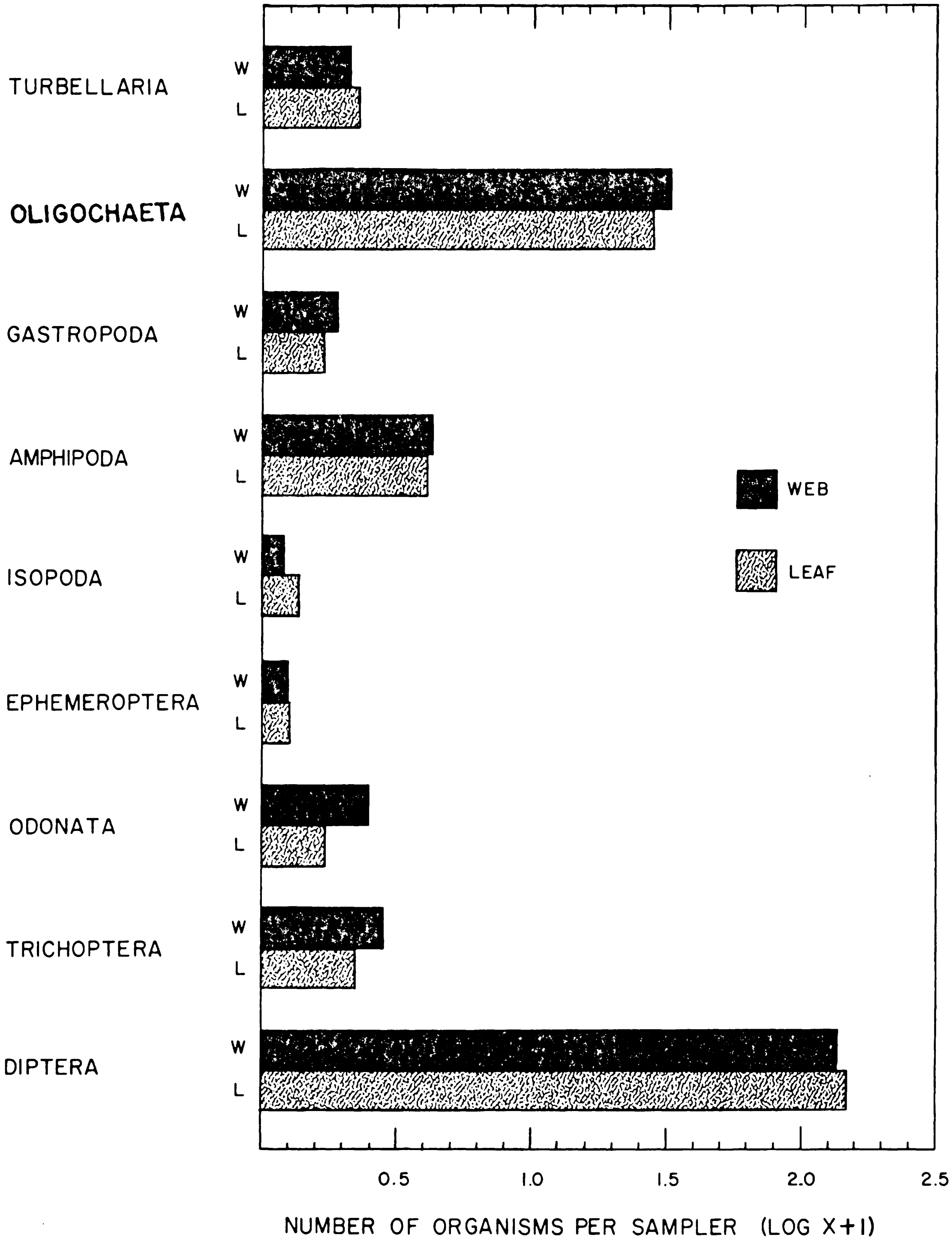

Fig. 16. Composition of macrobenthic community at Station H in 1973-74. These values are the mean of all depths.

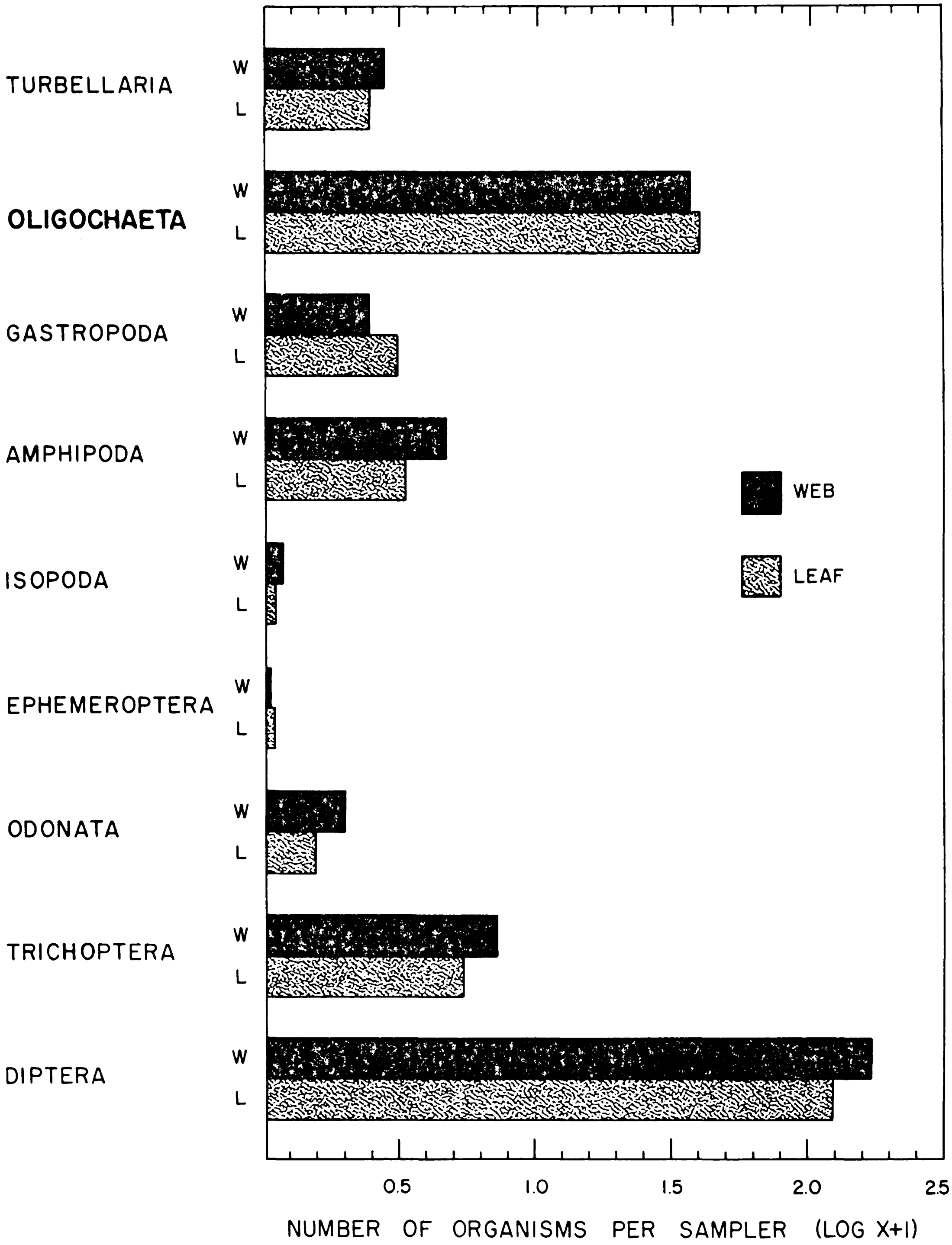

Fig. 17. Composition of macrobenthic community at Station H in 1974-75. These values are the mean of all depths.

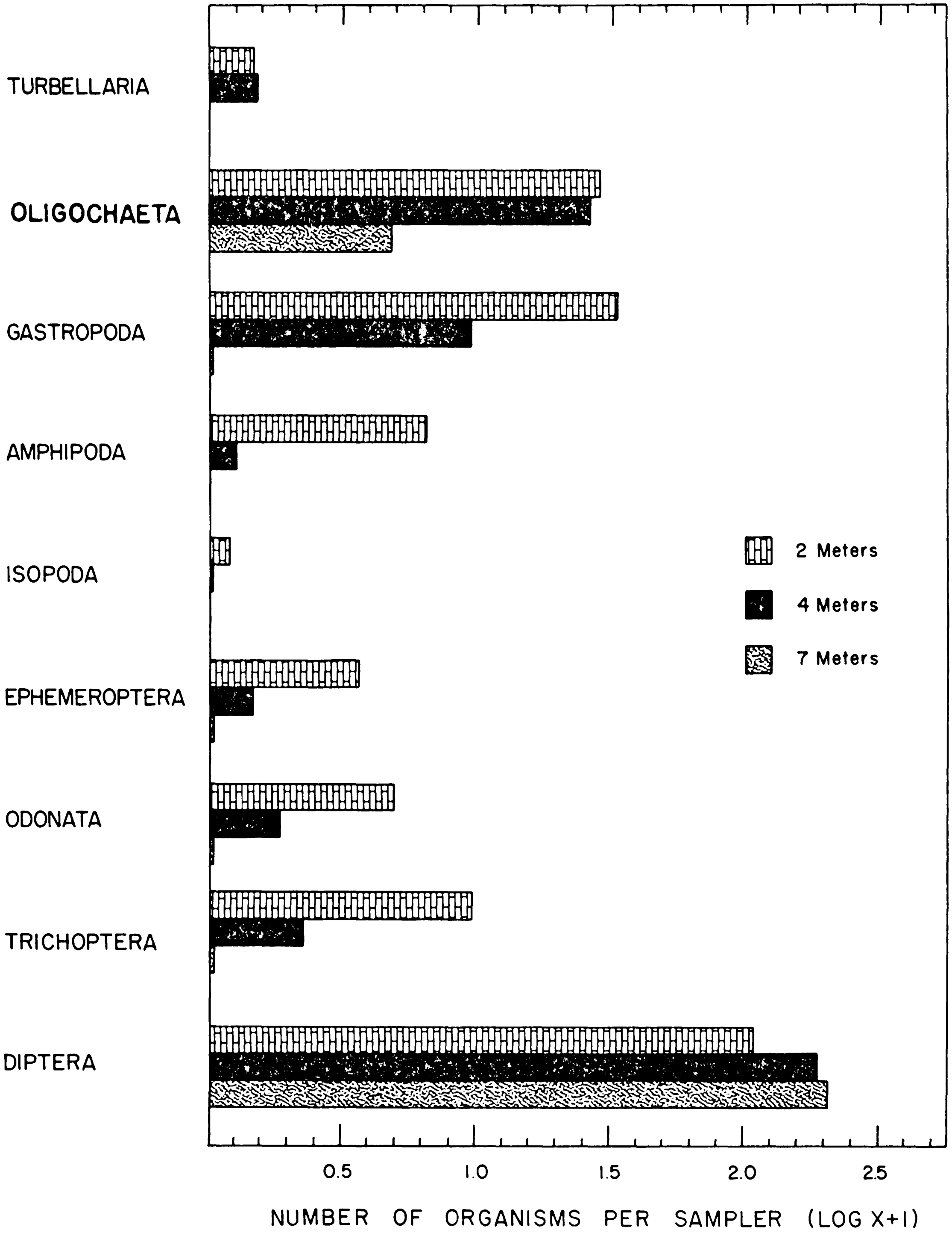

Fig. 18. Composition of macrobenthic community at each depth in lagoons during 1973-74 (web samplers). These values are the mean of Stations A, B, and C.

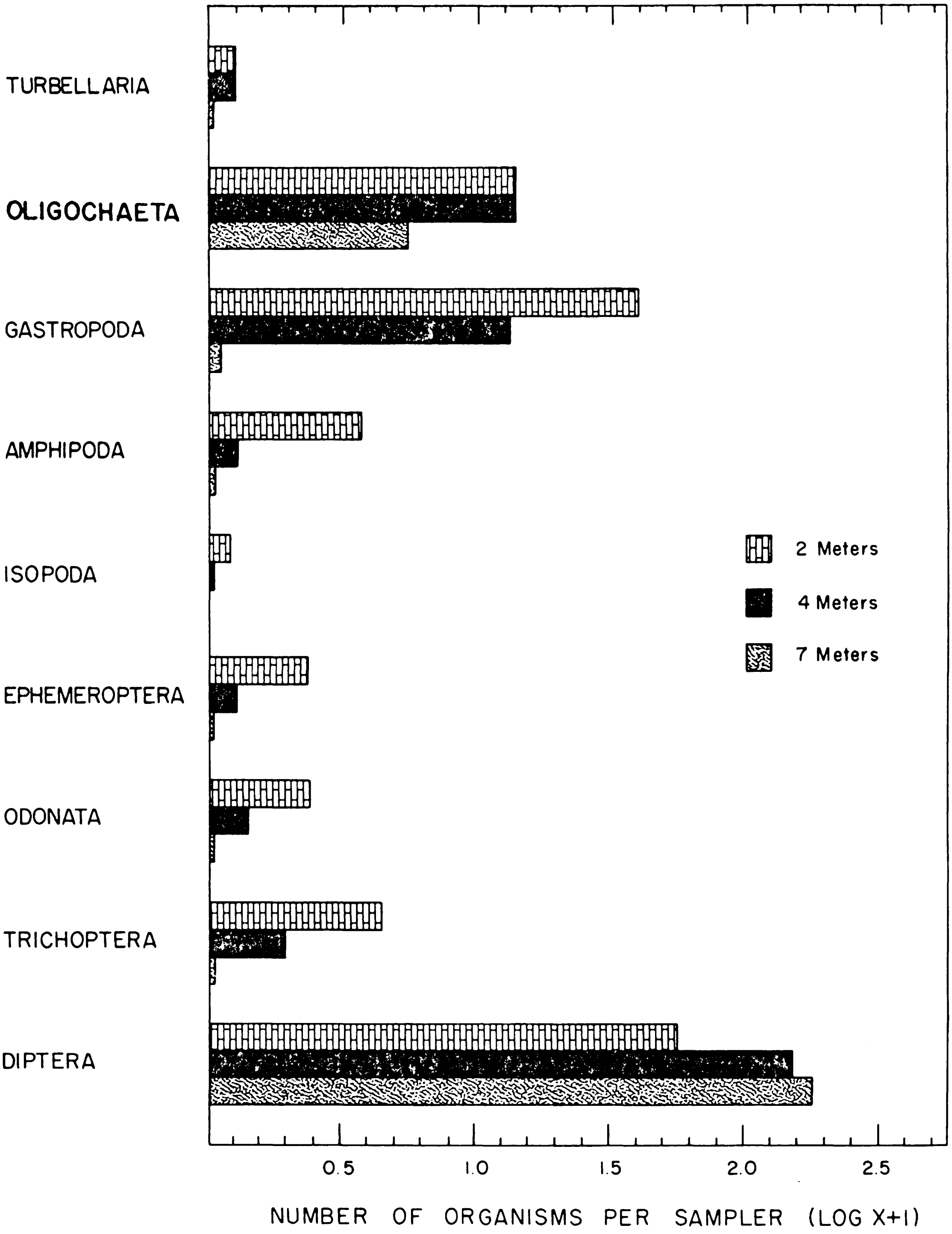

Fig. 19. Composition of macrobenthic community at each depth in lagoons during 1973-74 (leaf samplers). These values are the mean of Stations A, B, and C.

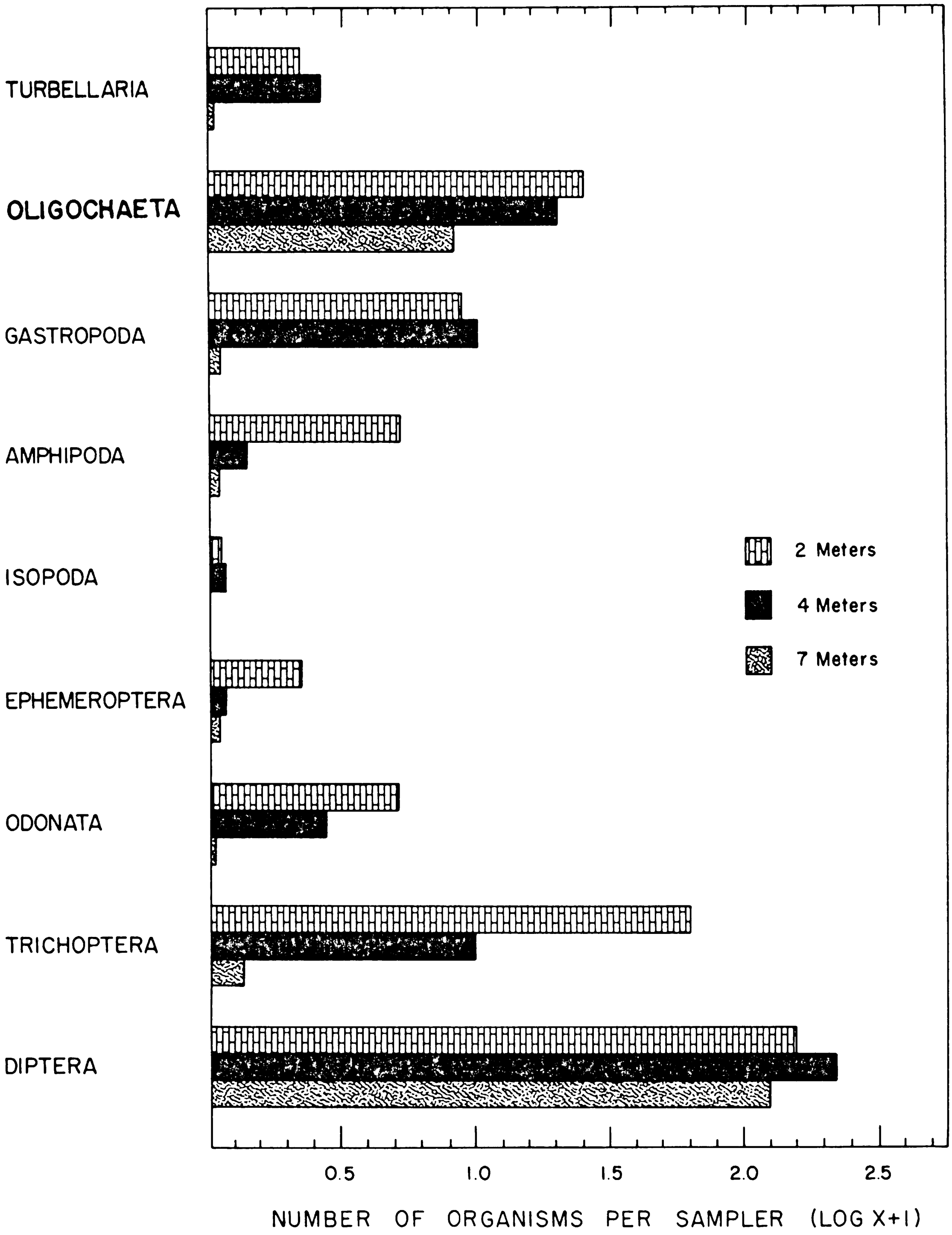

Fig. 20. Composition of macrobenthic community at each depth in lagoons during 1974-75 (web samplers). These values are the mean of Stations A, B, and C.

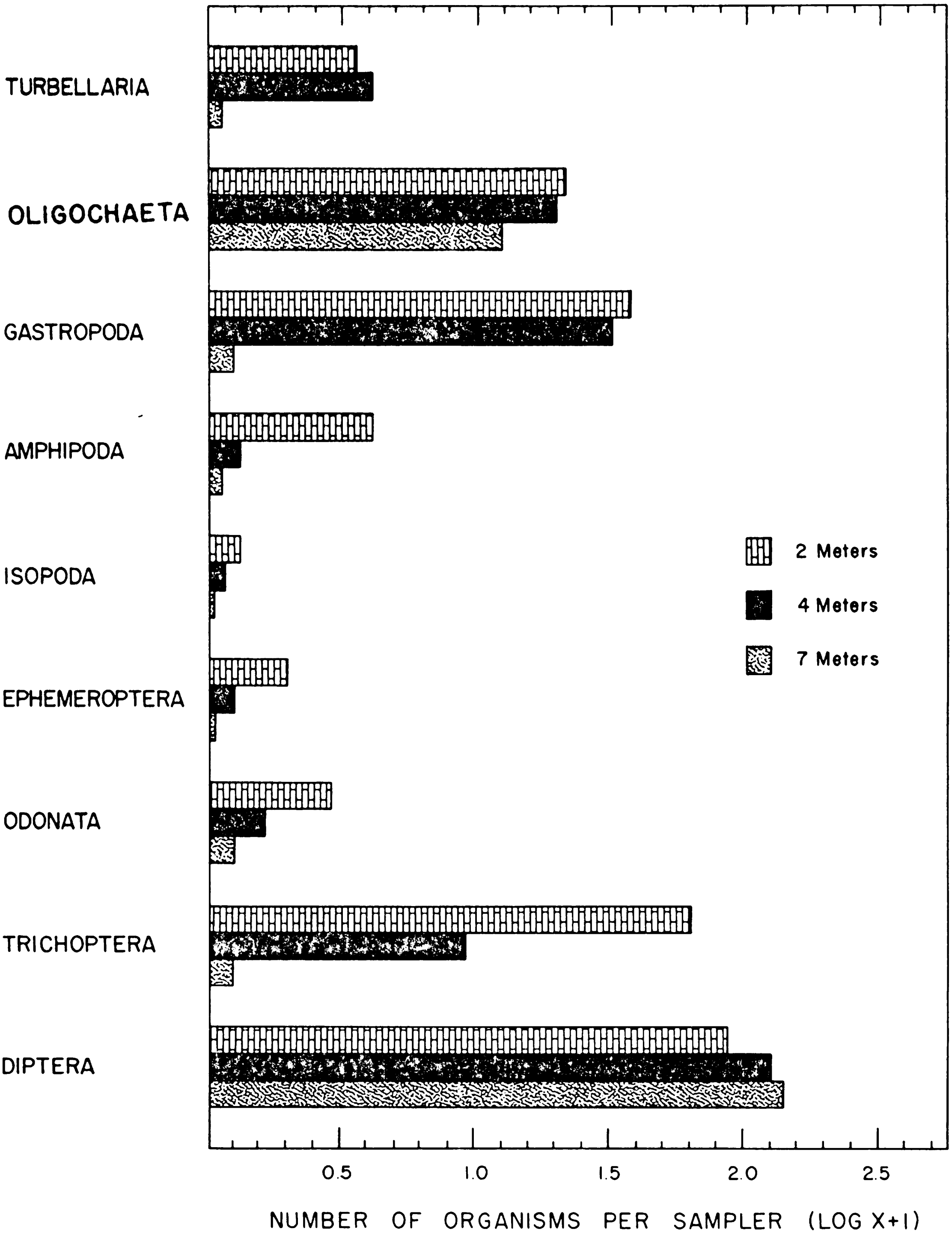

Fig. 21. Composition of macrobenthic community at each depth in lagoons during 1974-75 (leaf samplers). These values are the mean of Stations A, B, and C.

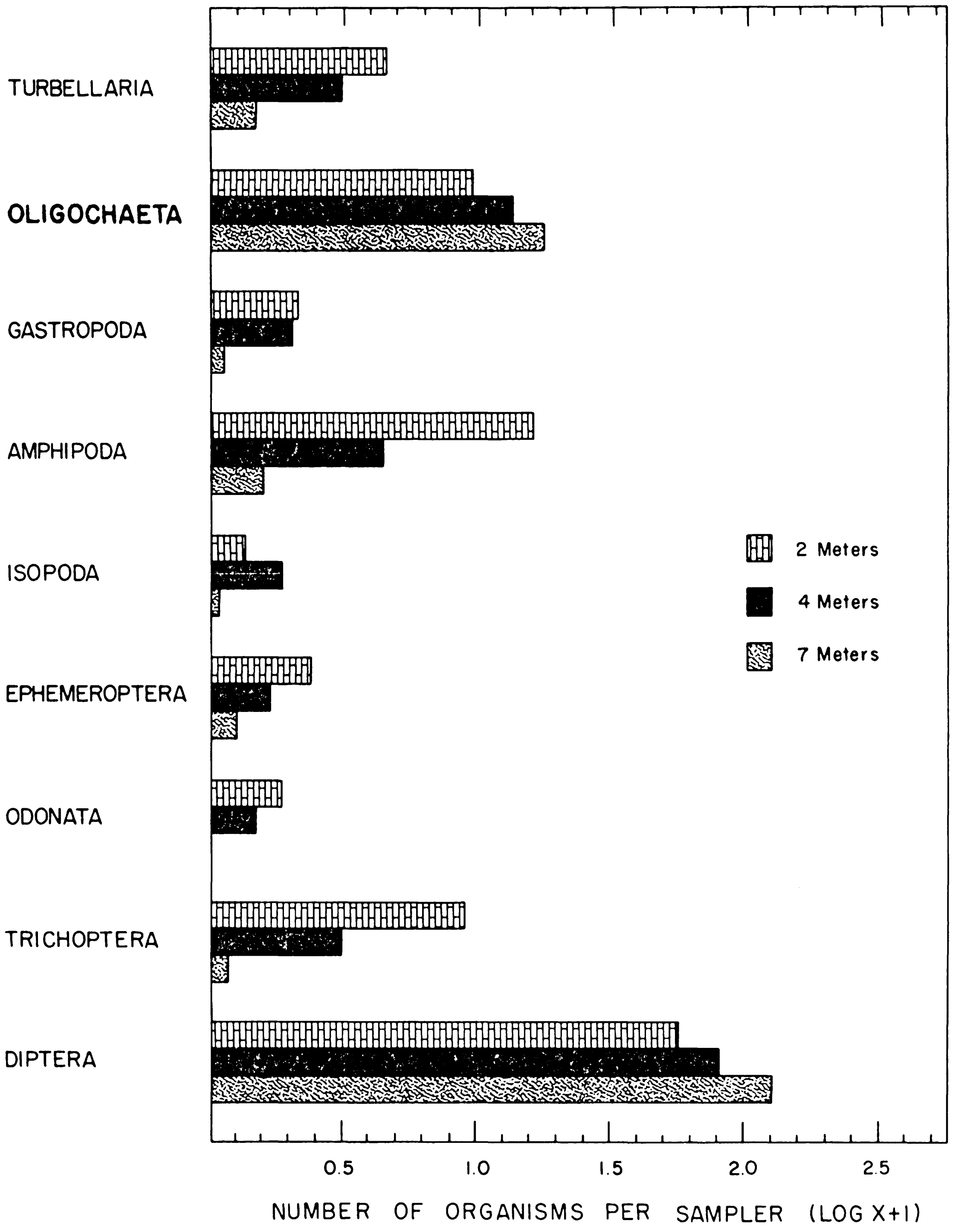

Fig. 22. Composition of macrobenthic community at each depth in lower reservoir during 1973-74 (web samplers). These values are the mean of Stations D, E, and F.

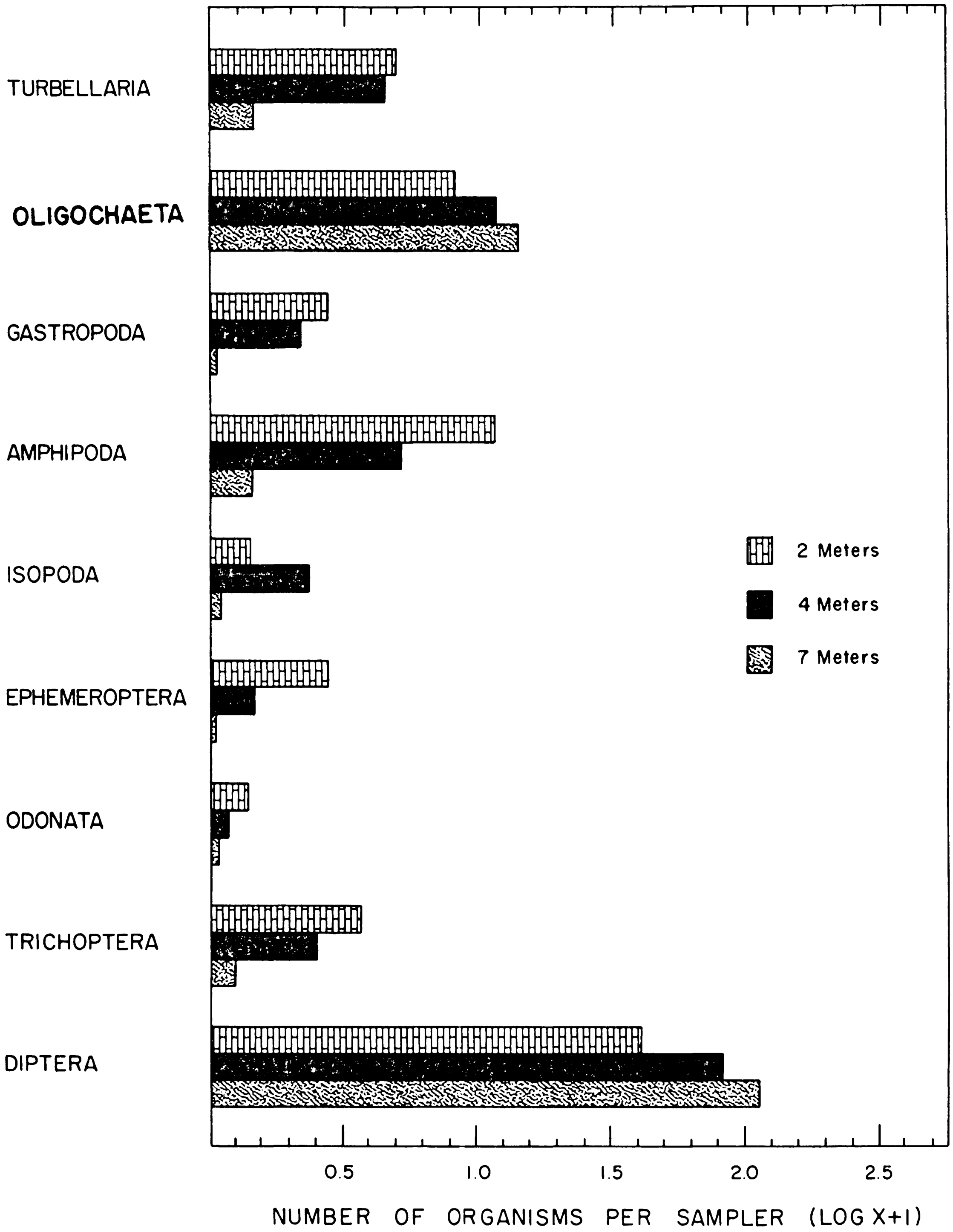

Fig. 23. Composition of macrobenthic community at each depth in lower reservoir during 1973-74 (leaf samplers). These values are the mean of Stations D, E, and F.

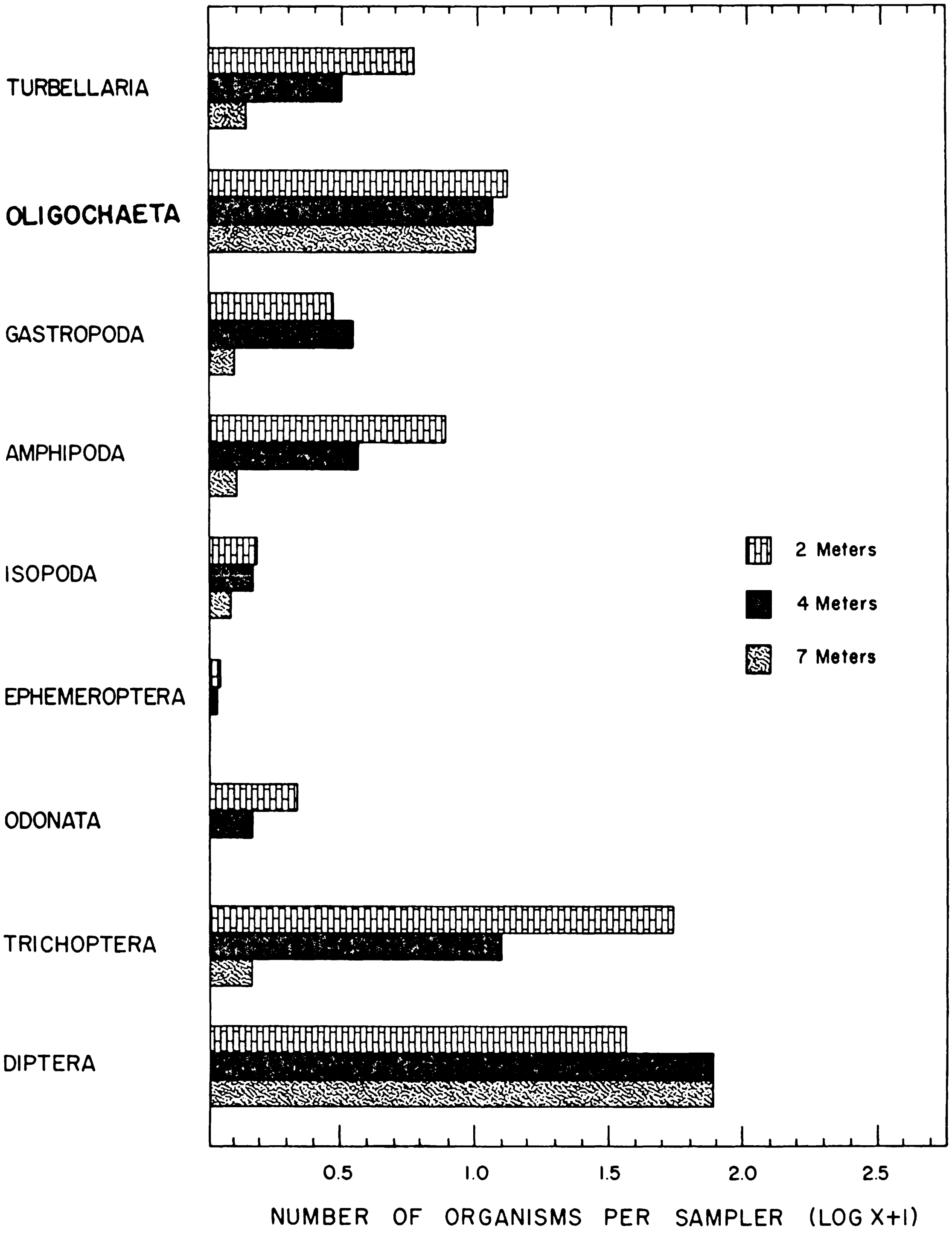

Fig. 24. Composition of macrobenthic community at each depth in lower reservoir during 1973-74 (web samplers). These values are the mean of Stations D, E, and F.

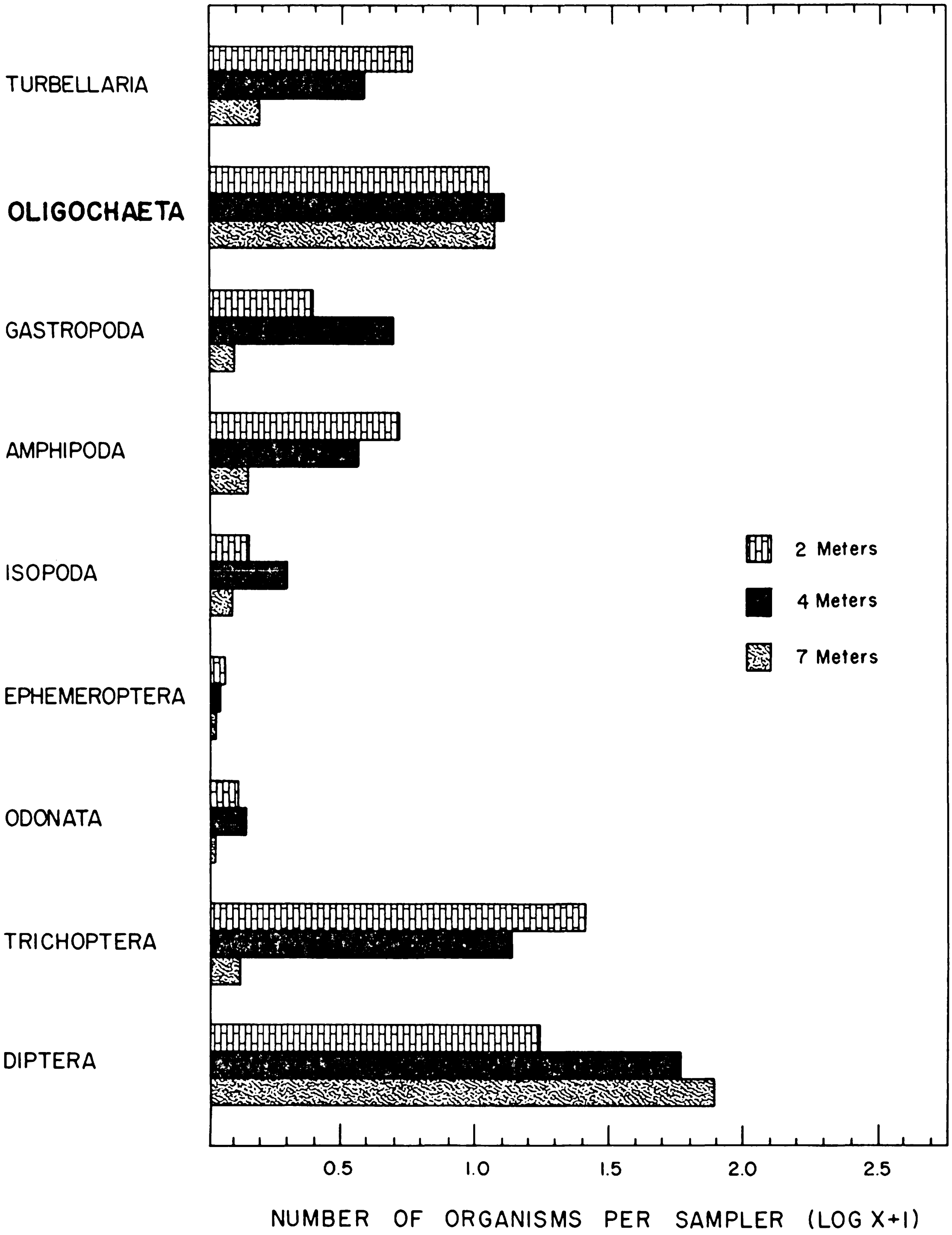

Fig. 25. Composition of macrobenthic community at each depth in lower reservoir during 1974-75 (leaf samplers). These values are the mean of Stations D, E, and F.

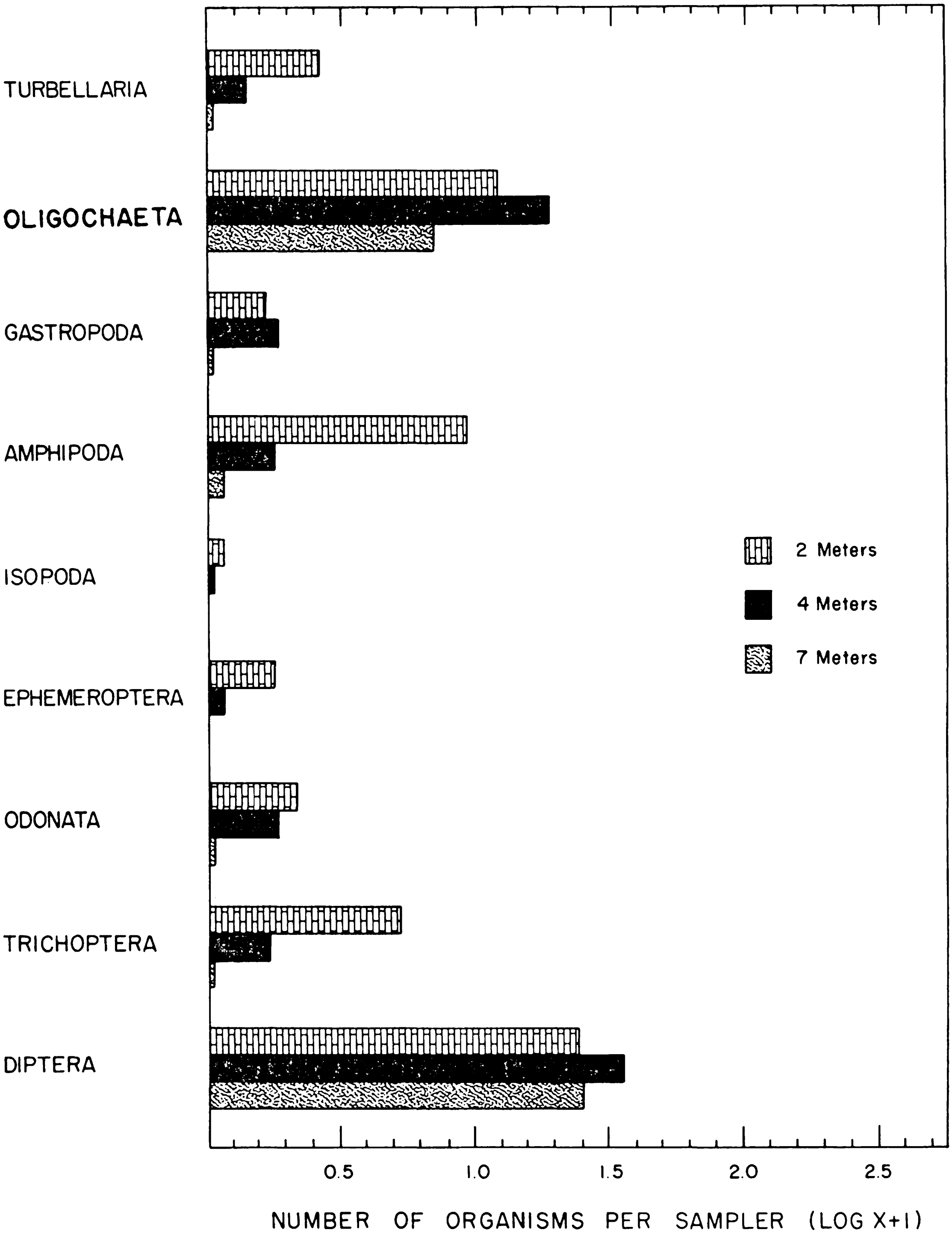

Fig. 26. Composition of macrobenthic community at each depth in upper reservoir during 1973-74 (web samplers). These values are the mean of Stations G and H.

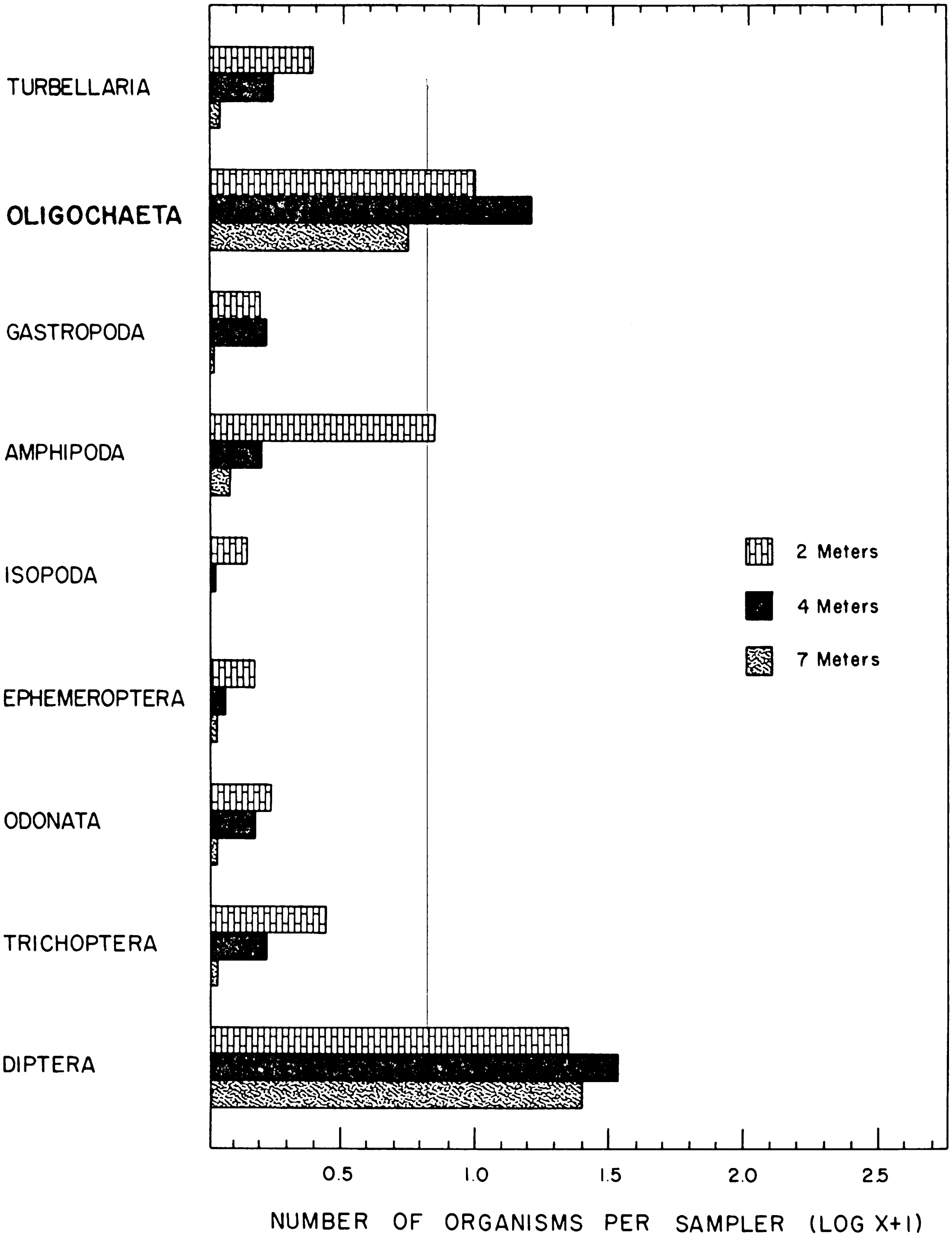

Fig. 27. Composition of macrobenthic community at each depth in upper reservoir during 1973-74 (leaf samplers). These values are the mean of Stations G and H.

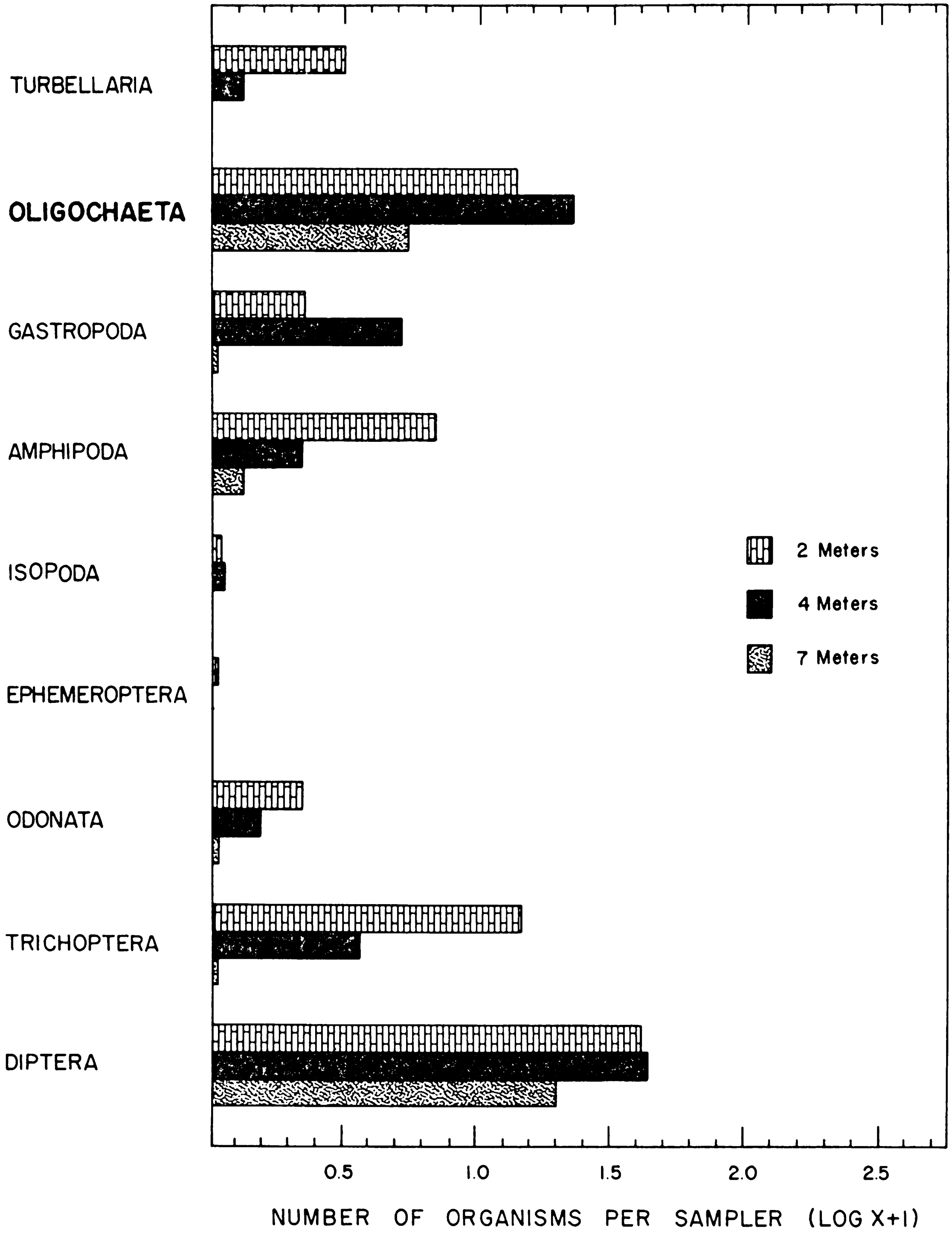

Fig. 28. Composition of macrobenthic community at each depth in upper reservoir during 1974-75 (web samplers). These values are the mean of Stations G and H.

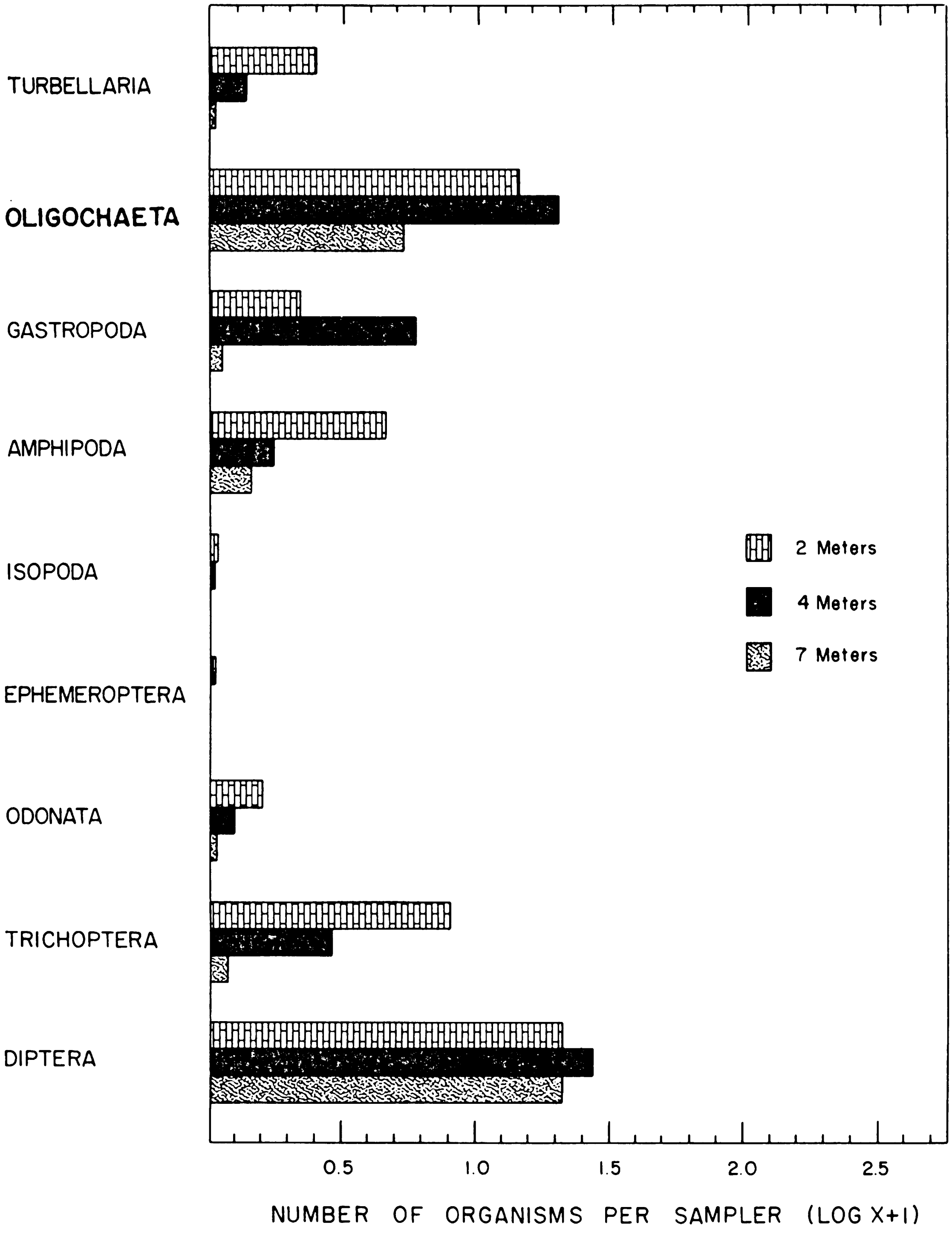

Fig. 29. Composition of macrobenthic community at each depth in upper reservoir during 1974-75 (leaf samplers). These values are the mean of Stations G and H.

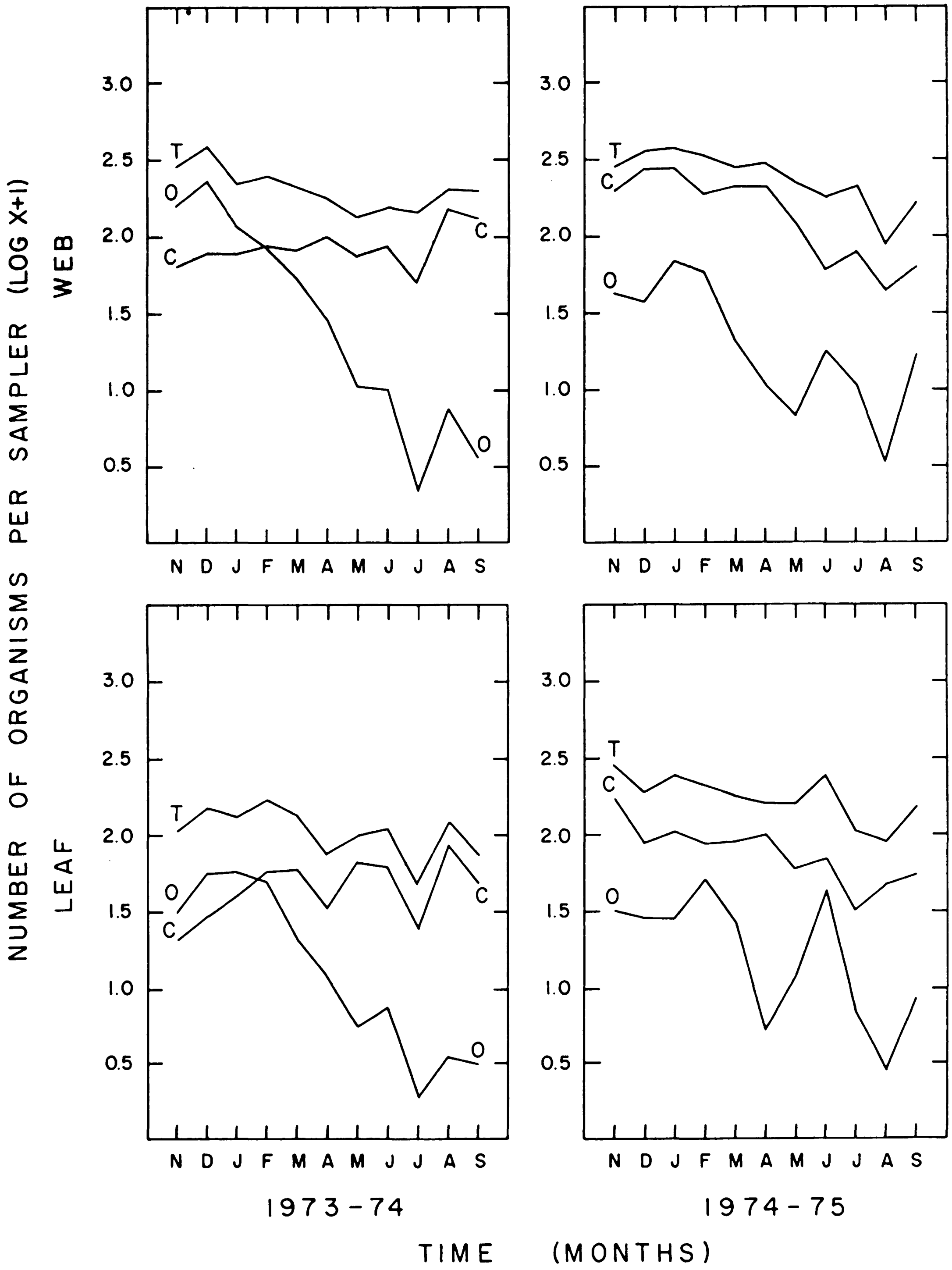

Fig. 30. Temporal distributions at 2 m in lagoons. These values are the mean of Stations A, B, and C. T = Total Organisms; C = Chironomidae; O = Oligochaeta.

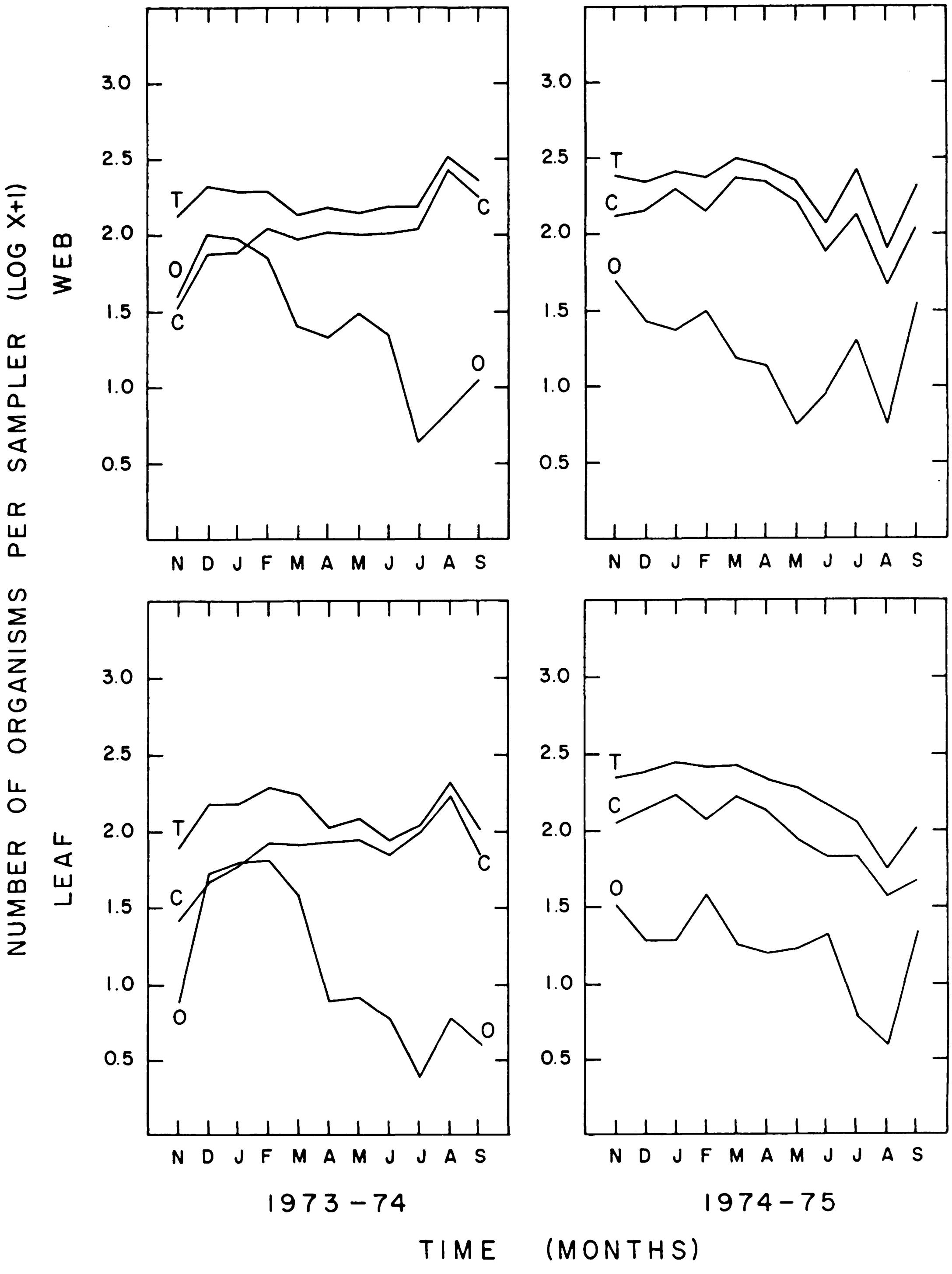

Fig. 31. Temporal distributions at 4 m in lagoons. These values are the mean of Stations A, B, and C. T = Total Organisms; C = Chironomidae; O = Oligochaeta.

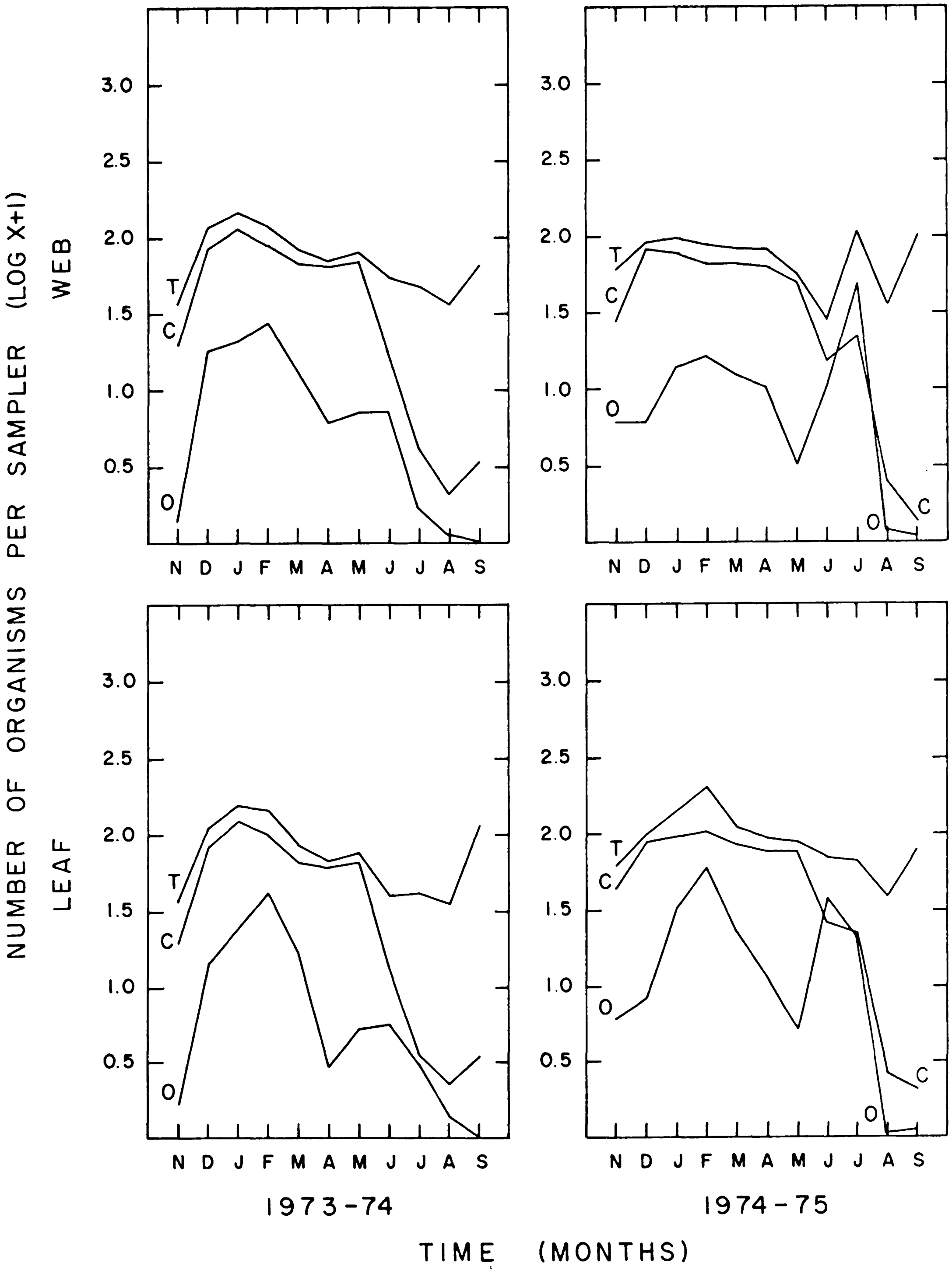

Fig. 32. Temporal distributions at 7 m in lagoons. These values are the mean of Stations A, B, and C. T = Total Organisms; C = Chironomidae; O = Oligochaeta.

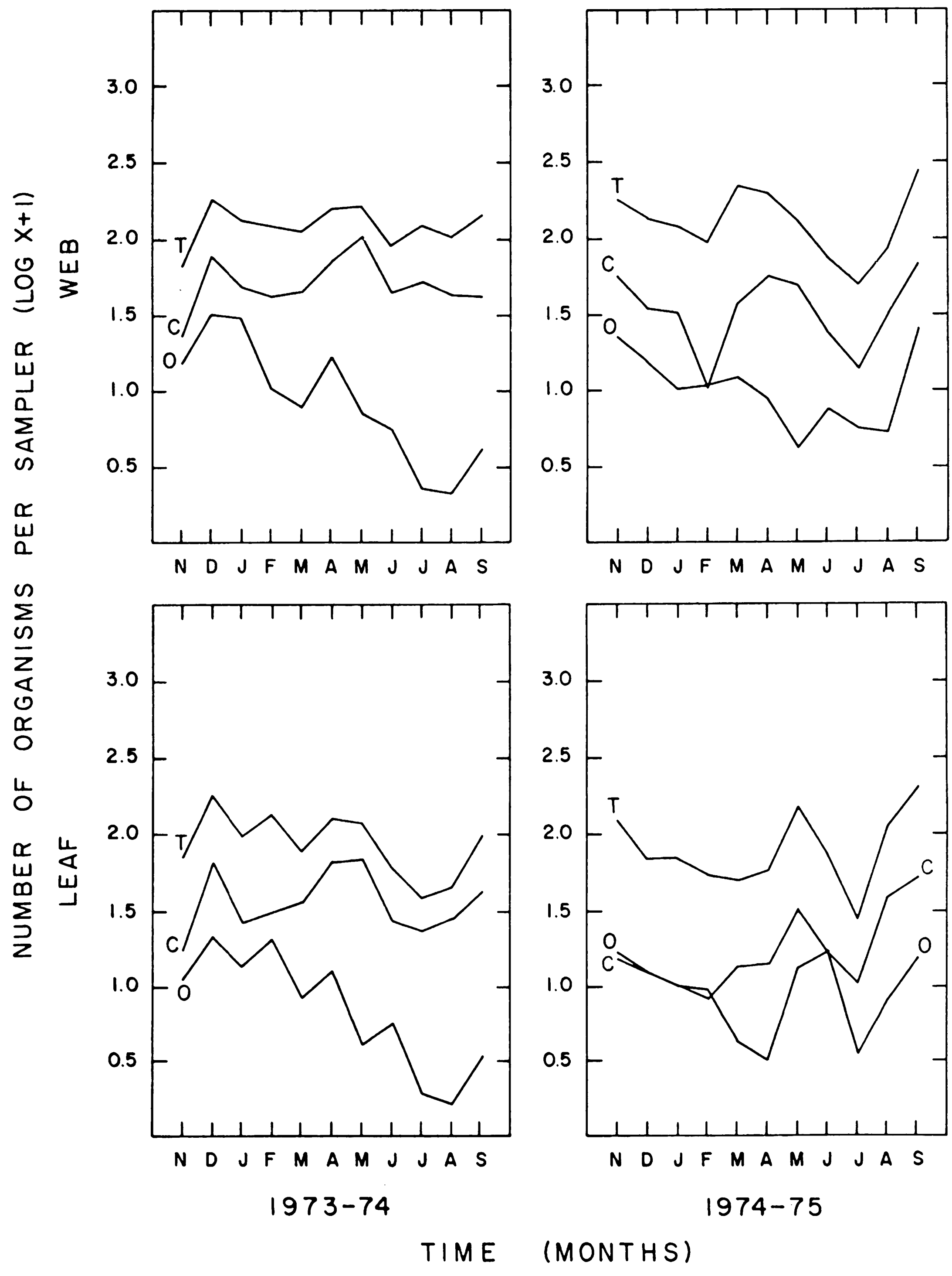

Fig. 33. Temporal distributions at 2 m in lower reservoir. These values are the mean of Stations D, E, and F. T = Total Organisms; C = Chironomidae; O = Oligochaeta.

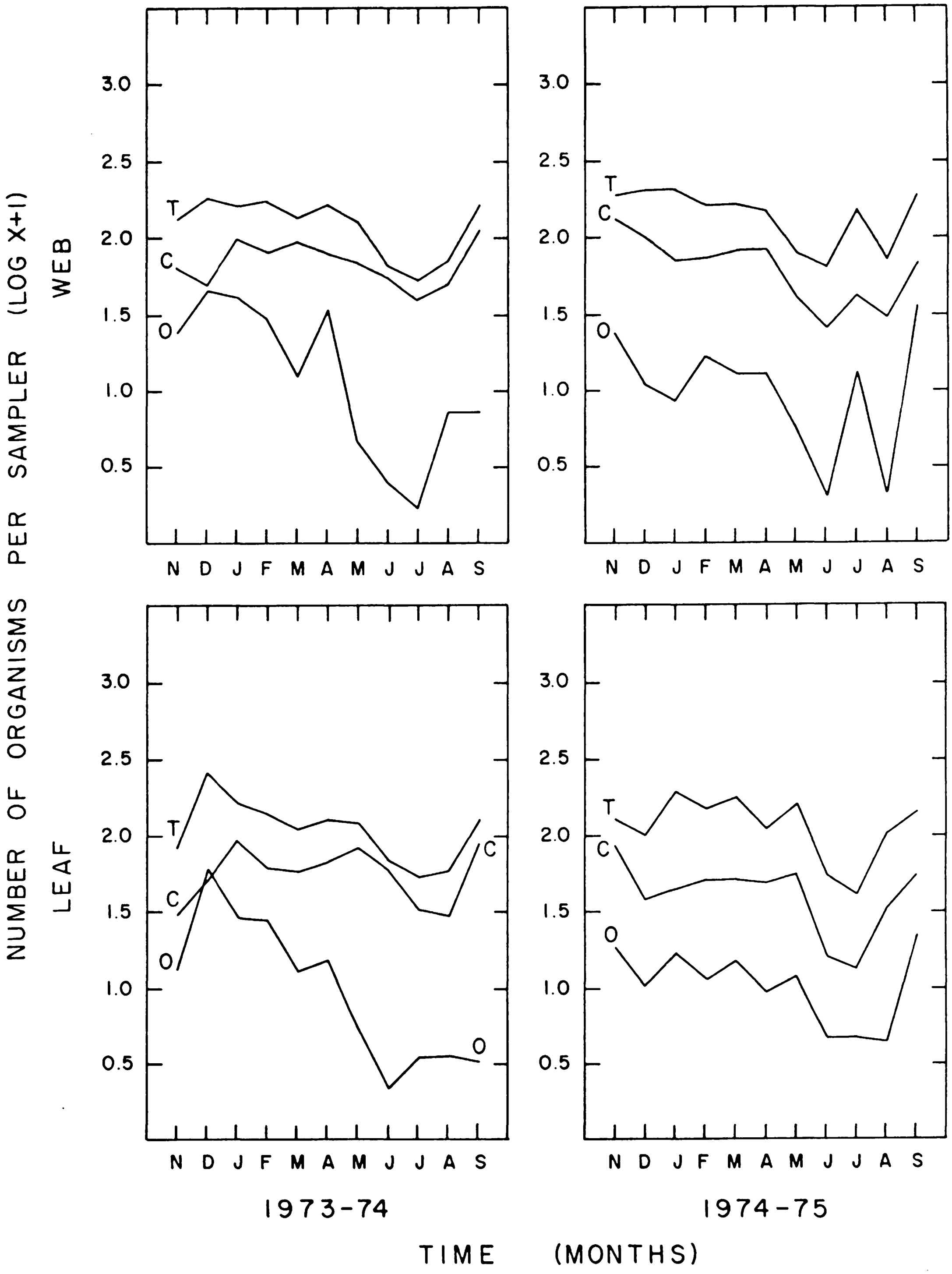

Fig. 34. Temporal distributions at 4 m in lower reservoir. These values are the mean of Stations D, E, and F. T = Total Organisms; C = Chironomidae; O = Oligochaeta.

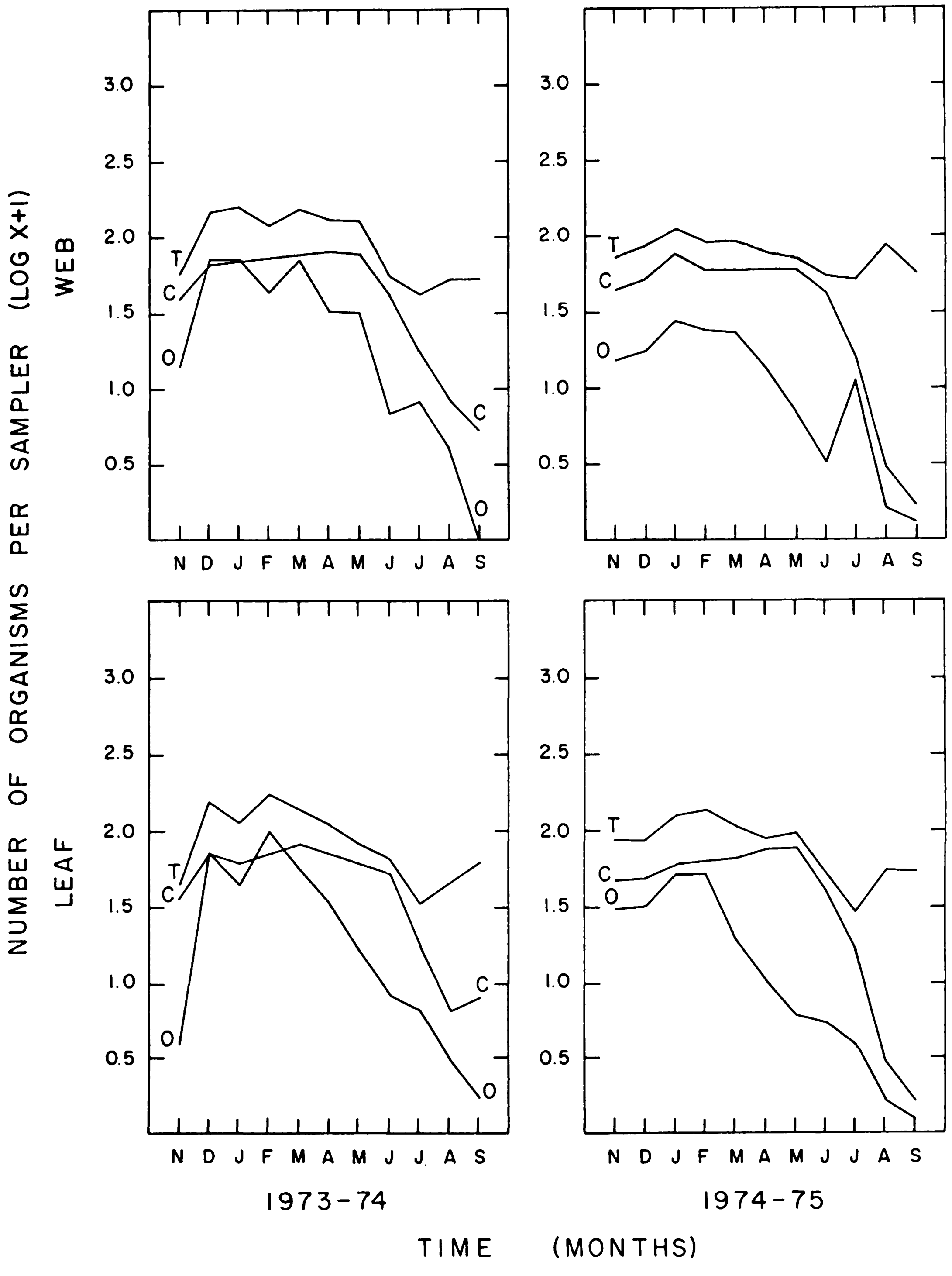

Fig. 35. Temporal distributions at 7 m in lower reservoir. These values are the mean of Stations D, E, and F. T = Total Organisms; C = Chironomidae; O = Oligochaeta.

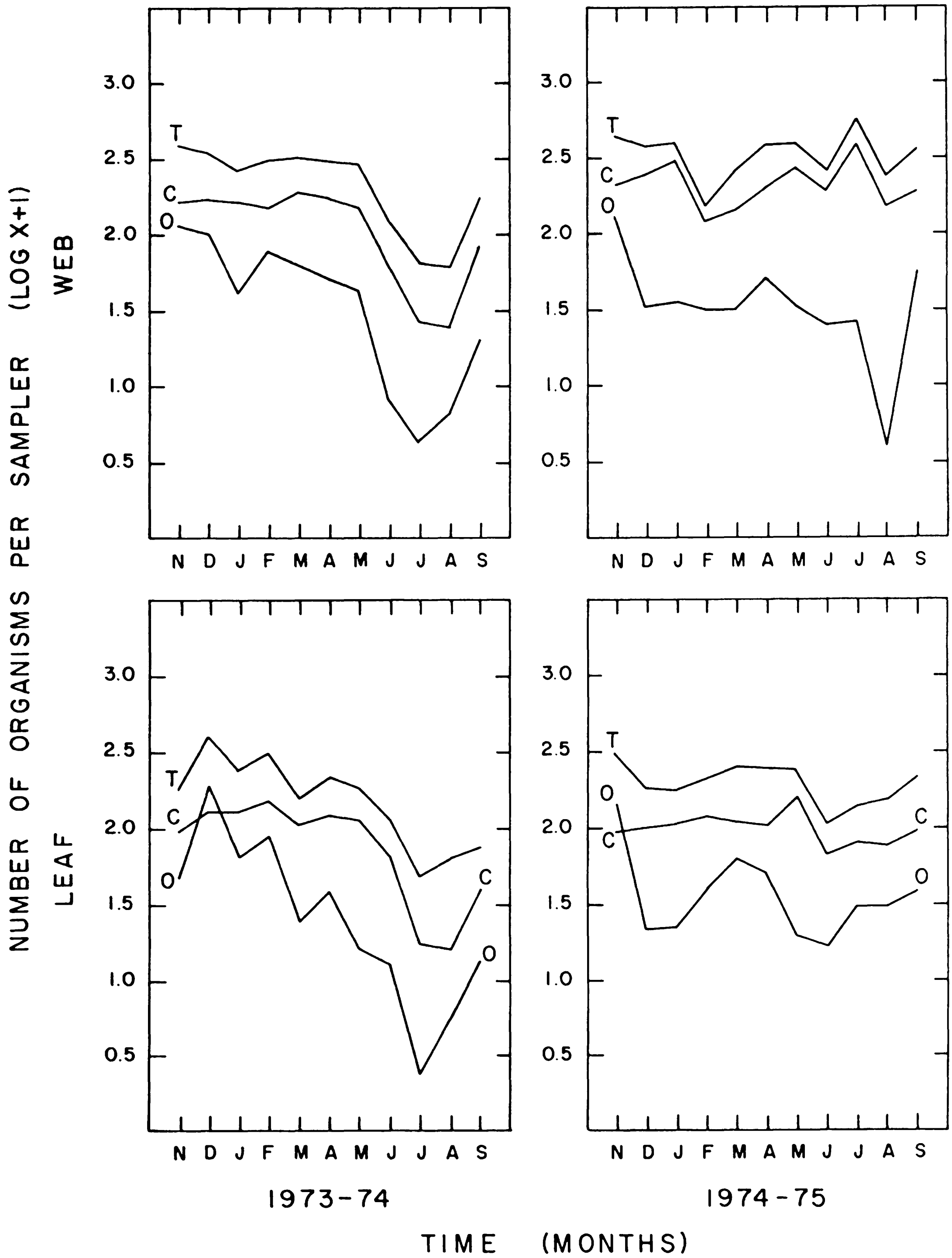

Fig. 36. Temporal distributions at 2 m in upper reservoir. These values are the mean of Stations G and H. T = Total Organisms; C = Chironomidae; O = Oligochaeta.

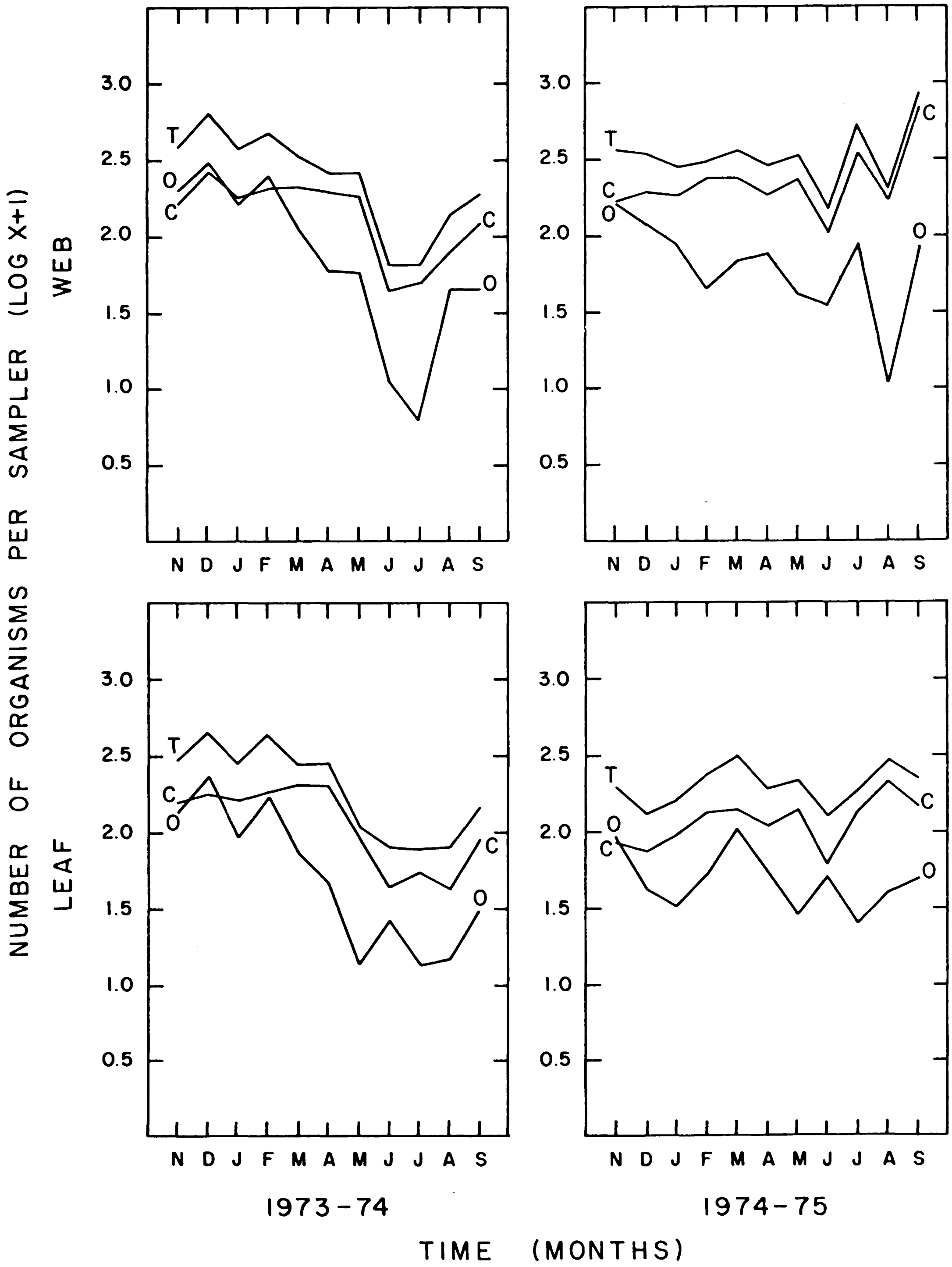

Fig. 37. Temporal distributions at 4 m in upper reservoir. These values are the mean of Stations G and H. T = Total Organisms; C = Chironomidae; O = Oligochaeta.

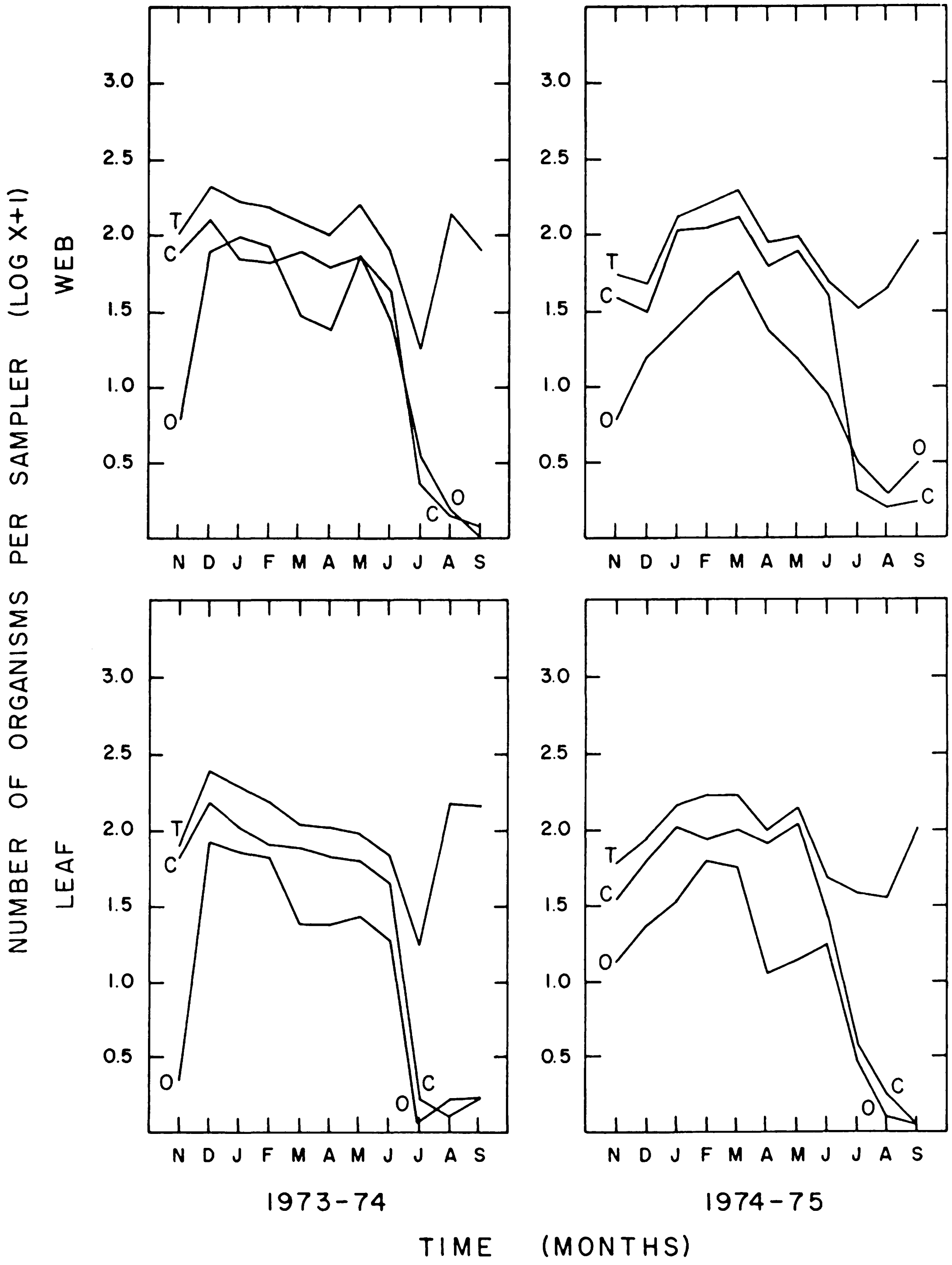

Fig. 38. Temporal distributions at 7 m in upper reservoir. These values are the mean of Stations G and H. T = Total Organisms; C = Chironomidae; O = Oligochaeta.

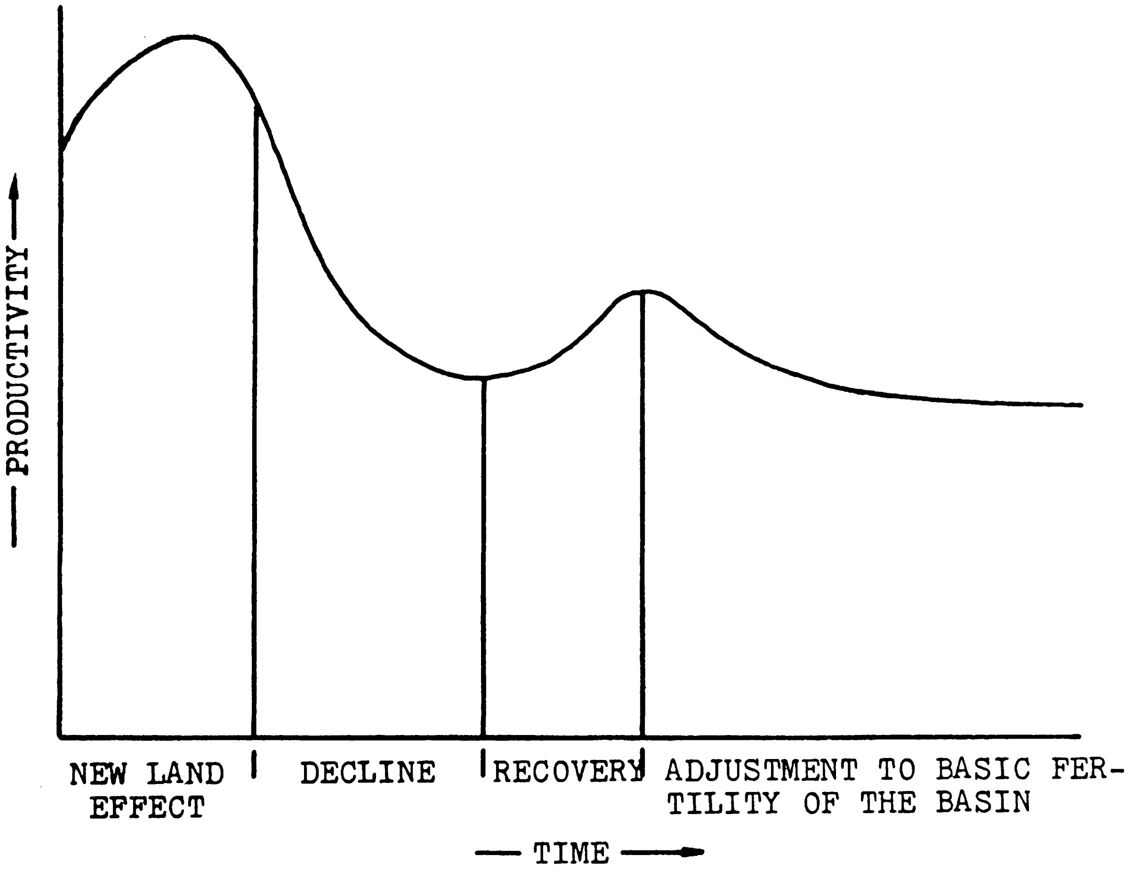

Fig. 39. Successional change in productivity of a newly impounded reservoir (U. S. Atomic Energy Commission, Directorate of Licensing, 1973).

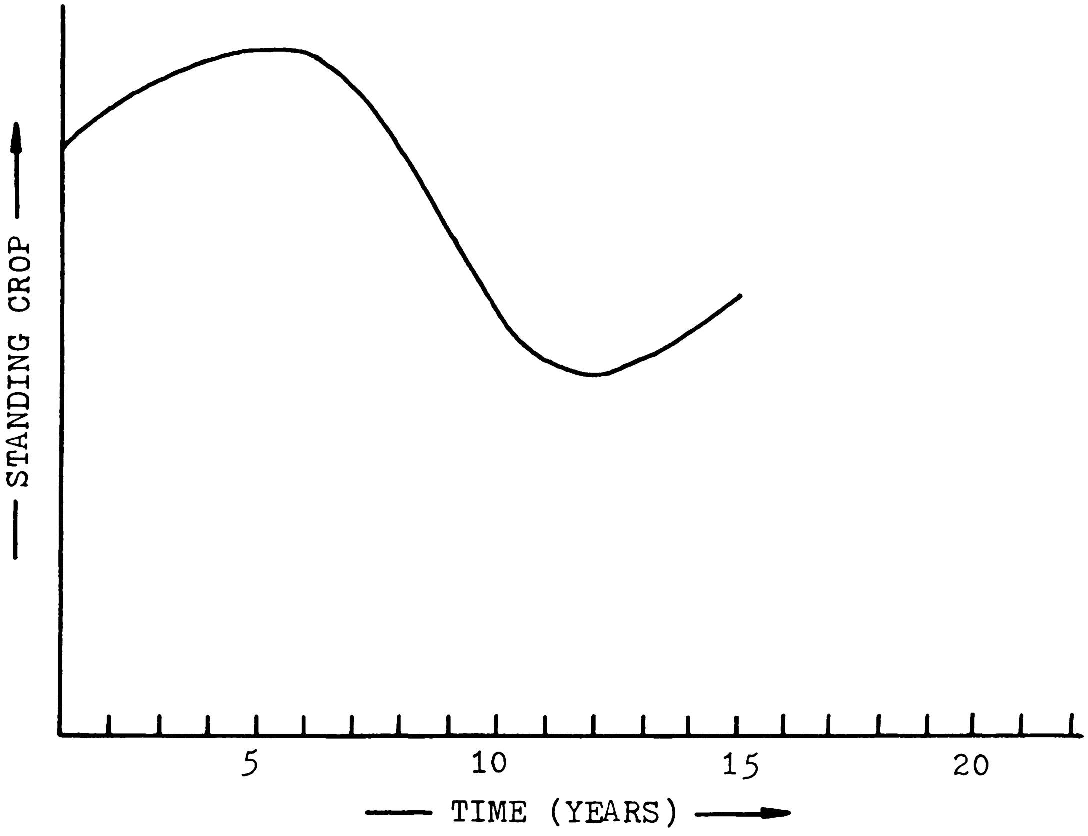

Fig. 40. Successional change in standing crop of macrobenthos in a newly impounded reservoir.

THE MACROBENTHOS OF A NEW RESERVOIR, LAKE ANNA, LOUISA COUNTY, VIRGINIA

by

Joseph Reese Voshell, Jr.

(ABSTRACT)

The macrobenthos of a new reservoir in central Virginia, Lake Anna, was studied for the first three years after impoundment, 1972-1975. Prior to this, extensive macrobenthic collections had been made in the river destined for impoundment, the North Anna River. The biota of this river had been seriously affected by acid mine drainage for over 100 years.

Macrobenthos consists of the organisms living on the bottom or the solid-liquid interface. The occurrence of these organisms is significant, because they are major items in the diet of many fish, and are thus important in the flow of energy through an ecosystem. The basic objectives of this study were to determine the changes in macrobenthic community structure brought about by impoundment, and then to observe the successional changes which occurred in the following years. This information was then compared to a hypothetical model predicting the productivity of new reservoirs.

It was discovered that traditional grab sampling was not reliable in new reservoirs because of the abundant submerged terrestrial vegetation. An original sampling method was developed which involved the use of SCUBA to place and retrieve artificial substrate samplers. This SCUBA method was compared to grab sampling, and found to more reliably estimate macrobenthic community structure.

Following impoundment, there was an immediate change in macrobenthic community structure. Colonization of the new reservoir occurred very quickly, especially during the first summer period. The acid mine drainage did not affect the distribution of macrobenthos in the new reservoir, probably because of dilution. Identification of over 525,000 organisms revealed that they could be classified into three groups: first colonizers, omnipresent species, and second colonizers. A review of the food habits of these organisms indicated that there were four trophic functional groups: micropredators, macropredators, collector-microgatherers, and collector-microfilterers. The first colonizers consisted of three species, one of which was completely dominant in each of the first three functional groups the first year. The second colonizers consisted of many additional species, several of which shared dominance in each of the same three functional groups the second and third years. The omnipresent group consisted of midge larvae which were dominant in the fourth functional group, collector-microfilterers, in all three years.

This information, in conjunction with analysis of the horizontal, vertical, and temporal distribution, indicated

that the development of macrobenthic community structure in Lake Anna followed the general trends expected in ecological succession. These trends are increased number of species, increased equitability of species composition, and better organization of distribution. A comparison of the development of macrobenthos in new reservoirs with a model of expected productivity indicated that the abundance of macrobenthos may also exhibit the same trends as productivity. These trends are an initial increase in productivity for several years, followed by a sharp decline for several years, to be finally followed by a small increase and stabilization. This sequence of events probably requires at least 15 years for macrobenthos.