

DISTRIBUTION, PRODUCTION, AND UTILIZATION OF THE BENTHIC  
MACROINVERTEBRATE FAUNA OF IMPERIAL RESERVOIR ON THE  
LOWER COLORADO RIVER, YUMA COUNTY, ARIZONA

by

Terence Patrick Boyle

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A Dissertation Submitted to the Faculty of the

SCHOOL OF RENEWABLE NATURAL RESOURCES

In Partial Fulfillment of the Requirements  
For the Degree of

DOCTOR OF PHILOSOPHY  
WITH A MAJOR IN FISHERIES SCIENCE

In the Graduate College

THE UNIVERSITY OF ARIZONA

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THE UNIVERSITY OF ARIZONA  
GRADUATE COLLEGE

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## ACKNOWLEDGMENTS

I would like to extend my appreciation to my committee for their advice and critical reading of my dissertation. Dr. Foster Mayer also kindly read and helped advise the dissertation writing. I would like to especially thank Robert Hallock, Steven Alcorn and my wife, Susan, for aid in the field work, Janet Henry and Hazel Gillie for typing several drafts and the final typing, Dr. Jeanne Sebough for her help with the statistics, Phillip Lovely and my wife, Susan, for their work on figures, and the Arizona Department of Game and Fish for their financial support and use of facilities at Imperial Reservoir.

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## ABSTRACT

Data for a study of the benthic macroinvertebrates in Imperial Reservoir in Yuma County, Arizona was collected 1970-1973. Imperial Reservoir is an old, heavily sedimented reservoir on the lower Colorado River. An extensive dredging program revealed that the benthic habitat supported a low number of invertebrate species (four insects and two oligochaets) in comparison to other bodies of water. Probable reasons for the low number of species included high salinity, low organic detrital input into the reservoir, low habitat and substrate diversity, temporary low dissolved oxygen concentration, possible contamination with agricultural chemicals, and the remoteness of Imperial Reservoir from other aquatic environments.

Within Imperial Reservoir the benthic macroinvertebrate community was restricted to more isolated, calm, side lakes which altogether made up only 23% of the entire surface area of the reservoir. Within these side lakes benthic macroinvertebrates were found primarily on mud substrate. Invertebrates were not found beneath dense stands of Najas marina, a rooted submersed macrophyte. Only two species of invertebrates appear to inhabit rocky substrates. Community analysis suggested that there were no large differences among most habitats where benthic invertebrates were found.

A study of the microdistribution of each species of invertebrate indicated that there were two patterns of spatial dispersion:

(1) taxa which bred continuously appeared to have no life history related change in dispersion; and (2) taxa which formed recognizable cohorts appeared to spread out from initial egg mass and dispersion changed with time from clumped to random.

Secondary net production measures were made directly on predominant benthic invertebrates at two sites in Imperial Reservoir. Both sites had similar production values which were low when compared to production values from other bodies of water. Low benthic production in Imperial Reservoir was related to several environmental factors including high water temperature and temporary low oxygen concentration near the bottom during the summer, low input of organic detritus into the reservoir, and high predation on benthic invertebrates by fish.

Collection and analysis of the stomach contents of the bass, bluegill and redear sunfish revealed that the smaller fish of a species were more dependent on benthic invertebrates for food. Large bass did not use benthic invertebrates as heavily as either bluegill or redear.

## INTRODUCTION

Shallow aquatic ecosystems are among the most productive in the world (Odum 1971). The primary and secondary productivity of the benthic areas are especially important in small lakes and reservoirs due to their relative shallowness and high shoreline to surface area ratio (Hargrave 1969; Wetzel 1964; Winberg 1972). In a review of the hydrobiological research areas, Ivlev (1966) identified benthic invertebrates as a particularly important group of organisms in the bioenergetics of shallow lentic ecosystems. Benthic invertebrates function in ecosystems as herbivores, feeding directly on algae and aquatic macrophytes; as carnivores feeding on other invertebrates and small fish; and as detritivores, feeding on the decomposing organic material in benthic hydrosols (Cummins 1973). They are also responsible for re-suspending inorganic plant nutrients from the bottom muds into the water column (Brinkhurst 1972). Aquatic macroinvertebrates are classed as secondary producers (Winberg 1971; Edmonson and Winberg 1971), occupying a place in a general trophic pyramid between photosynthetic primary production and fish production. Secondary production estimates defy the facile community analysis possible in planktonic primary production since there is no single measurement such as radioactive carbon uptake or changes in dissolved oxygen concentration that can characterize the energetics of the community. Each of the populations, for at least the predominant taxa, must be individually assessed.

Many studies have been made on the composition of benthic fauna in north temperate lakes and reservoirs (Kajak 1960a, 1960b, 1963, 1964a, 1964b, 1972; Jonasson 1965, 1972; Thut 1969; Johnson and Brinkhurst 1971). Ball (1948), Allen (1951), Gerking (1954, 1962), Hayne and Ball (1956), and Hall, Cooper and Werner (1970) are examples of important studies that have shown benthic macroinvertebrates to be an important food of fish in streams and shallow lakes. However, relatively few direct secondary benthic production estimates have been done and most of these deal with a single predominant species (Anderson and Hooper 1956; Borutzky 1939; Cooper 1965; Jonasson 1972; Johnson and Brinkhurst 1971; Kajak and Ryback 1966; Kajak, Hillbricht-Ilkowska and Pieczuska 1972; Neess and Dugdale 1966).

There remains the need to study the production of benthic macroinvertebrates in relation to ecological distribution. This is especially important in reservoirs where benthic habitat is more diverse than in lakes. Moreover, the fisheries of smaller reservoirs rely heavily on the benthic fauna as a food source (McConnell 1971).

Imperial Reservoir, Yuma County, Arizona, chosen for this study of benthic macroinvertebrates, is typical of older reservoirs with reduced volume and depth due to sediment deposition. The encroachment of aquatic vegetation and the fouling of outlet gates and irrigation structures by river-born silt make it likely that some mitigation projects will take place in the future. Almost all man-made changes in the reservoir through dredging and channelization cause changes in the bottom, and these changes directly affect one of the most important groups of fish food organisms, the benthic fauna.

Imperial Reservoir and others like it still contain valuable fishery and wildlife resources. It currently supports a popular, productive sport fishery (0.5 fish per man hour, Weaver 1971), and this fishery should be considered in any future plans for changing this reservoir. Basic studies are needed to better understand the ecological basis for support of these valuable biological resources.

The objectives of this study are: (1) to determine the type of benthic habitat supporting benthic macroinvertebrates and the factors affecting distribution; (2) to estimate the secondary net production of the predominant invertebrate taxa; and (3) to estimate the importance of benthic invertebrates to the fishery.

## MATERIALS AND METHODS

### Description of the Study Area and Vegetation Characteristics

Imperial Reservoir is located on the Colorado River at longitude 114°27'; latitude 32°43' in the lower Colorado desert, which averages 9 cm. of precipitation per annum and has an annual evaporative column of 264 cm. (Sellers and Hill 1974). The Bureau of Reclamation built the dam in 1938 creating a reservoir intended principally for storage. The initial size was 7,800 acres (2,955 hectares) with a capacity of 85,000 acre-feet ( $1.05 \times 10^8 \text{ m}^3$ ) (California Department of Water Resources 1968). The heavy silt load of the Colorado River quickly reduced the original capacity until today the dam acts solely to divert irrigation waters east to the Yuma and Mohawk-Welton area in Arizona and west to the Imperial Valley of California.

The water level of the reservoir is controlled by the outlet of water through dams upstream and the diversion of water into the irrigation channels at Imperial Dam. Fluctuation of the water level in the reservoir amounts to less than 0.6 m., and only rarely does water go over the dam.

Much of the reservoir, formerly open water, has become filled with sandbars and islands which have been colonized and stabilized by dense stands of rooted emergent vegetation. The physiognomy of the reservoir is similar to a river delta or a coastal marshland and can be divided into three main features: (1) river channels with



substantial currents and sand bottoms (22% surface area); (2) dense stands of emergent vegetation -- mainly cattails (Typha latifolia) with rushes (Scirpus spp.) and reeds (Phragmitis communis) widespread (55% of surface area); and (3) small lakes separated from the river channels by beds of T. latifolia or formed from the mouths of submerged arroyos along the margin of the reservoir (23% of surface area).

Weaver (1971) and Hallock (1973) noted the hypertrophic nature of the reservoir. The range of benthic soils in Imperial Reservoir can be classified as sand in the bottom of river channels, sapropel and claycolloid ooze in the bottoms of side lakes and gravel-boulder along some shorelines (Veatch 1931).

#### Chemical-physical Measurements

Dissolved oxygen concentrations and temperatures were measured with a polarographic-thermister probe (YSI model 54) and hydrogen ion measurements were taken with a portable pH meter (Beckman model 1009). These measurements were from surface water and water from the mud-water interface. Percent light transmission was measured at the bottom of two side lakes with a submarine photometer, and transparency was measured with a Secchi disc. Phleger core samples taken in summer and winter from different sites were observed for depth of soil oxygenation as indicated by the division between gray and black soil and thickness of bottom type. In order to estimate the effect of proximity to the river one composite hydrosol sample was taken from three places in the reservoir and tested by the Agricultural Experiment Station, University of Arizona for percent dry weight of carbon, nitrogen, and phosphorus and mechanical analysis.

## Benthic Macroinvertebrates

### Distribution

The general distribution of benthic macrofauna was determined in six benthic habitates of Imperial Reservoir.

1. River channels with substantial currents and sand bottoms.
2. Submerged sand bars.
3. Beneath rooted submersed vegetation.
4. Edge of rooted emergent vegetation.
5. Small lakes around the margin of the reservoir.
6. Submerged mud flats near the dam.

A series of Ekman dredge samples were taken in these habitats throughout the Reservoir on nine dates between July 1970 and March 1971. The benthic macroinvertebrates were collected by washing the samples in a number 30 mesh (0.5 mm pore size) screen-bottomed bucket. The invertebrates were separated from debris retained by the sieve using a sugar-floatation method (Anderson 1959). Results of this initial distribution survey were used to select eight sample sites (Fig. 1) from among small lakes on the margin of the reservoir. These sites were selected to represent a range of habitat factors in Imperial Reservoir which included: (1) percentage of shoreline occupied by dense cattail beds; (2) area and depth of sample site; (3) degree of potential exchange with a main channel; (4) presence of rooted submerged macrophytes at sample sites; and (5) presence of rock or mud substrates (Table 1).

Sites 1 and 8 represent the extremes of several habitat factors shown in Table 1. Both sites were sampled with 20 dredge samples

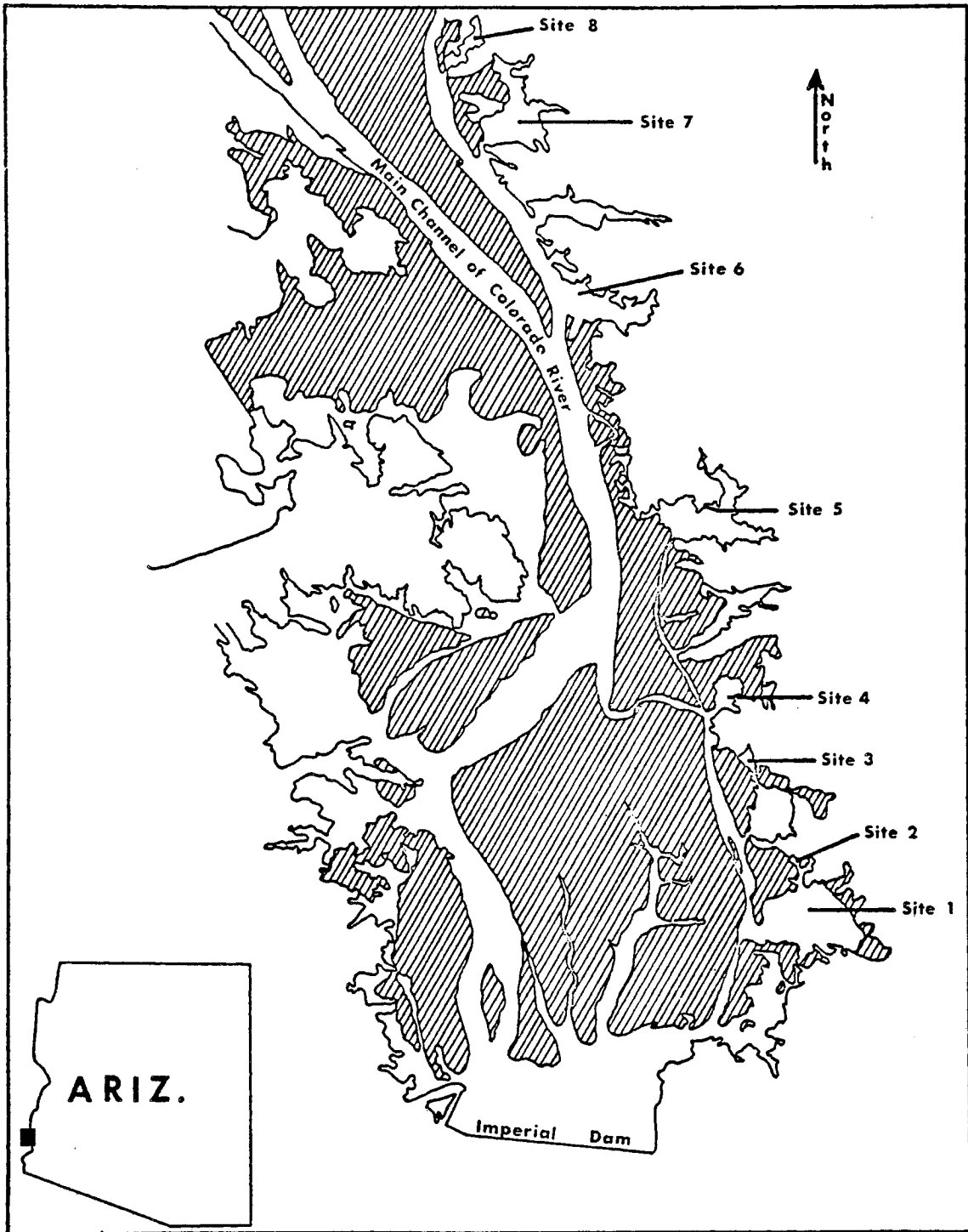


Figure 1. Map of Imperial Reservoir showing the eight sample sites. -- The shaded area represents major beds of Typha latifolia. Linear scale is provided by the dam which is one-half mile long.

Table 1. Summary of habitat quality and physical factors of eight sampling sites in Imperial Reservoir.

Site	Area in Hectares	Depth of Benthic Zone Sampled	% Shoreline with Rooted Vegetation	Distribution of <u>Najas marina</u>	Connection with Main Channel
1	25.4	4 m	94	Marginal, to 1 m deep	Inlet 15 m wide, Outlet 2 m wide
2	1.3	2 m	33	Complete cover	Inlet 4 m wide*
3	1.3	3 m	40	Marginal, to 1 m deep	Inlet 3 m wide*
4	5.3	2 m	66	Clumps with bare areas	Inlet 10 m wide
5	23.5	4 m	0	None present, rocks	Long narrow channel 2-4 m wide
6	12.9	4 m	0	None present	Inlet 25 m wide
7	16.9	3 m	16	Clumps with bare areas	Inlet 3 m wide
8	4.0	4 m	0	None present	Inlet 1.5 m wide

\*Indicates sample site reached from main channel. only by passing through another body of water.

biweekly from March 1971 to March 1972. Site 1 was a larger side lake (25.4 ha) with water from the main channel entering on the west side and leaving through an outlet on the south. The lake was surrounded by a nearly continuous stand of T. latifolia and the shore composed mostly of mud. The bottom was relatively flat; the deepest point was 4 m. Site 8 was one of the smaller lakes (4.0 ha) and water exchange occurred with the river through a narrow shallow opening which was frequently blocked by a sand bar. The shores were steep and rocky with scanty marginal vegetation. The maximum depth was 4 m. Sites 2, 3, 4, 6, and 7 were sampled in December 1971 and July 1972 to provide a comparison of taxa among side lakes with different habitat qualities intermediate to those at Sites 1 and 8.

In order to determine the occurrence of benthic organisms on rock substrates, 12 polyethylene tubs (40 cm. long x 30 cm wide x 18 cm. deep) filled with local rocks were submerged at Site 5 in April 1972. Four tubs were removed August 1972 and in January and April 1973. The rocks were scraped over a screen-bottomed bucket and the invertebrates were separated as was done with the Ekman dredge samples. Invertebrates were identified using keys in Pennak (1953), Usinger (1956), and Bryce and Hobart (1972). Dr. Donald Webb of the Illinois Natural History Survey, University of Illinois, Urbana, kindly corroborated in the insect sample identification.

Once during the summer of 1972, several individuals from each taxa were dissected and the intestinal contents smeared on a glass slide and examined under a microscope.

## Production

Production estimates were based on the samples taken from Sites 1 and 8. The benthic organisms from each Ekman dredge sample were separated by taxon, counted, and dried at 60°C for 24 hours, weighed on a Mettler balance to the nearest 0.1 mg, ashed in a muffle furnace at 600°C for 0.5 hour, and the ash reweighed to determine the ash-free dry weight. A direct production estimate was calculated when a given taxon was found in distinct cohorts. Where the end of one generation overlapped with the beginning of another, they were separated on the basis of head capsule width of the instars.

Two computation procedures were used to calculate net production (MacFayden 1949). The first equation used was after Edmonson and Winberg (1971). Production for an interval of time was determined by:

$$P = \frac{N_t + N_o}{2} (\bar{W}_t - \bar{W}_o),$$

where  $N_o$  is the mean number of individuals within a taxon in a series of samples;  $N_t$  is the mean of a subsequent series of samples; and  $\bar{W}_o$  and  $\bar{W}_t$  their respective mean weights. The second net production estimate was calculated as:

$$P_i = G(B),$$

where  $P_i$  is the net production for the time interval,  $t$ ,  $G$  is the coefficient of growth in weight (specific growth rate) during  $t$  determined as:

$$G = \ln W_t - \ln W_o$$

and  $B$  is the mean standing crop during the sample interval (Ricker 1946; Allen 1951; Chapman 1968).

## Utilization

Utilization of benthic organisms by fish was estimated by analysis of the stomach contents of redear sunfish (Lepomis microlophus), bluegill sunfish (Lepomis macrochirus) and largemouth bass (Micropterus salmoides). The fish were obtained monthly (July 1972 to July 1973) at Site 1 by electrofishing shortly after dusk with the aid of floodlights. Fifteen fish (>6 cm) of each species were sampled per time. The total length of each fish was measured to the nearest centimeter. Stomachs were removed within an hour of capture and preserved in formalin.

Food analysis was done by identifying the organisms in stomach contents to the lowest possible taxon, and by determining relative food volume using the points method (Hynes 1950). Each food item was assigned a number of points depending on the size of the organism and the number present. The base for comparison was the fourth instar of Clinotanypus spp. which was assigned one point. The points were considered only in geometric progression (i.e., 1, 2, 4, 8, 16, etc.).

## Statistical Analysis

The statistical methods of determining means, confidence intervals, correlations, and contingency tables were performed after Steel and Torrie (1960). The non-parametric Spearman ranked correlation coefficient was used when exact quantities could not be assigned to a variable or when there seemed to be a risk involved assuming a bivariate normal distribution of a variable (Siegel 1956). The dispersion pattern, or microdistribution, of benthic invertebrates was

analyzed for the samples taken at Sites 1 and 8 using the variance to mean ratio and Morisita's index of aggregation ( $I\sigma$ ) (Elliott 1971; Poole 1974). The biannual distribution data was analyzed for recurrent taxa with the geometric mean of the proportion of joint occurrences based on presence or absence of taxa in an individual dredge sample (Fager 1957; Fager and Longhurst 1968; Fager and McGowan 1963).



## RESULTS

The results section is divided into four main parts: (1) the study area vegetative characteristics affecting benthic macroinvertebrates; (2) the distribution of benthic macroinvertebrates; (3) the production of selected predominant invertebrates; and (4) the utilization of benthos by three species of fish.

### Vegetative Characteristics

Because of changes over time, vegetative characteristics are best considered within the concept of succession. Vegetative succession in Imperial Reservoir can be described in two time frames: changes which occurred with the annual change of seasons; and changes in vegetational physiognomy of the reservoir that occurred through the years. Seasonal succession began in late March when epibenthic algae, mainly filamentous diatoms, formed mats 3 to 5 cm thick. The water column at this time was relatively transmissive to light (Figs. 2 and 3).

Rooted submersed vegetation, Najas marina, and rooted emergent vegetation began to grow in shallow water in April. N. marina formed dense monospecific stands in all calm waters to a depth of about 1.5 m except over rock substrates. Some growth of N. marina occurred deeper in areas sheltered from river currents and wind turbulence. Peak biomass of this macrophyte occurred in August. Growth slowed in August, stopped in September, and then the plants died by November. Typha

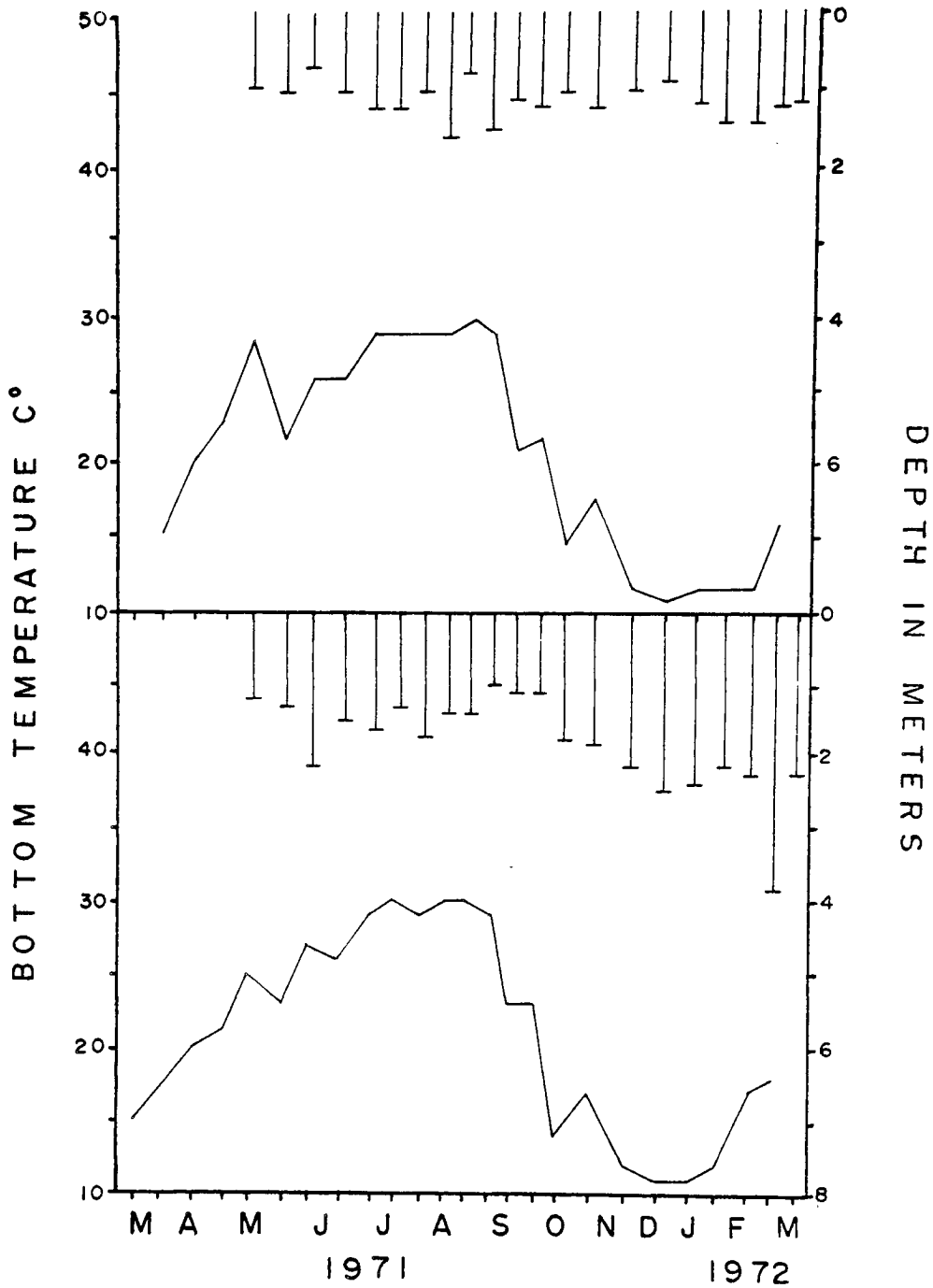


Figure 2. Annual bottom temperature at Site 1 (upper graph) and Site 8 (lower graph). -- Secchi disc depth are represented by lines suspended from the top of the figures.

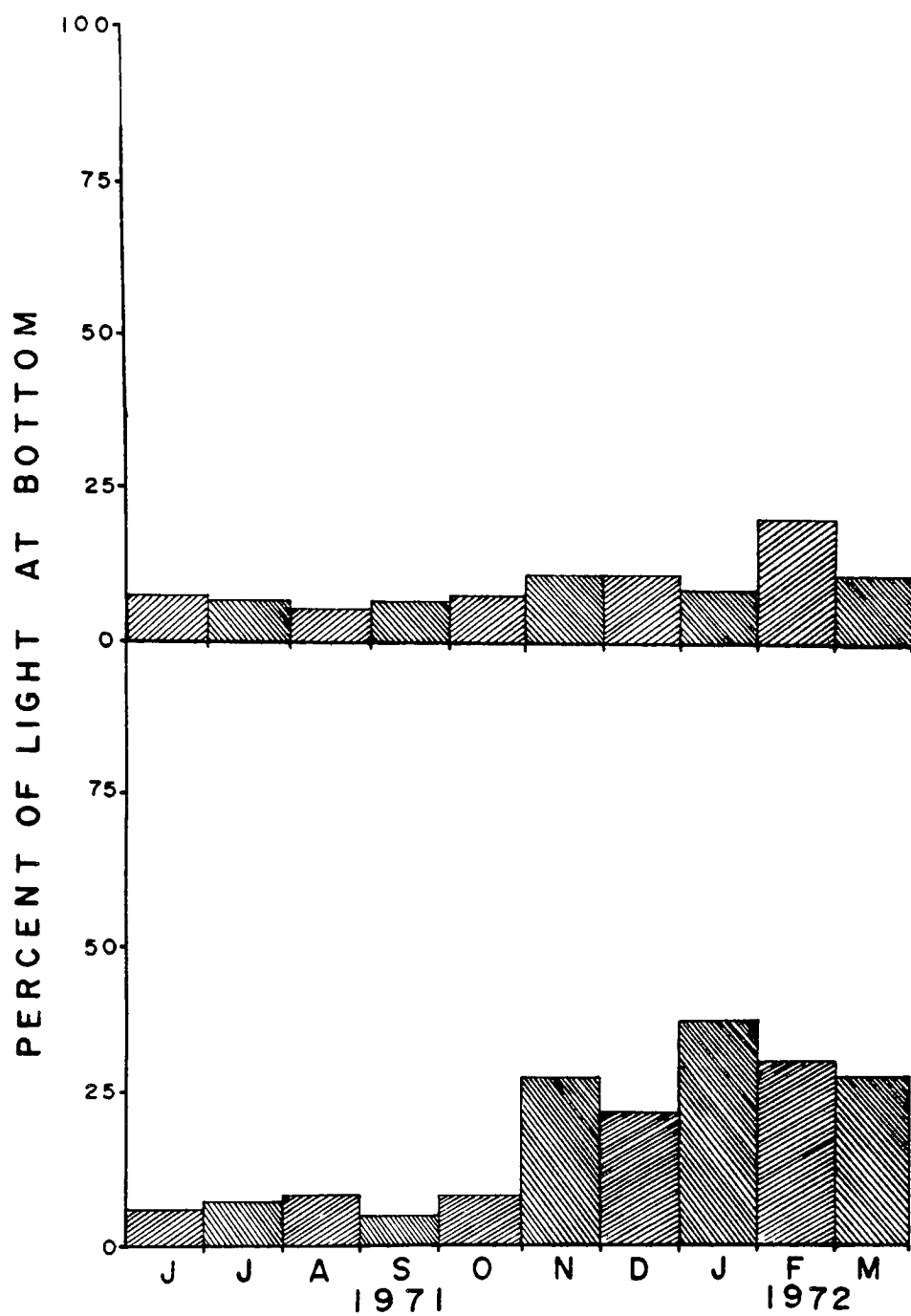


Figure 3. Monthly means of percentage light measured at the bottom relative to the surface. -- Upper histogram represents Site 1, lower histogram represents Site 8.

latifolia had a growth pattern similar to N. marina, however after the autumn die-off the leaves remained standing.

The major factors affecting perennial vegetational succession were the deposition of sediment and the formation of sand bars which were colonized by T. latifolia. This process resulted in encroachment of open water by beds of submersed and emergent rooted vegetation, the choking of smaller channels with vegetation and sediment, and the increased isolation of small areas of water in the center of the reservoir, and especially at the mouths of drowned arroyos.

#### Chemical-physical Characteristics

The mechanical analysis of sediment samples showed that Sites 1 and 8 were composed mainly of river born silt (Table 2). These two sites were typical of side lakes immediately adjacent to the river. Site 2 was typical of more isolated backwaters and was shallower and more separated from the river. The hydrosol consisted of primarily coarse sand (Table 2). Site 2, which was covered by N. marina in the growing season, had less nitrogen, phosphorus, and carbon than Site 1 or 8, where N. marina was very scarce.

Bottom core samples taken during the summer at Sites 1 and 8 showed an anoxic layer, indicated by a zone of black sulfide, 2 to 3 cm down from the hydrosol-water interface. During the winter this anoxic layer was 6 or more centimeters deep. This annual pattern was reversed under dense stands of N. marina at Site 2. In the summer the root system oxygenated the benthic soil to a depth of at least a meter. After death of the macrophytes, in the autumn, the anaerobic layer came to within 2-3 cm of the hydrosol-water interface.

Table 2. Nutrient and mechanical analysis of hydrosol in three sample sites in Imperial Reservoir.

Site	Characteristics					
	% N	% P	% C	% Sand	% Silt	% Clay
1	1.05	0.1510	.32	13.6	77.9	8.5
2	0.46	0.0124	.12	86.3	11.2	2.5
8	2.77	0.0489	1.83	11.0	62.0	20.0

Dissolved oxygen measurements taken during the day were generally at or above saturation throughout the water column, averaging 8.6 mg/l in the growing season and 10.6 mg/l during the winter months. Little difference existed between oxygen measurements taken at the surface and those taken at the mudwater interface during the day. However, predawn samples showed that respiration was much greater near the mudwater interface than at the surface, and at times the oxygen concentration levels fell to 1 mg/l (Hallock, personal communication 1975).

At Sites 1 and 8 pH measurement ranged from 7.4 to 8.5 with only one value below 8.1. The pH 7.4 was observed at Site 1 when the rooted macrophytes died in the fall.

The annual pattern of bottom water temperature for Sites 1 and 8 is shown in Figure 2. Thermal stratification was infrequent and weakly developed due to currents and frequent strong winds. Only once was the difference between top and bottom temperature as great as 3°C and this occurred in the more protected Site 8.

Light measurements taken at Sites 1 and 8 show that the water column was more transmissive in the winter and that the water in Site 8 was somewhat clearer than Site 1 (Figs. 2 and 3). The trophic status of Imperial Reservoir was calculated using Secchi disc data and a trophic state index (TSI) (Carlson 1977). The TSI is based on an empirical relationship between the transparency of the water, the concentration of chlorophyll extracted from phytoplankton, and the total phosphorous concentration of the water. The TSI of Imperial Reservoir in the warmer months (April-October) fell between 60 and 70, which indicated a highly eutrophic condition.

## Benthic Macroinvertebrates

### Taxa Life History

Four taxa of insects of the order Diptera, Clinotanypus sp., Chironomus plumosus, Pentaneura sp., and Chaoborus punctipennis, and two aquatic annelid worms of the class Oligochaeta, Limnodrilus hoffmeisteri and Branchiura sowerbyi were found in Eckman dredge samples taken July 1970 through February 1971. The taxonomy of dipterans in general and especially aquatic species of the family Chironomidae is difficult and poorly worked, therefore, two of the larvae could only be identified as a species form (sp.). For clarity in subsequent discussions in this text the taxa will be referred to by their generic names.

The general life cycle of all insects was similar. The imago form was aerial, non-feeding and short-lived. The eggs were laid in masses or singly, either on the waters' surface, attached to an object in the water, or injected into the water while the imago clung to an object on the surface. The eggs developed where they fell on the bottom, and the larval stage consisted of four instars, with each instar being larger in size and longer in duration than those preceding. The fourth instar metamorphosed into a pupa which swam to the surface of the water, shed its pupal exoskeleton, and metamorphosed into an imago or adult form.

Insects in the family Chironomidae, Clinotanypus sp., Chironomus plumosus and Pentaneura sp., appeared to feed on both detrital material and numerous forms of algae (Table 3). Some forms of

Table 3. Qualitative analysis of gut contents of three Chronomid larvae during August 1971. -- An X indicates presence.

Material Found in Gut	<u>Clinotanypus</u> sp.	<u>Chronomus plumosus</u>	<u>Pentaneura</u> sp.
Detritus particles	X	X	X
Algal Taxa			
<u>Nitzschia</u>		X	
<u>Cymbella</u>	X	X	X
<u>Gomphonema</u>		X	
<u>Achnanthes</u>	X	X	
<u>Navicula</u>		X	
<u>Diploneia</u>		X	X
<u>Fragilaria</u>	X	X	X
<u>Hydrocera</u>	X	X	



Pentaneura are also described as predaceous (Pennak 1953). Chaoborus punctipennis, of the Dipteran family Culicidae, was a member of the benthic community by day and ascended into the water column to feed during the night. The individuals examined either had their stomachs empty or everted. Jonasson (1972) reports Chaoborus, preying on zooplankton in the water column.

Both Oligochaet worms belonged to the family Tubificidae. The variation in the size of individuals within a single Ekman dredge sample implied that breeding was, if not continuous, at least, intermittent throughout the year.

Five of the taxa collected exhibited varying shades of red due to coloring by haemoglobin-like respiratory pigments which would enable them to survive at low oxygen tensions. Other adaptations to near anoxic conditions were the external gill filaments present on Chironomus plumosus and especially well developed on Branchiura sowerbyi. Chaoborus punctipennis was the only benthic dweller collected which did not exhibit morphological or physiological adaption to low oxygen conditions, however, it could escape low oxygen tensions near the bottom at night by swimming into the overlying water.

### Distribution

Three aspects of invertebrate distribution were considered in this study: (1) macrodistribution -- the determination of which habitat types in Imperial Reservoir supported populations of benthic macroinvertebrates; (2) biannual distribution patterns in small side lakes of the reservoir to determine what factors affected presence of individual taxa of benthic macroinvertebrates; and (3) distribution of

benthic macroinvertebrates at Sites 1 and 8 through time and changes in dispersion pattern, or microdistribution.

Macrodistribution. No benthic macroinvertebrates were found in any of the samples from sand bars (Table 4) although the shells of recently dead asiatic clams, Corbicula fluminea, appeared when the water level was lowered for any length of time. Clams found in the reservoir were not collected by the Ekman dredge sampling. Distribution was inferred from observation of shells on sand bars and local isolated beds of live clams found on the edge of channels where the current was swift. Ekman dredge samples from the edge of rooted emergent vegetation showed few benthic insects or oligochaet worms and only in samples from mid-summer (Table 4). No benthic macroinvertebrates were found beneath rooted submersed macrophytes or on the bottoms of river channels. However, after the plants died in the autumn, a population of Chironomus appeared in some places formerly covered by N. marina. The general habitat type consistently supporting heaviest population of benthic macroinvertebrates was the bottom of small lakes located around the edge of the reservoir.

Biannual Distribution. During the summer benthic insect larvae were found at seven sampling sites (1, 3-8). At this time Site 2 was covered by a dense mat of the rooted submersed macrophyte, N. marina and no insects were found. Clinotanypus sp. occurred at all sampling sites except at Site 2 and Site 5 where the substrate was composed of rock (Table 5). Chironomus occurred at all sites except under beds of N. marina at Site 2. It was also the only insect found in the rocky

Table 4. Reservoir wide distributional sampling in six different habitat types. -- First number in numerator of ratio is the number of Ekman dredges with Chironomid larvae, the second the number with Oligochaet worms and the denominator is the total number of Ekman samples taken in that habitat on the date shown to the left.

	River Channels	Sand Bars	Edge of Rooted Emergents	Beneath Najas marina	Peripheral Lakes	Submerged Mud Flats
7/25	$\frac{(0)(0)}{5}$	$\frac{(0)(0)}{5}$	$\frac{(1)(2)}{5}$	$\frac{(0)(0)}{5}$	$\frac{(5)(5)}{5}$	$\frac{(0)(0)}{5}$
8/15	$\frac{(0)(0)}{5}$	$\frac{(0)(0)}{5}$	$\frac{(1)(0)}{5}$	$\frac{(0)(0)}{5}$	$\frac{(5)(4)}{5}$	$\frac{(0)(0)}{2}$
9/5	$\frac{(0)(0)}{3}$	$\frac{(0)(0)}{3}$	$\frac{(0)(0)}{2}$	$\frac{(0)(0)}{3}$	$\frac{(10)(10)}{10}$	
9/26	$\frac{(0)(0)}{2}$	$\frac{(0)(0)}{2}$	$\frac{(0)(0)}{2}$	$\frac{(0)(0)}{3}$	$\frac{(15)(12)}{15}$	
10/17	$\frac{(0)(0)}{2}$	$\frac{(0)(0)}{2}$	$\frac{(0)(0)}{2}$	$\frac{(0)(0)}{2}$	$\frac{(14)(13)}{15}$	
11/7	$\frac{(0)(0)}{2}$	$\frac{(0)(0)}{2}$	$\frac{(0)(0)}{2}$	$\frac{(0)(0)}{2}$	$\frac{(12)(14)}{15}$	
12/5	$\frac{(0)(0)}{2}$	$\frac{(0)(0)}{2}$	$\frac{(0)(0)}{2}$	$\frac{(2)(0)}{2}$	$\frac{(14)(13)}{15}$	
1/30	$\frac{(0)(0)}{2}$	$\frac{(0)(0)}{2}$	$\frac{(0)(0)}{2}$	$\frac{(2)(0)}{2}$	$\frac{(12)(13)}{15}$	
2/20	$\frac{(0)(0)}{2}$	$\frac{(0)(0)}{2}$	$\frac{(0)(0)}{2}$	$\frac{(2)(0)}{2}$	$\frac{(12)(15)}{15}$	

Table 5. Biannual distribution of benthic macroinvertebrates at eight sites in Imperial Reservoir. -- Values indicate the number of Ekman samples out of a total of five that contained individuals of that group. An asterisk indicates presence in rock filled tubs. Site 7 was not sampled during winter.

Taxon	Sample Site							
	1	2	3	4	5	6	7	8
	<u>Summer Samples</u>							
<u>Clinotanypus</u>	5	0	3	2	0	2	3	5
<u>Chironomus</u>	4	0	1	2	*	3	3	1
<u>Pentaneura</u>	2	0	0	1	0	0	0	0
<u>Chaoborus</u>	0	0	2	0	0	0	1	4
<u>Limnodrilus</u>	3	0	2	2	*	3	1	3
<u>Branchiura</u>	4	0	1	2	0	2	0	0
	<u>Winter Samples</u>							
<u>Clinotanypus</u>	5	0	4	2	0	3	-	5
<u>Chironomus</u>	0	4	5	3	*	3	-	5
<u>Pentaneura</u>	0	0	0	1	0	0	-	5
<u>Chaoborus</u>	0	0	1	0	0	0	-	5
<u>Limnodrilus</u>	1	0	2	3	*	3	-	2
<u>Branchiura</u>	5	0	2	3	0	2	-	0

area. Populations of Chironomus did appear at Site 2 in the winter sampling. Pentaneura appeared in samples at Sites 1, 4, and 8. Chaoborus was found at only Sites 3, 7, and 8 in the summer and Sites 3 and 8 in the winter. The Oligochaet worm, Limnodrilus was found summer and winter in all samples but those from Site 2. The gilled Oligochaet Branchiura had an identical pattern summer and winter, and was found at Site 1 in nearly all samples, less frequently at Sites 3, 4, and 6, and not found at all in samples from Sites 7 and 8 (Table 5).

The sample sites were ranked according to the distribution data in Table 5 and the information on the area, percent of marginal vegetation, and potential for water exchange with the main channel as appears in Table 1. The association of the three environmental variables with the distribution of each taxa collected in the summer-winter distributional samples was tested with Spearman's rank correlation coefficient (Table 6).

Size of sample site was correlated significantly ( $P < 0.05$ ) only with Chironomus and only for the summer data. Percent of shore with rooted vegetation showed a positive correlation ( $P < 0.05$ ) only with Pentaneura and only in summer. In the summer collections, potential exchange with the main channel was significantly positively correlated ( $P < 0.05$ ) with Chironomus, Limnodrilus, and Branchiura. In the winter collection, only Branchiura appeared to have a significant positive correlation and Chironomus showed a significant negative correlation with potential exchange with the main channel.

Taxa with similar distribution in time and space suggest similar environmental requirements, possible interdependence, or similar

Table 6. Spearman rank correlations ( $r_s$ ) of summer and winter distribution of the six taxa with the sample sites arranged in three gradients. -- I ranked by size in acres, II ranked by percent of shore with dense marginal vegetation, and III ranked by potential for exchange of water with the main channel. Upper value is the  $r_s$  with the significance level below.

	I Size of Site	II % Margin with Heavy Vegetation	III Ranked Association with River
	<u>Summer</u>		
<u>Clinotanypus</u>	$\frac{.18}{\text{N.S.}}$	$\frac{-.62}{\text{N.S.}}$	$\frac{.15}{\text{N.S.}}$
<u>Chironomus</u>	$\frac{.93}{.01}$	$\frac{.27}{\text{N.S.}}$	$\frac{.78}{.05}$
<u>Pentaneura</u>	$\frac{0}{\text{N.S.}}$	$\frac{.83}{.05}$	$\frac{.67}{\text{N.S.}}$
<u>Chaoborus</u>	$\frac{-.39}{\text{N.S.}}$	$\frac{-.49}{\text{N.S.}}$	$\frac{.55}{\text{N.S.}}$
<u>Limnodrilus</u>	$\frac{.36}{\text{N.S.}}$	$\frac{-.13}{\text{N.S.}}$	$\frac{.71}{.05}$
<u>Branchiura</u>	$\frac{.47}{\text{N.S.}}$	$\frac{.49}{\text{N.S.}}$	$\frac{.73}{.05}$
	<u>Winter</u>		
<u>Clinotanypus</u>	$\frac{.38}{\text{N.S.}}$	$\frac{.28}{\text{N.S.}}$	$\frac{.44}{\text{N.S.}}$
<u>Chironomus</u>	$\frac{-.69}{\text{N.S.}}$	$\frac{-.62}{\text{N.S.}}$	$\frac{-.88}{\text{N.S.}}$
<u>Pentaneura</u>	$\frac{.03}{\text{N.S.}}$	$\frac{.34}{\text{N.S.}}$	$\frac{.03}{\text{N.S.}}$
<u>Chaoborus</u>	$\frac{.07}{\text{N.S.}}$	$\frac{-.51}{\text{N.S.}}$	$\frac{.54}{\text{N.S.}}$
<u>Limnodrilus</u>	$\frac{.24}{\text{N.S.}}$	$\frac{-.15}{\text{N.S.}}$	$\frac{.24}{\text{N.S.}}$
<u>Branchiura</u>	$\frac{.65}{\text{N.S.}}$	$\frac{.04}{\text{N.S.}}$	$\frac{.71}{.05}$

ecological origins (Fager 1957). The summer-winter distributional data were subjected to recurrent group analysis in order to test if the various taxa of benthic macroinvertebrates found in Imperial Reservoir formed assemblages (Fager 1957; Fager and McGowan 1963; Fager and Longhurst 1968) (Table 7). All pairs of taxa were considered importantly associated if their index of affinity was 0.50 or greater (Fager and Longhurst 1968).

On the basis of recurrent group analysis using Fager's index of affinity only one group was formed from the summer distributional data (Fig. 4). Here, the taxa most often found together were Limnodrilus, Chironomus and Branchiura. Clinotanypus was associated with Limnodrilus and Branchiura. Two groups were formed in the winter collection: a larger group comprised of Clinotanypus, Chironomus, Limnodrilus and Branchiura and a separate group made up of Chaoborus and Pentaneura.

Dispersion and Time. The temporal and spatial distribution of the benthic macroinvertebrates was examined using the 20 replicate dredge samples taken biweekly from March 1971 to March 1972 at Sites 1 and 8. The distribution for each taxon through time was plotted as the mean and a 95% confidence limit for each of 20 samples (Figs. 5-14).

Clinotanypus at Site 1 showed three generations, or recognizable cohorts, in the sampling year (Fig. 5). Chironomus had one cohort which lasted from April to September 1971, at Site 1 (Fig. 6). Pentaneura may have had one cohort April to August and then appeared sporadically at several other times during the year (Fig. 7). Limnodrilus did not form cohorts and appeared throughout the year in widely varying numbers (Fig. 8). Branchiura appeared throughout the spring

Table 7. Distribution data for summer and winter collection among the various sample sites. -- The values in the summer and winter columns are the geometric means of the proportion of joint occurrences corrected for sample size which is used in the determination of recurrent groups of animals. Only those values above 0.50 were considered significant.

	Summer	Winter
<u>Clinotanypus-Chironomus</u>	0.35	0.64
<u>Clinotanypus-Pentaneura</u>	0.27	0.44
<u>Clinotanypus-Chaoborus</u>	0.47	0.44
<u>Clinotanypus-Limnodrilus</u>	0.71	0.63
<u>Clinotanypus-Branchiura</u>	0.55	0.66
<u>Chironomus-Pentaneura</u>	0.34	0.44
<u>Chironomus-Chaoborus</u>	0.07	0.44
<u>Chironomus-Limnodrilus</u>	0.74	0.56
<u>Chironomus-Branchiura</u>	0.55	0.66
<u>Pentaneura-Chaoborus</u>	-0.19	0.71
<u>Pantaneura-Limnodrilus</u>	0.33	0.24
<u>Pentaneura-Branchiura</u>	0.41	-0.03
<u>Chaoborus-Limnodrilus</u>	0.61	0.22
<u>Chaoborus-Branchiura</u>	-0.04	-0.03
<u>Branchiura-Limnodrilus</u>	0.67	0.55



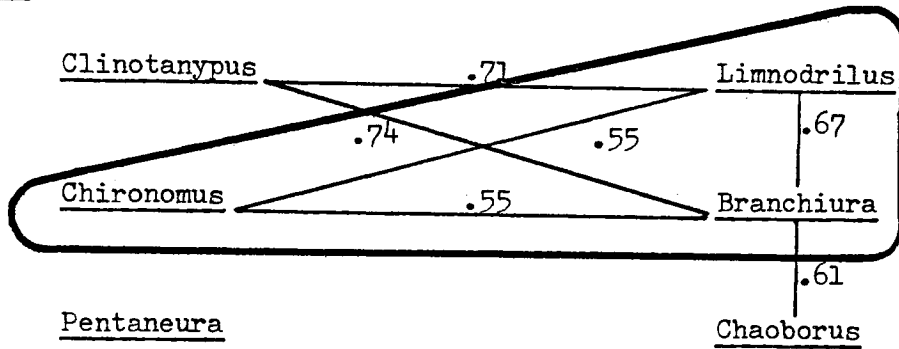
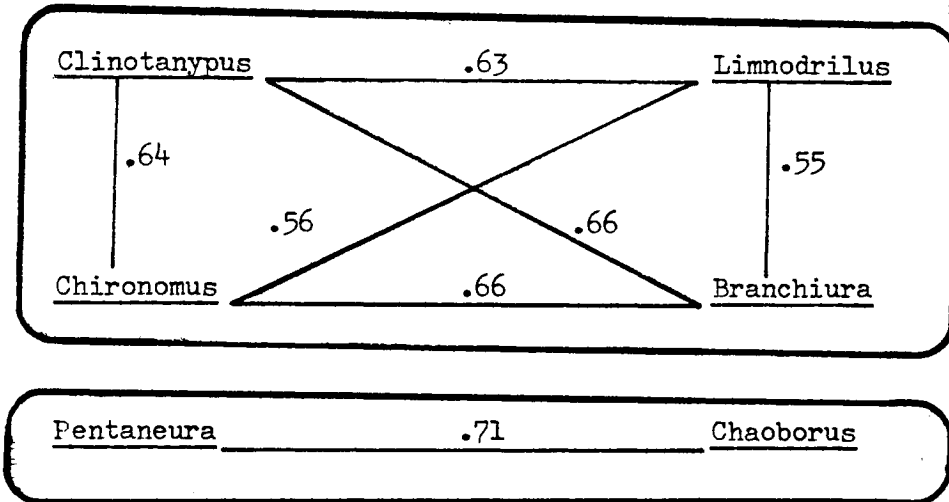
SummerWinter

Figure 4. Groupings of benthic macroinvertebrates from seven sample sites in Imperial Reservoir. -- Connecting lines were drawn only when the value of the index of affinity was greater than 0.5.

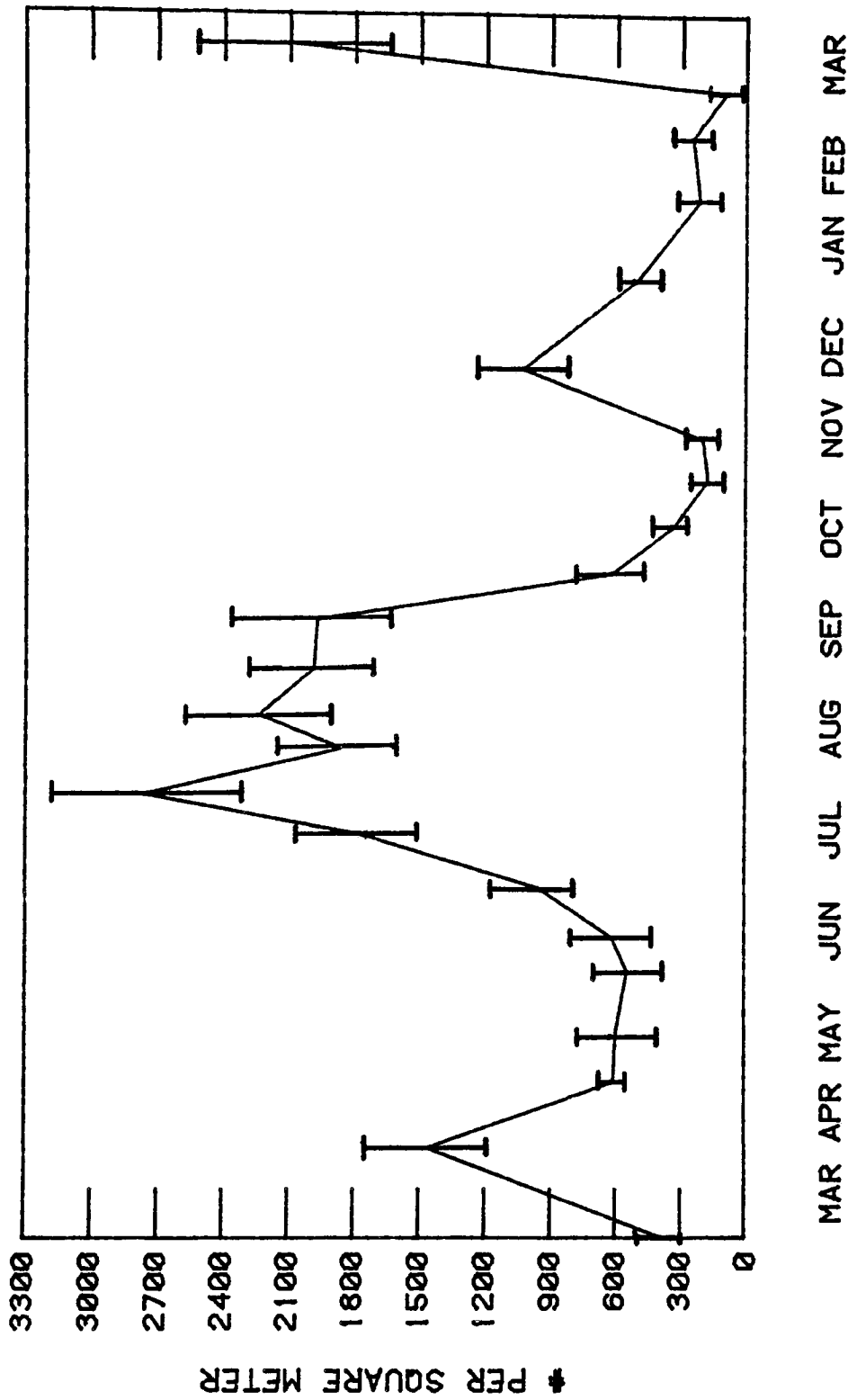


Figure 5. Population fluctuations of *Clinotanypus* sp. at Site 1. -- Vertical bars represent the 95% confidence interval about the mean for each set of 20 samples taken on each date.

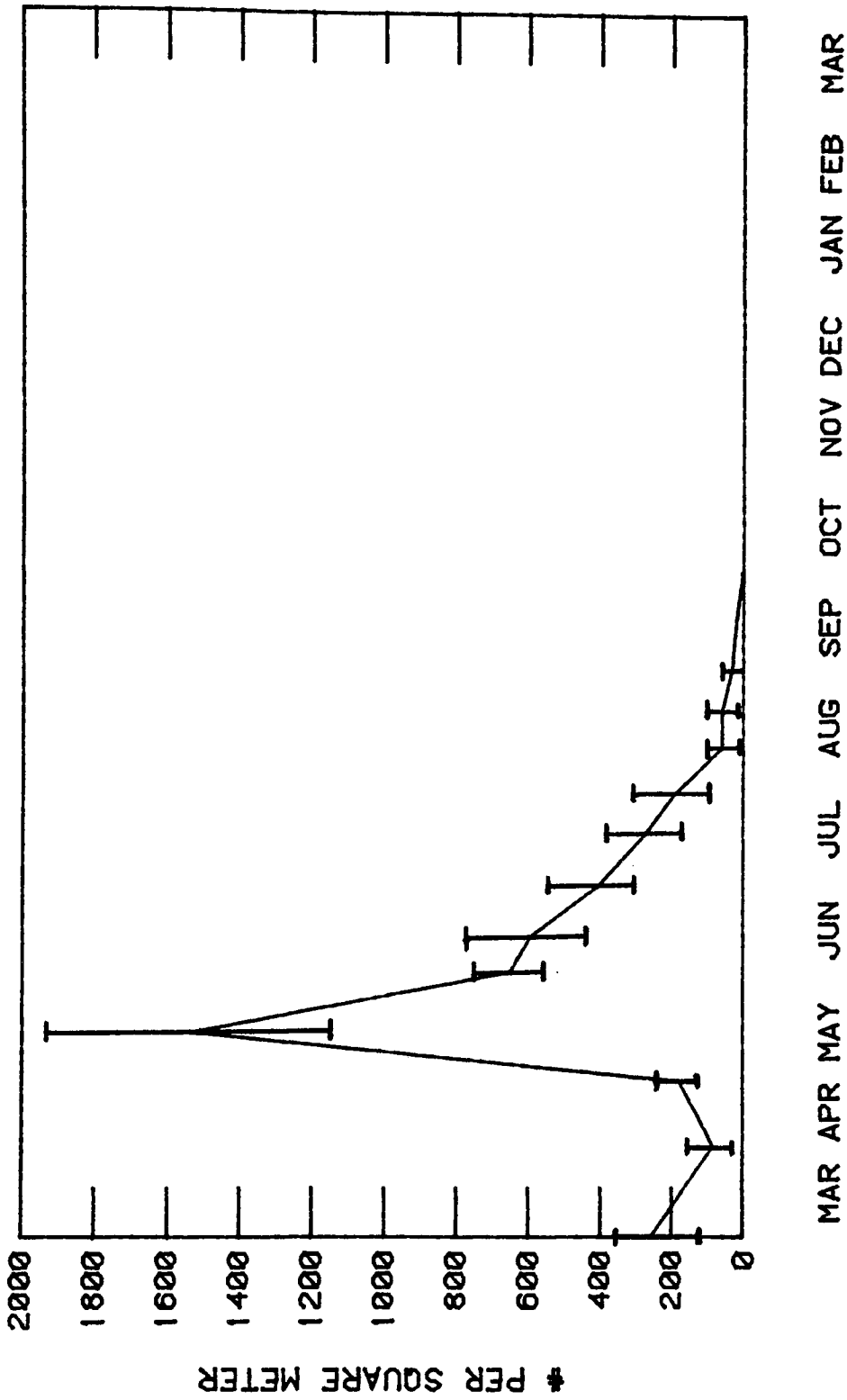


Figure 6. Population fluctuations of *Chironomus plumosus* at Site 1. --- Vertical bars represent the 95% confidence interval about the mean for each set of 20 samples taken on each date.

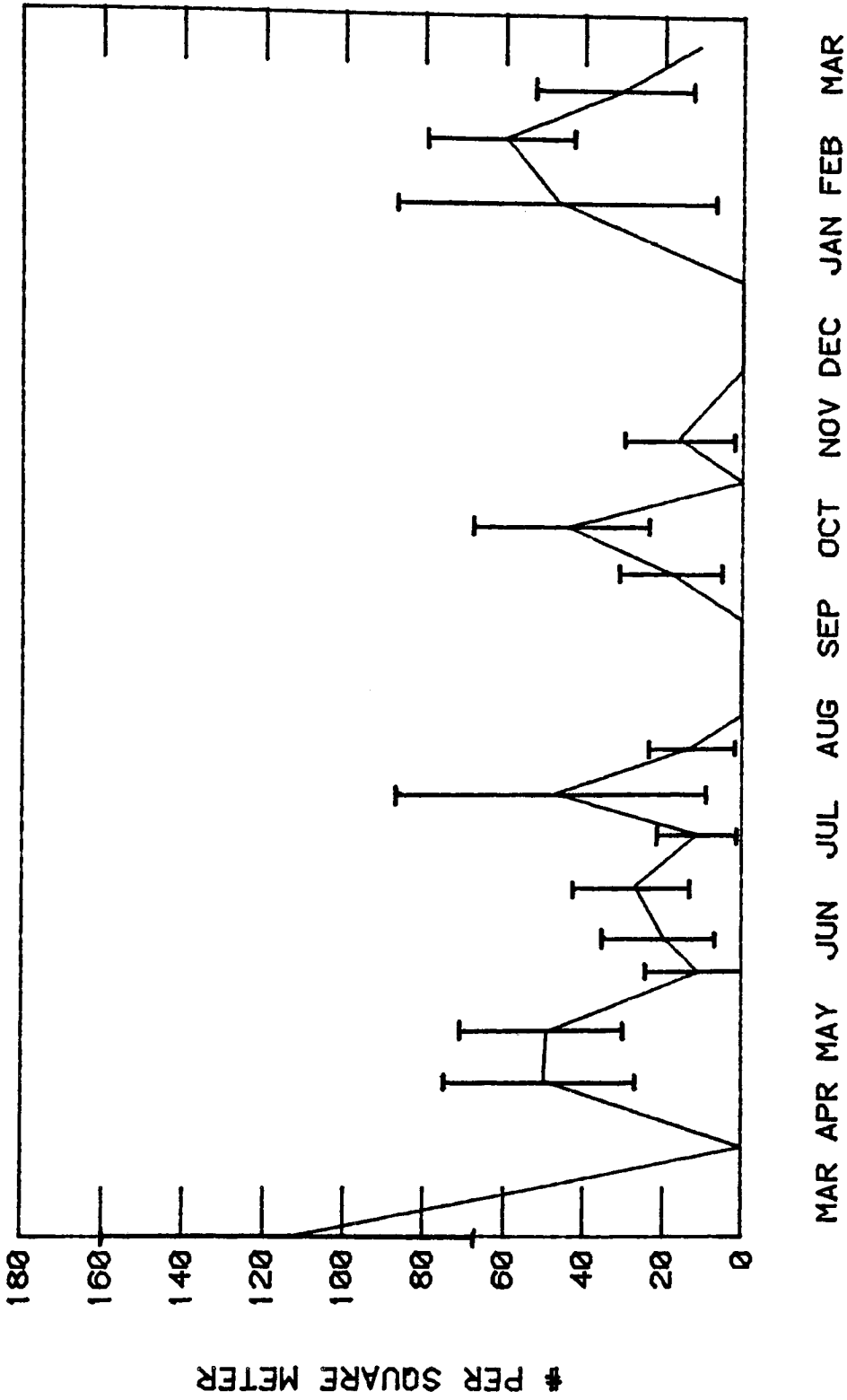


Figure 7. Population fluctuations of Pentaneura sp. at Site 1. --- Vertical bars represent the 95% confidence interval about the mean for each set of 20 samples taken on each date.

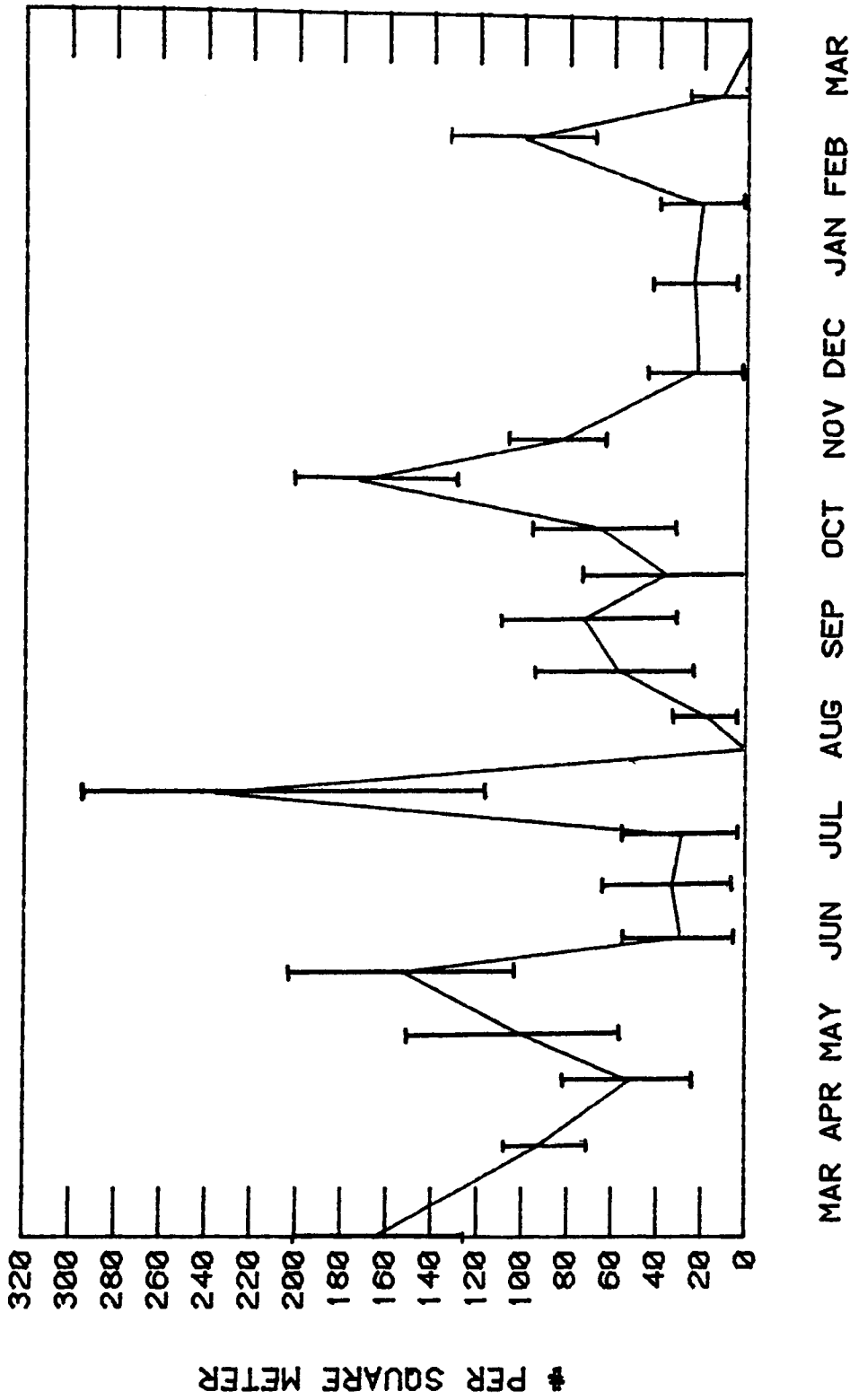


Figure 8. Population fluctuations of *Limnodrilus hoffmeisteri* at Site 1. --- Vertical bars represent the 95% confidence interval about the mean for each set of 20 samples taken on each date.

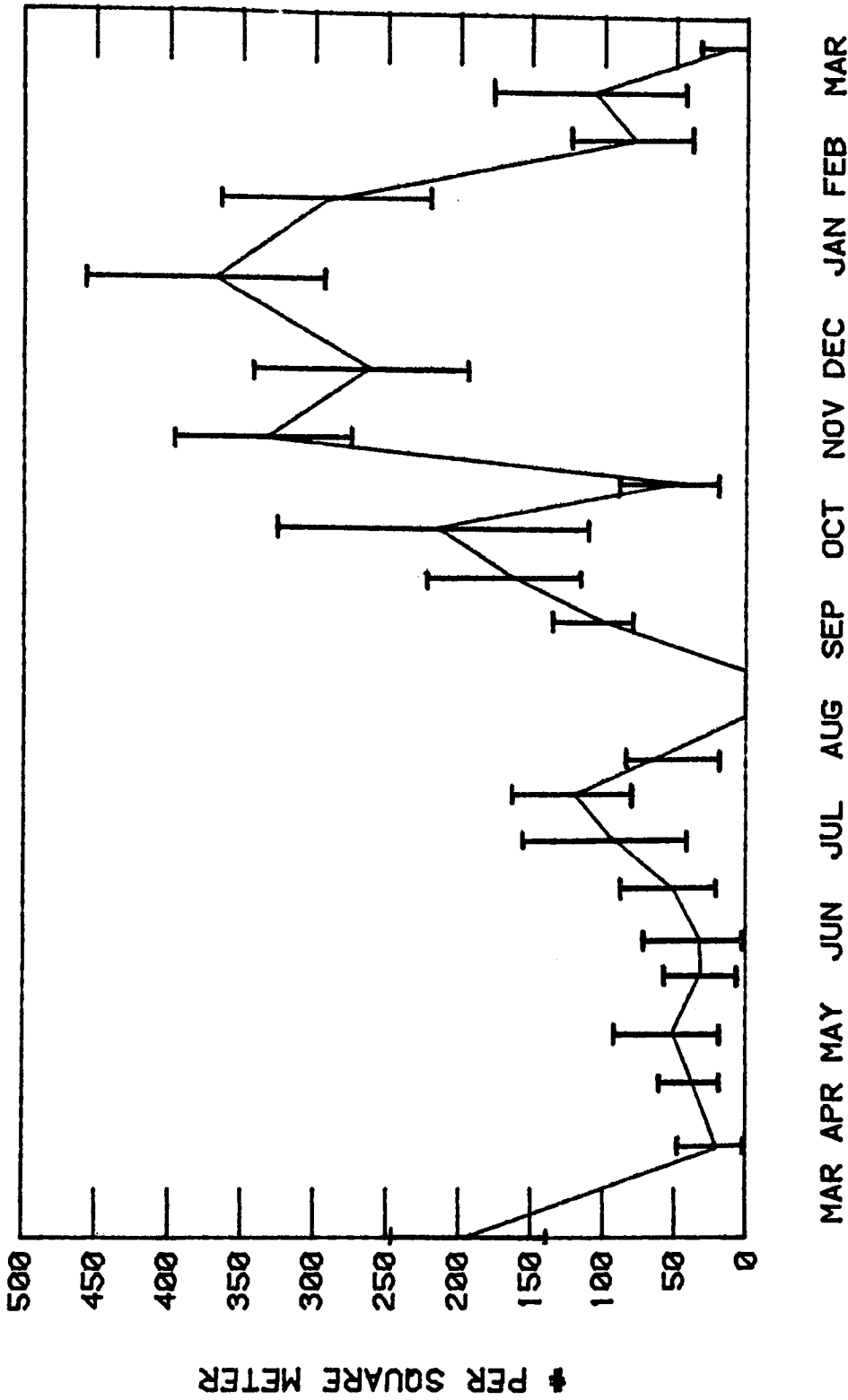


Figure 9. Population fluctuations of *Branchiura sowerbyi* at Site 1. -- Vertical bars represent the 95% confidence interval about the mean for each set of 20 samples taken on each date.

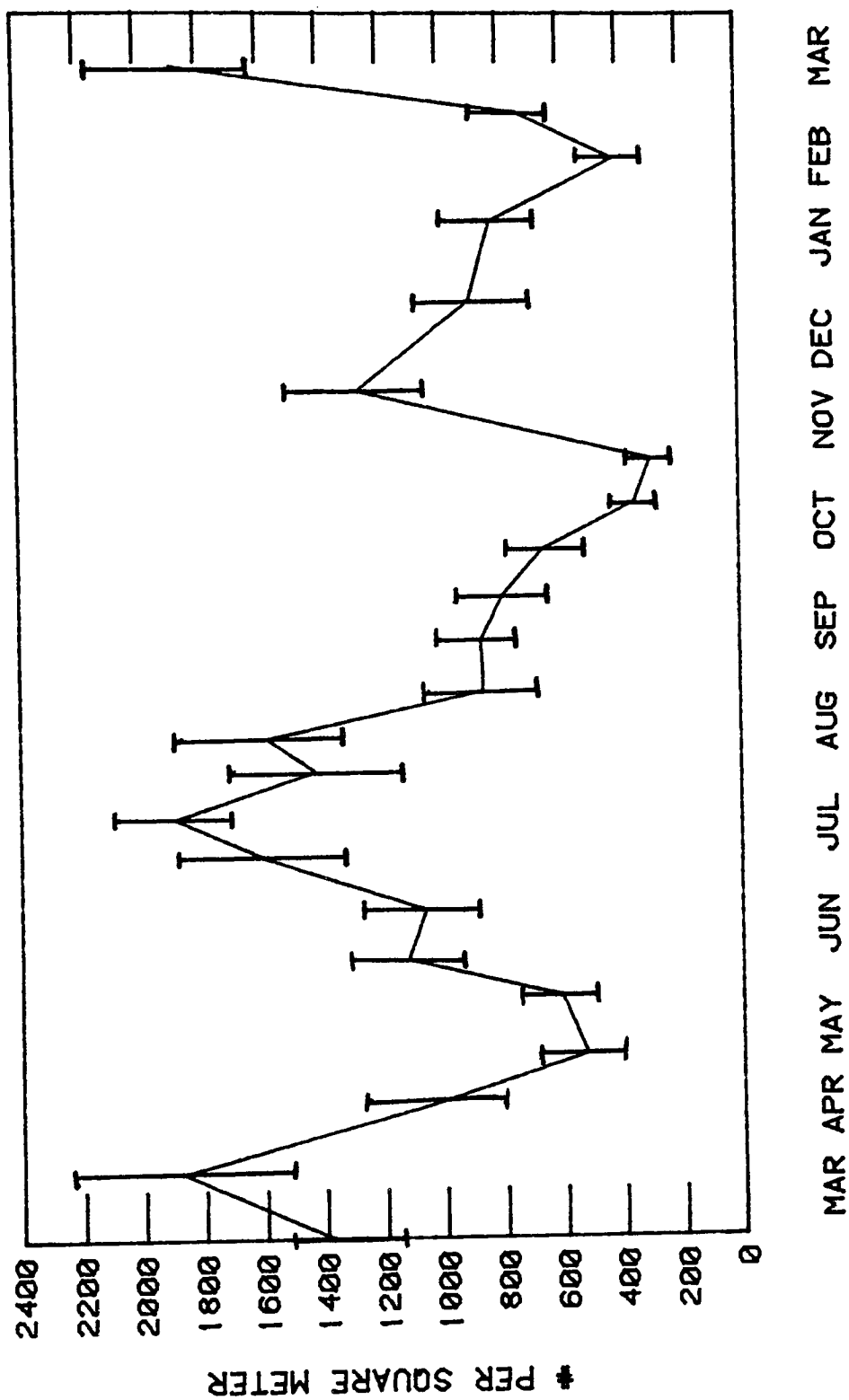


Figure 10. Population fluctuations of *Clinotanypus* sp. at Site 8. --- Vertical bars represent the 95% confidence interval about the mean for each set of 20 samples taken on each date.

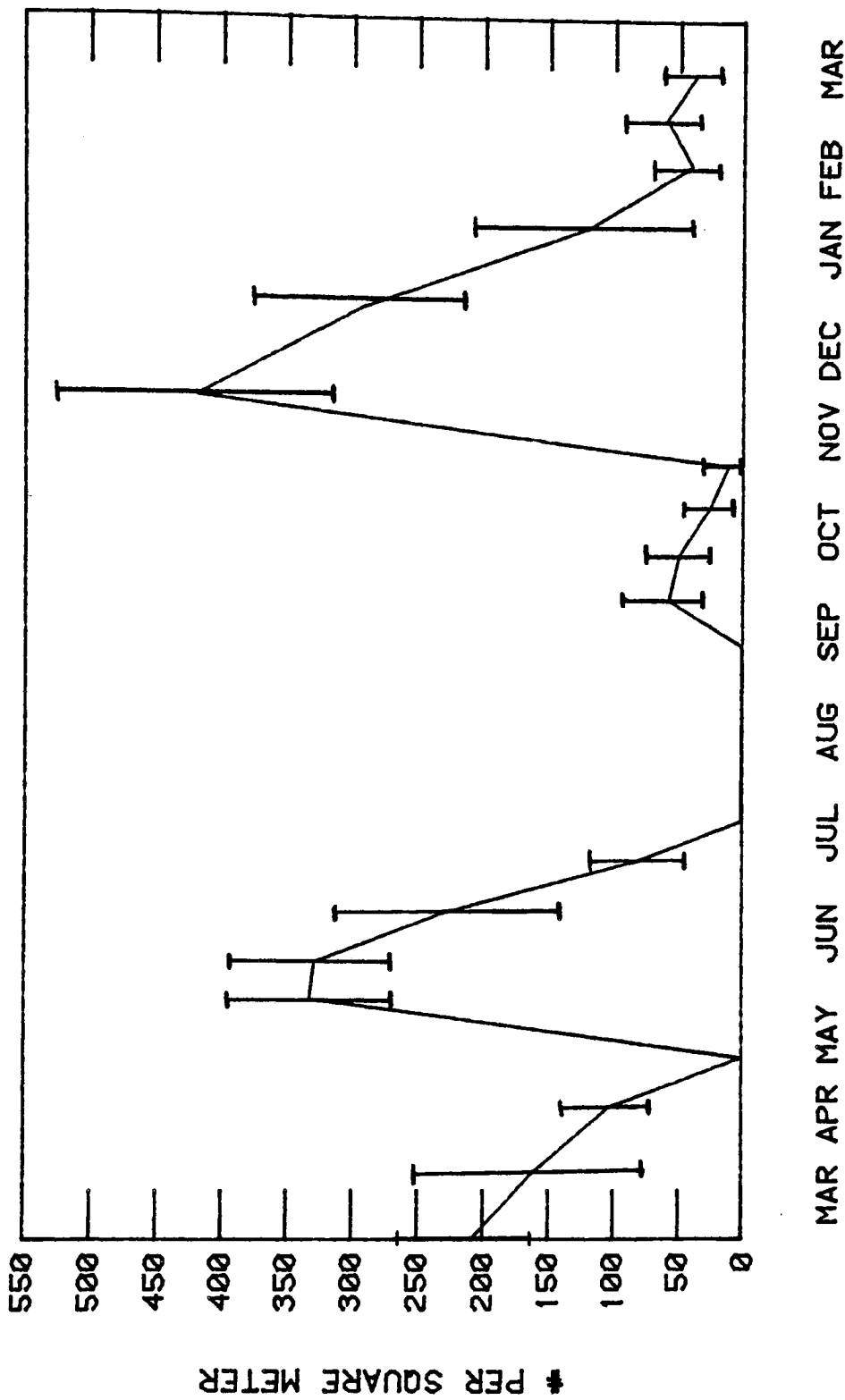


Figure 11. Population fluctuations of *Chironomus plumosus* at Site 8. -- Vertical bars represent the 95% confidence interval about the mean for each set of 20 samples taken on each date.



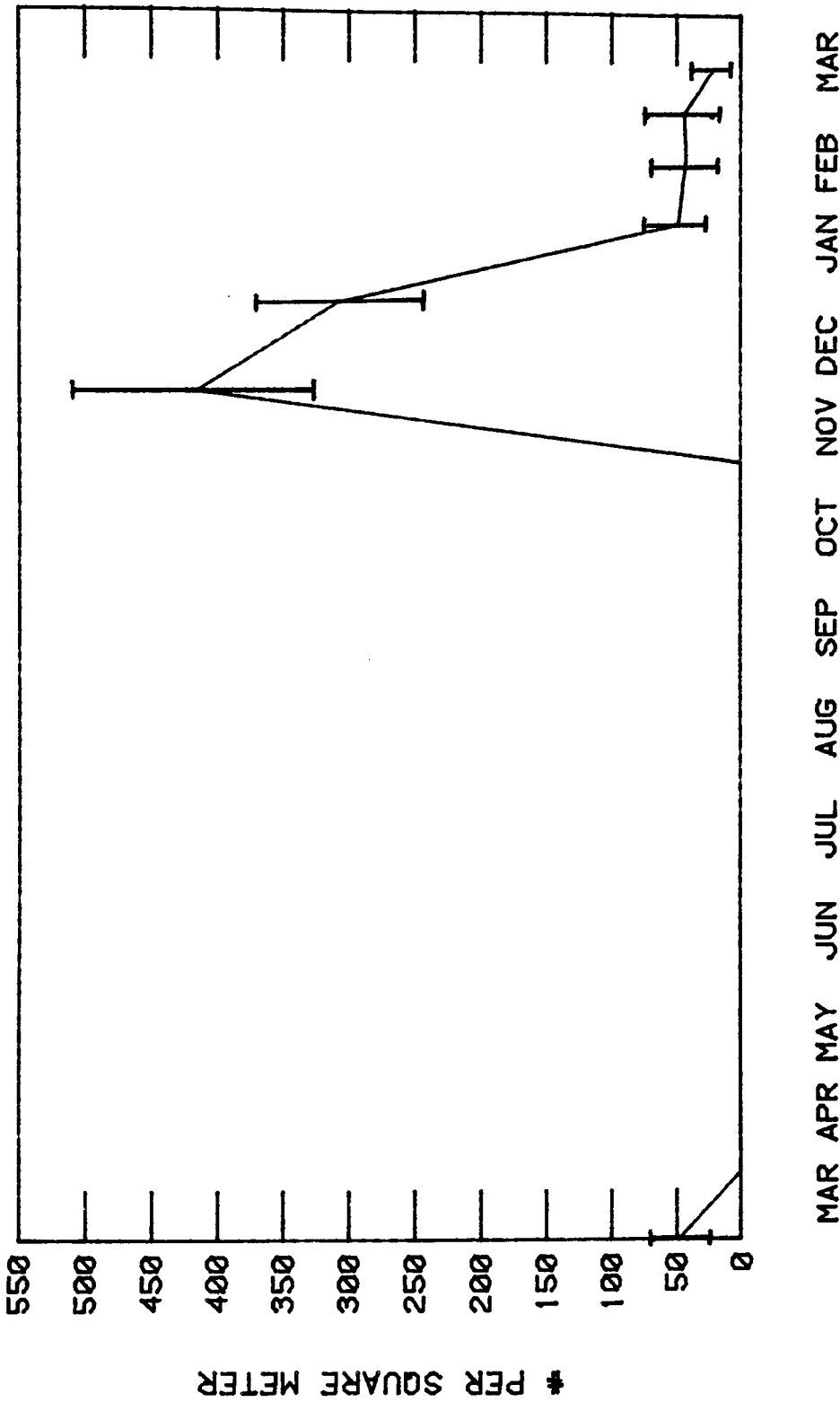


Figure 12. Population fluctuations of Pentaneura sp. at Site 8. -- Vertical bars represent the 95% confidence interval about the mean for each set of 20 samples taken on each date.

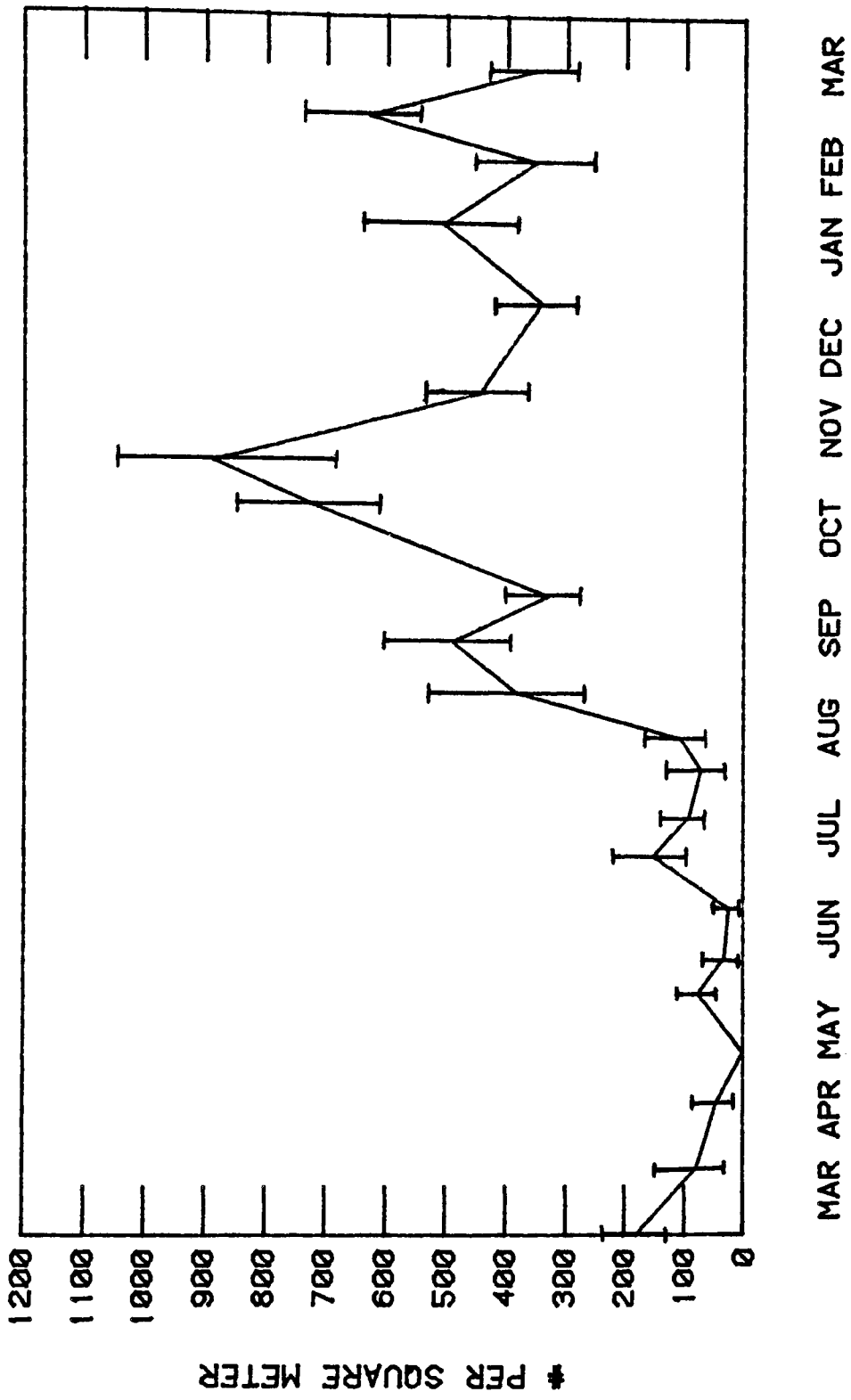


Figure 13. Population fluctuations of *Chaoborus punctipennis* at Site 8. -- Vertical bars represent the 95% confidence interval about the mean for each set of 20 samples taken on each date.

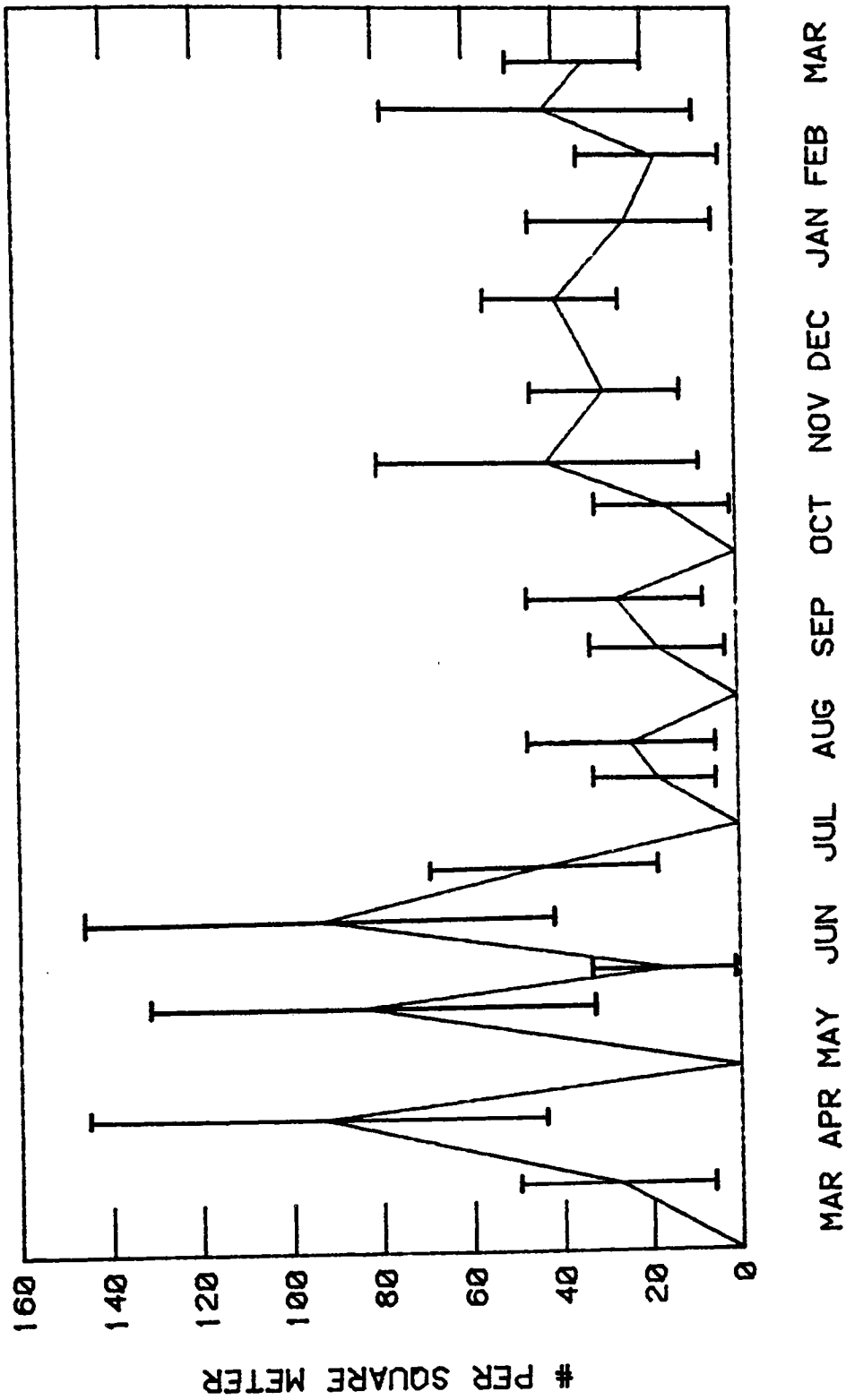


Figure 14. Population fluctuations of *Limnodrilus hoffmeisteri* at Site 8. -- Vertical bars represent the 95% confidence interval about the mean for each set of 20 samples taken on each date.

and early summer and then was absent in August and September, it appeared at higher numbers throughout the autumn and winter (Fig. 9).

At Site 8, Clinotanypus showed three cohorts in the spring shorter than that at Site 1 and then an additional cohort in the late autumn and winter (Fig. 11). Pentaneura had a single cohort during the winter at Site 8 (Fig. 12). Chaoborus was collected in low numbers throughout the spring and summer at Site 8 and in higher numbers in the autumn and winter (Fig. 13). Limnodrilus was found in all seasons of the year but not during all sample times (Fig. 14).

Microdistribution. The spatial distribution pattern, or micro-distribution, of each taxon was measured in three ways: (1) a chi-square test of departure of the variance to mean ratio from a value of 1.0 (Elliott 1971); (2) a chi-square test of Morisita's index (Elliott 1971); and (3) an F test of the departure of Morisita's index from a value of 1.0 (Poole 1974). Three categories of microdistribution patterns could be assigned to the chi-square values (Elliott 1971) and two to the F test (Poole 1974). Chi-square values of over 32.8 indicated a significant departure of both the variance to mean ratio and Morisita's index from a value of 1.0 and the population could be classified as contagious, a statistical term for the tendency to occur in aggregates. Populations with chi-square test values for either the variances to mean ratio or Morisita's index which fell between 32.8 and 8.9 were classified as randomly distributed. A chi-square value below 8.9 indicated a regularly distributed population. As a double check of the chi-square test a computed F value was compared with an F distribution of (n-1) degrees of freedom in the numerator (Poole 1974). Computed

F values with significant  $P \geq 0.05$  were considered to have an index greater than 1.0 and were classified as contagious. Populations of significance levels  $P \leq 0.05$  were considered random. Both chi-square values and the F tests indicated similar trends in the dispersion patterns of the benthic macroinvertebrates throughout the year (Appendix 1).

The chi-square of Morisita's index of aggregation was plotted over time for each taxon (Figs. 15-24). Horizontal lines separate areas of clumped distribution (above 32.8), random distribution (32.8 to 8.9), and regular distribution (below 8.9).

At Site 1, Clinotanypus was mostly clumped (Fig. 15). Chironomus became increasingly random with time (Fig. 16). Pentaneura was mostly random but appeared clumped on two occasions (Fig. 17). Limnodrilus was mostly random, occasionally clumped, and one occasion regular (Fig. 18). Branchiura was mostly found to be clumped but at various times was found randomly distributed (Fig. 19). Clinotanypus was found mostly clumped at Site 8; a few times it was found randomly distributed (Fig. 20). The first set of samples of Pentaneura was also clumped; all others were classed as random (Fig. 21). Chaoborus, Chironomus and Limnodrilus were found both clumped and random with no apparent pattern.

Since Morisita's index of aggregation is independent of sample size (Elliott 1971; Poole 1974), it is possible to test the association between development of a cohort, as manifested by the change in numbers over time, and changes in the value of the chi-square test of Morisita's index. The implied test is for change in dispersal pattern with age of a cohort. Since Clinotanypus and Chironomus at both sites and

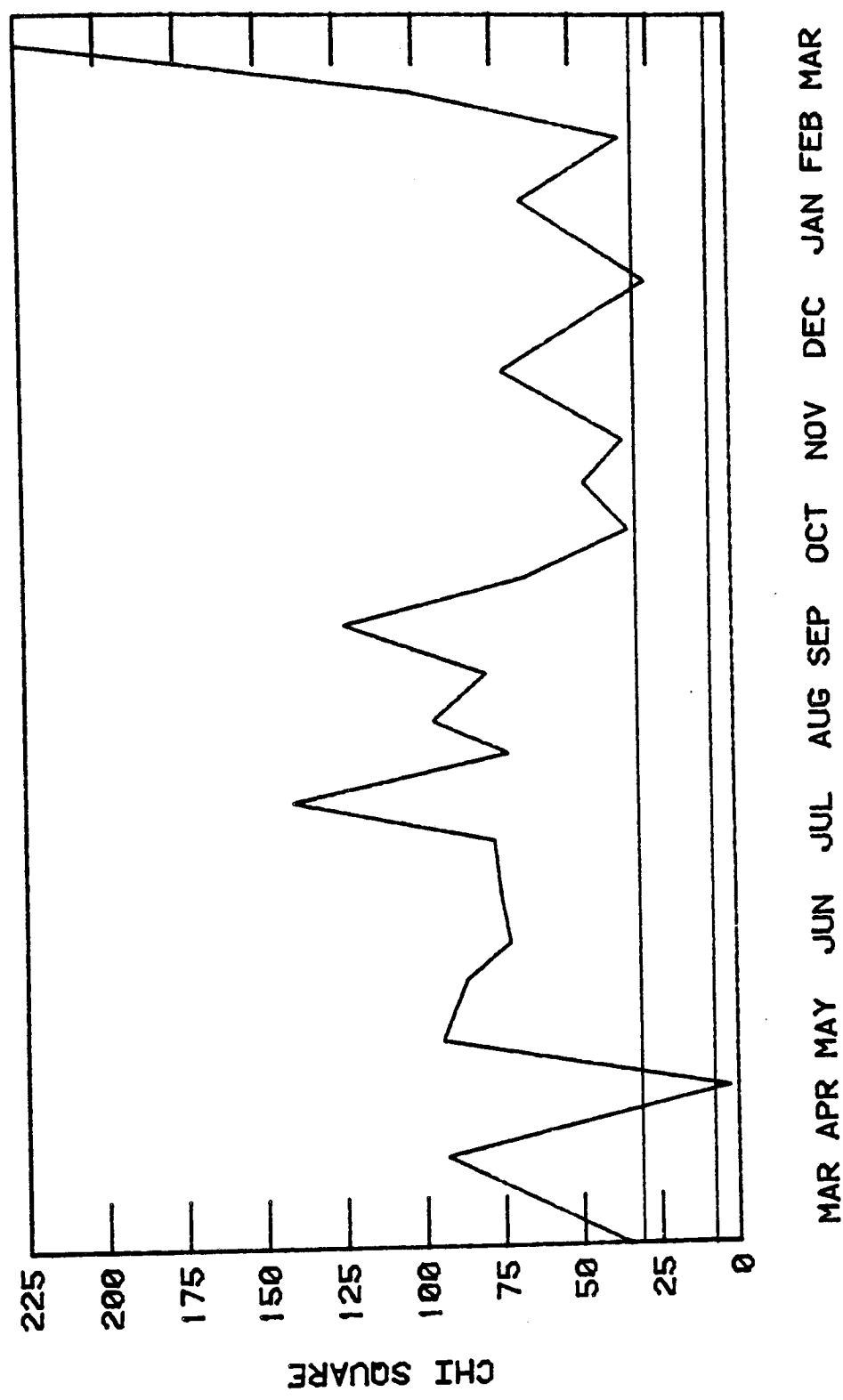
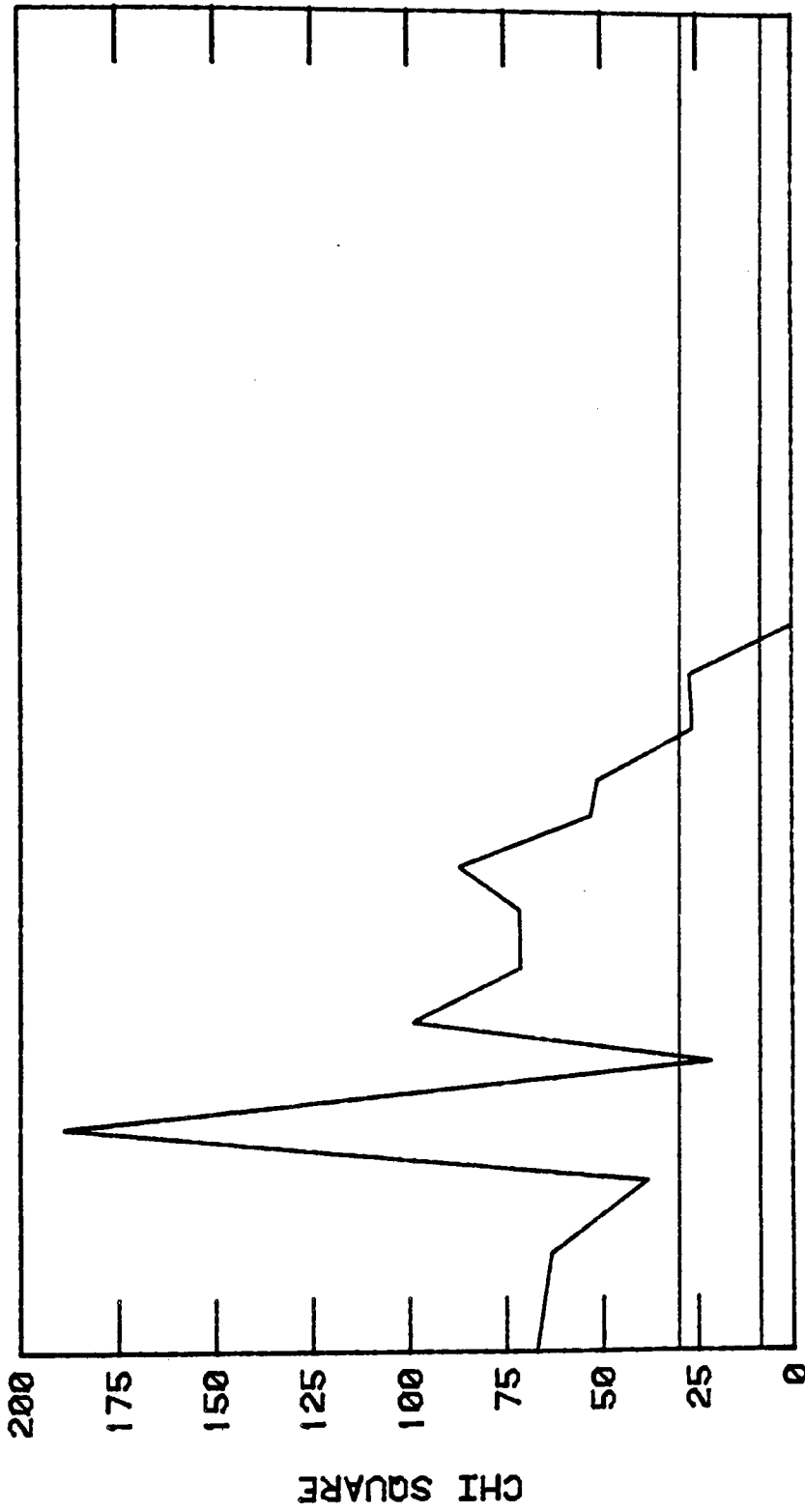
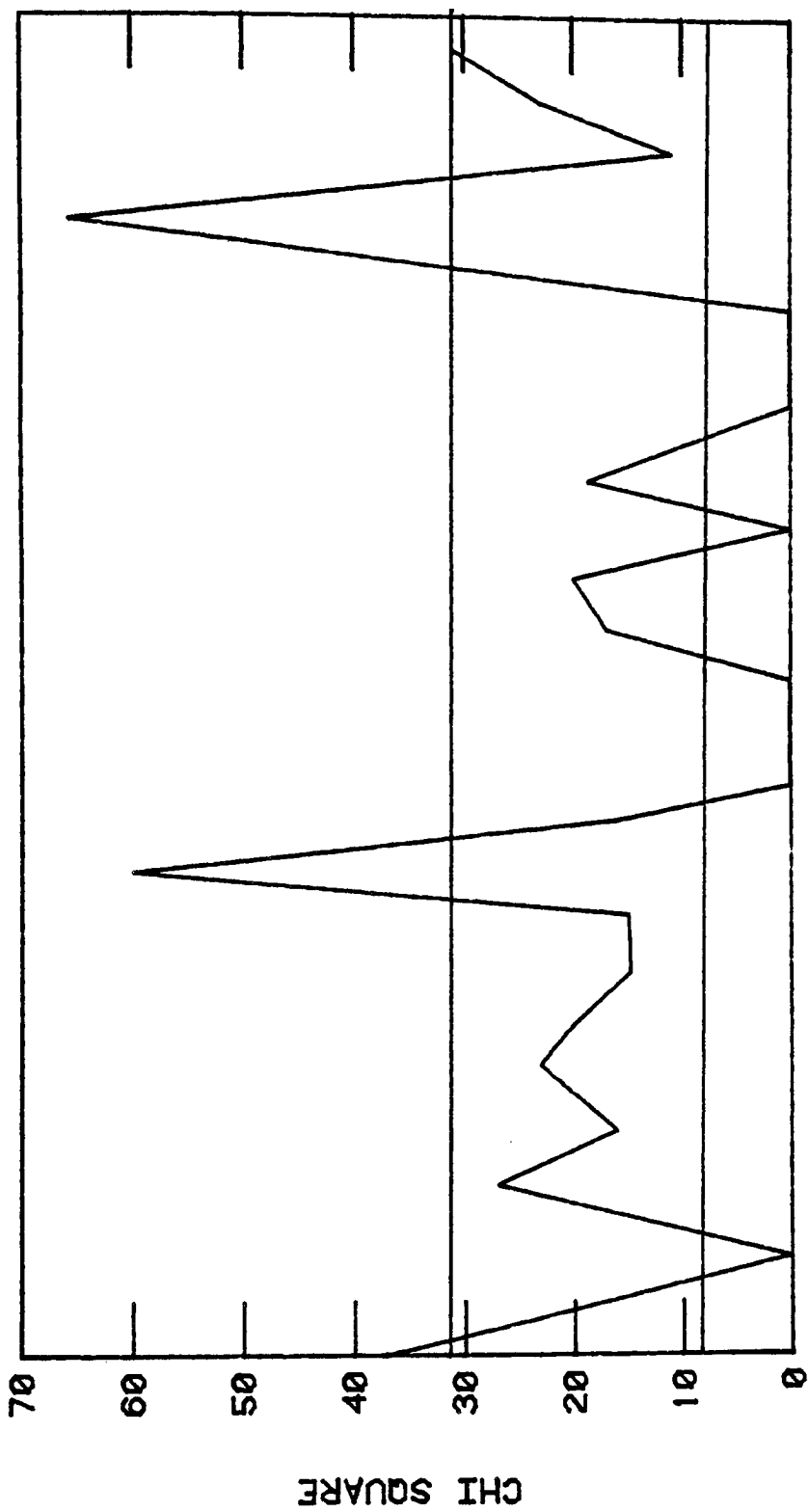


Figure 15. Microdistributional pattern of Clinotanypus sp. at Site 1 as tested for with the chi-square of Morisita's index of aggregation. -- The two horizontal lines above the abscissa divide the graph into regions of clumped distribution (upper), random distribution (middle), and regular distribution (between abscissa and first vertical line).



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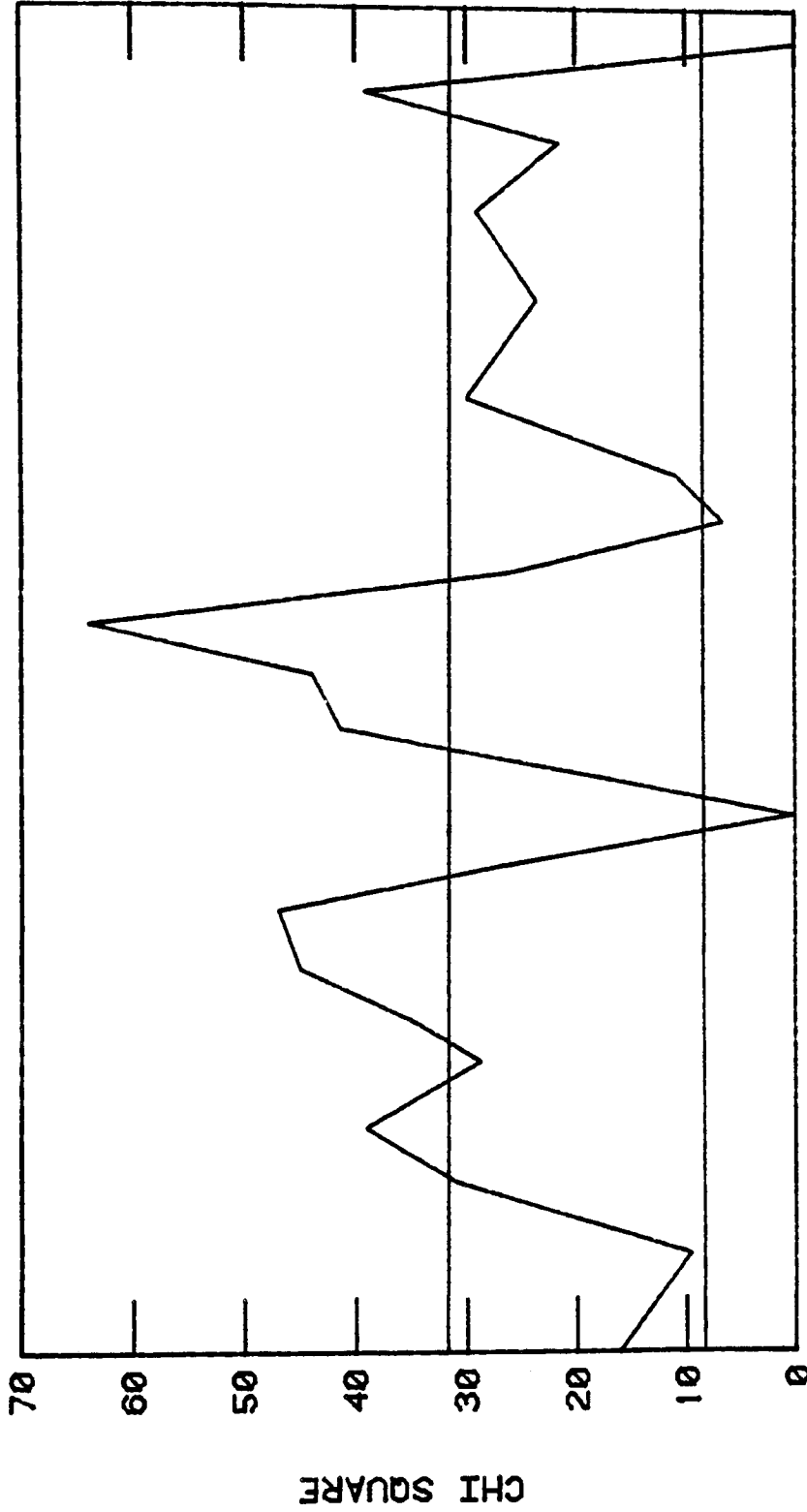
Figure 16. Microdistributional pattern of *Chironomus plumosus* at Site 1 as tested for with the chi-square of Morisita's index of aggregation. --- The two horizontal lines above the abscissa divide the graph into regions of clumped distribution (upper), random distribution (middle), and regular distribution (between abscissa and first vertical line).



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Figure 17. Microdistributional pattern of Pentaneura sp. at Site 1 as tested for with the chi-square of Morisita's index of aggregation. -- The two horizontal lines above the abscissa divide the graph into regions of clumped distribution (upper), random distribution (middle), and regular distribution (between abscissa and first vertical line).





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Figure 18. Microdistributional pattern of *Limnodrilus hoffmeisteri* at Site 1 as tested for with the chi-square of Morisita's index of aggregation. -- The two horizontal lines above the abscissa divide the graph into regions of clumped distribution (upper), random distribution (middle), and regular distribution (between abscissa and first vertical line).

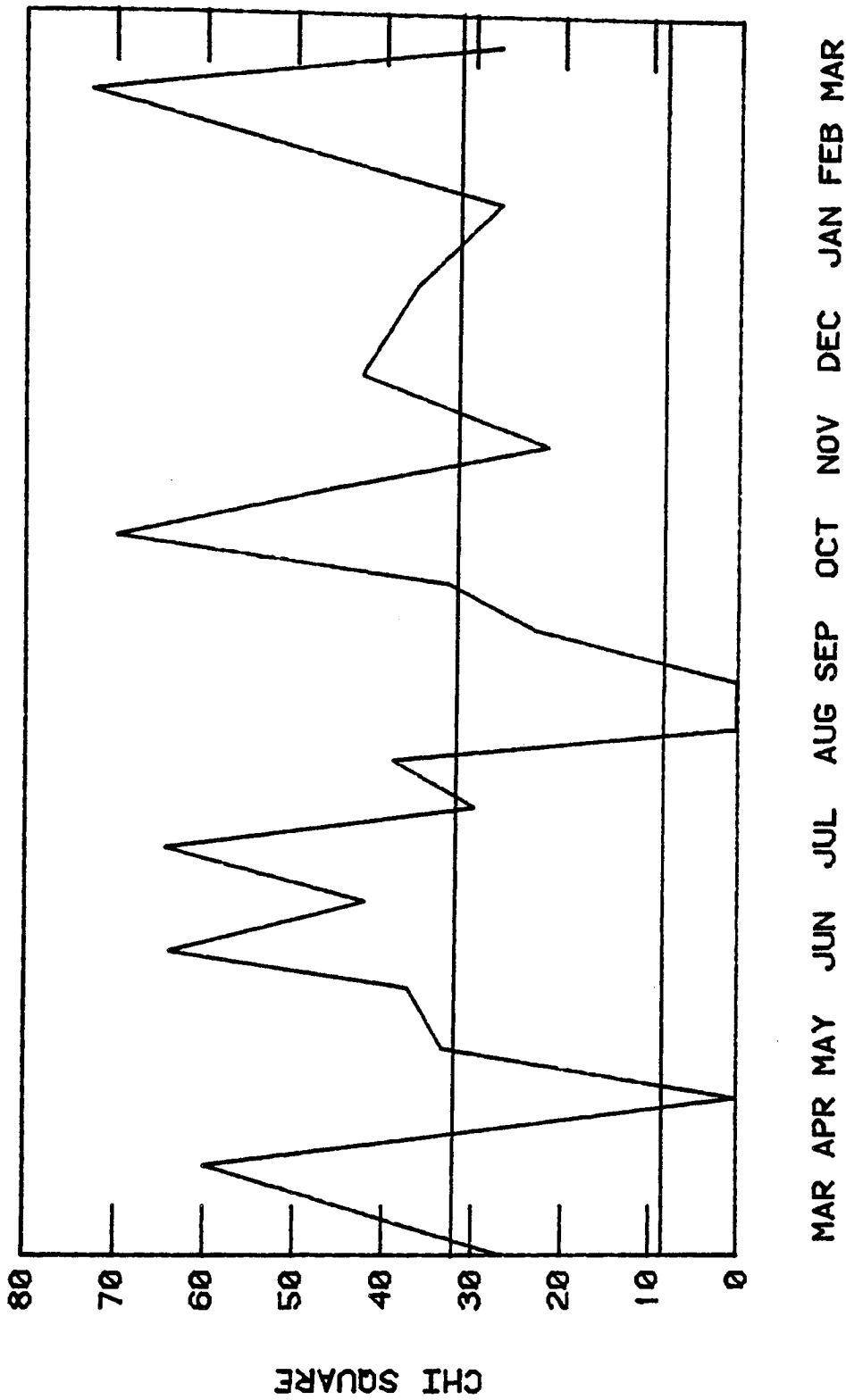


Figure 19. Microdistributional pattern of *Branchiura sowerbyi* at Site 1 as tested for with the chi-square of Morisita's index of aggregation. -- The two horizontal lines above the abscissa divide the graph into regions of clumped distribution (upper), random distribution (middle), and regular distribution (between abscissa and first vertical line).

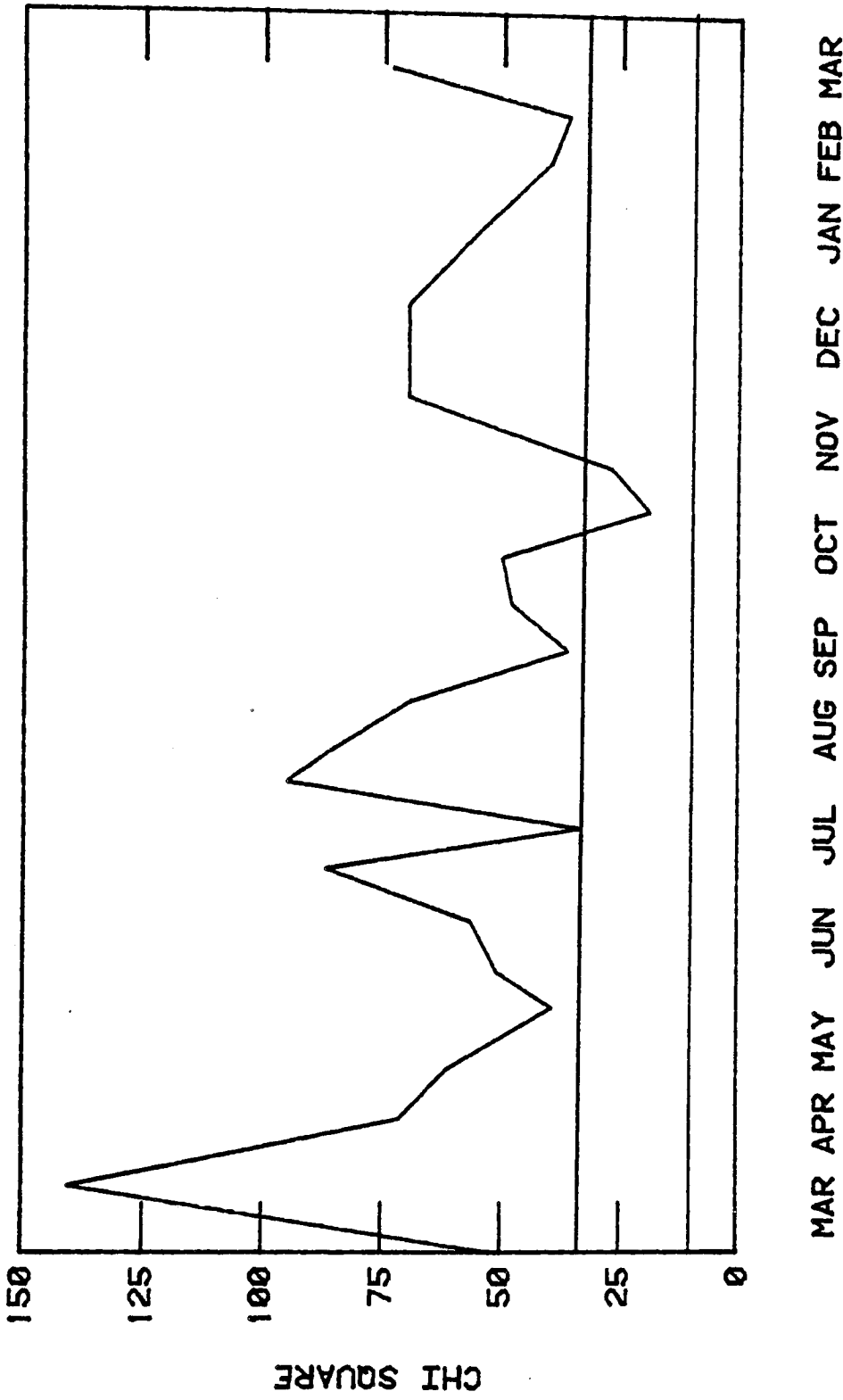


Figure 20. Microdistributional pattern of Clinotanypus sp. at Site 8 as tested for with the chi-square of Morisita's index of aggregation. -- The two horizontal lines above the abscissa divide the graph into regions of clumped distribution (upper), random distribution (middle), and regular distribution (between abscissa and first vertical line).

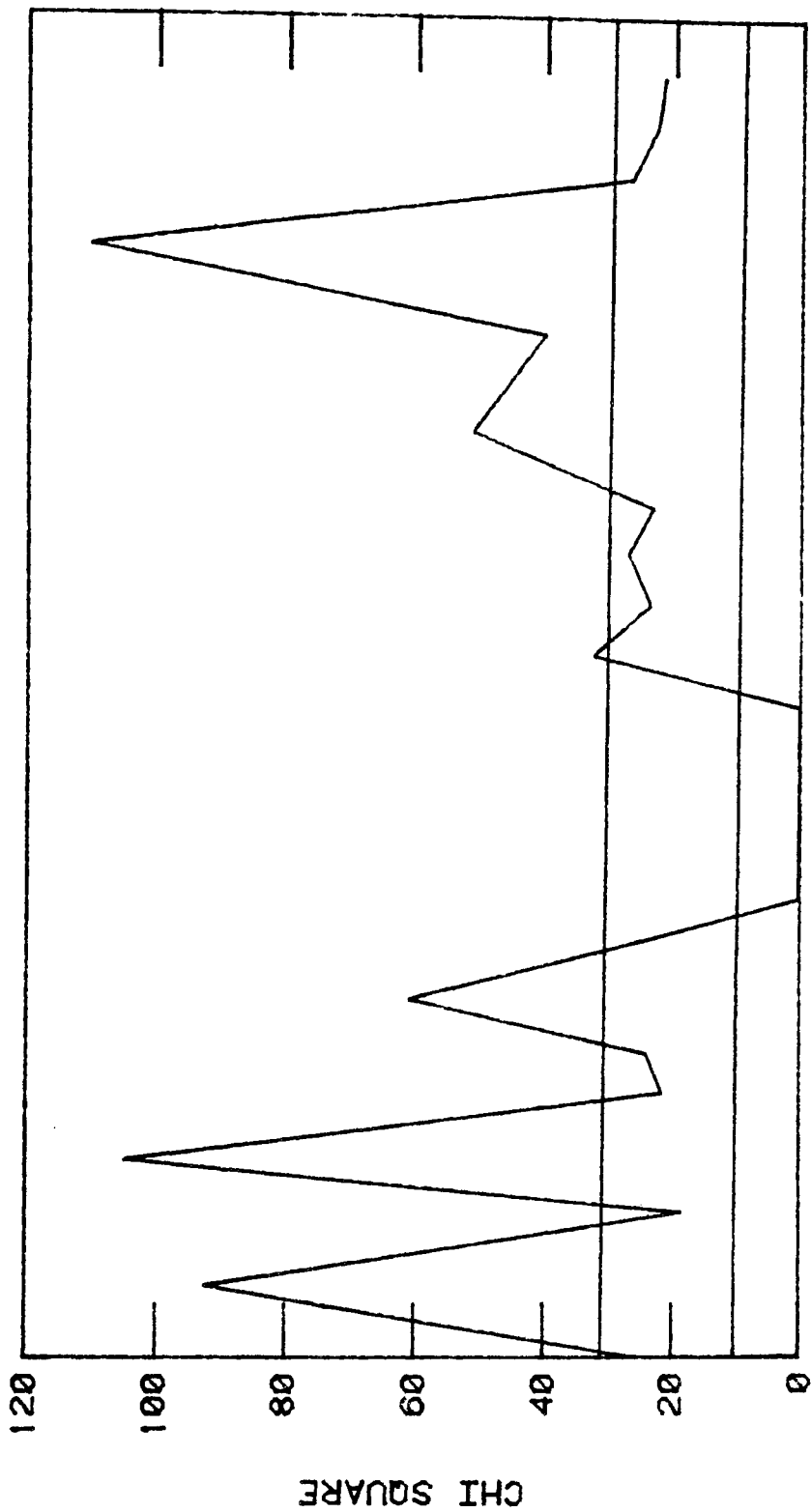


Figure 21. Microdistributional pattern of *Chironomus plumosus* at Site 8 as tested for with the chi-square of Morisita's index of aggregation. -- The two horizontal lines above the abscissa divide the graph into regions of clumped distribution (upper), random distribution (middle), and regular distribution (between abscissa and first vertical line).

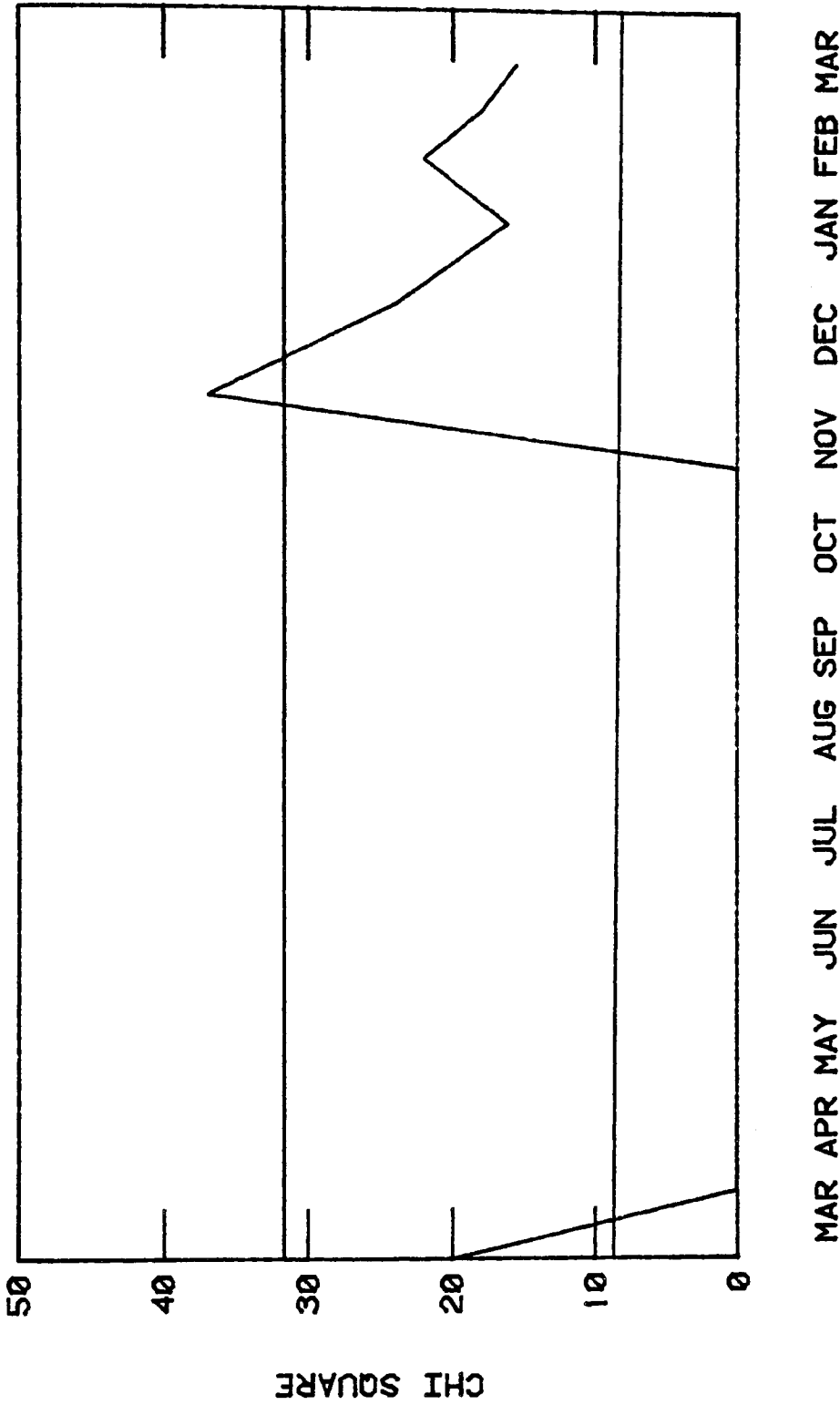


Figure 22. Microdistributional pattern of *Pentaneura* sp. at Site 8 as tested for with the chi-square of Morisita's index of aggregation. --- The two horizontal lines above the abscissa divide the graph into regions of clumped distribution (upper), random distribution (middle), and regular distribution (between abscissa and first vertical line).

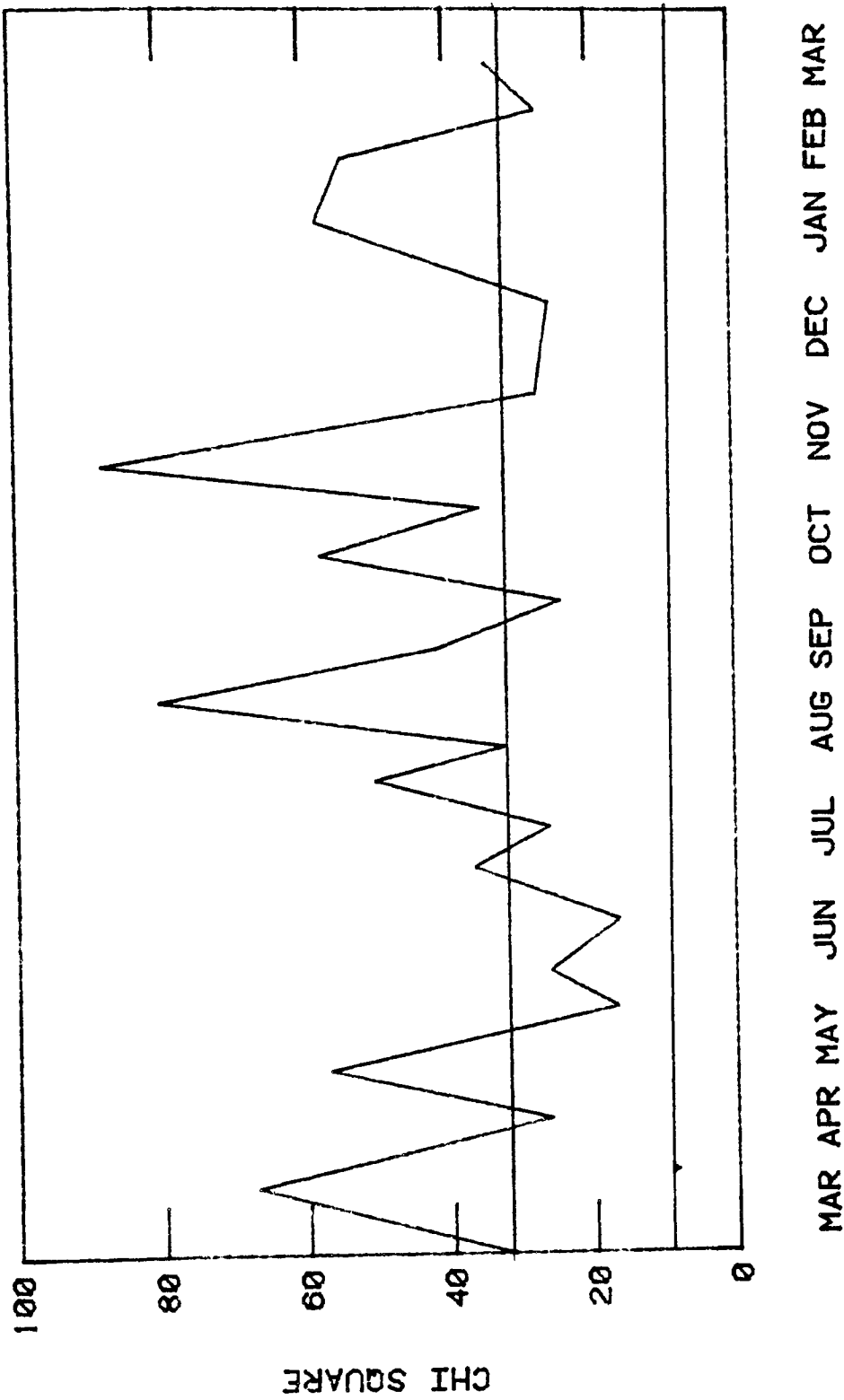


Figure 23. Microdistributional pattern of *Chaoborus punctipennis* at Site 8 as tested for with the chi-square of Morisita's index of aggregation. -- The two horizontal lines above the abscissa divide the graph into regions of clumped distribution (upper), random distribution (middle) and regular distribution (between abscissa and first vertical line).

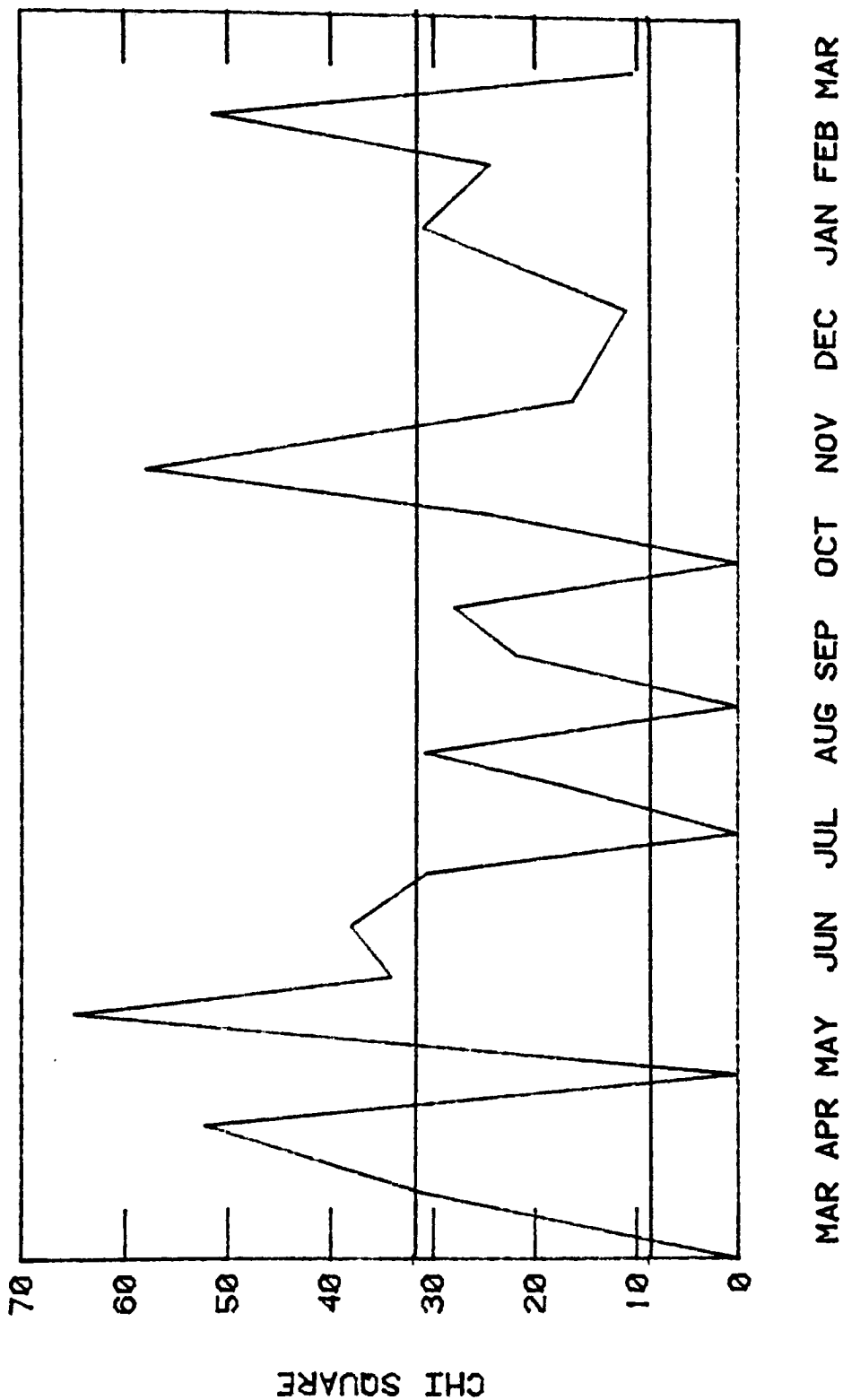


Figure 24. Microdistributional pattern of *Limnodrilus hoffmeisteri* at Site 8 as tested for with the chi-square of Morisita's index of aggregation. -- The two horizontal lines above the abscissa divide the graph into regions of clumped distribution (upper), random distribution (middle), and regular distribution (between abscissa and first vertical line).

Pentaneura at Site 8 exhibited obvious cohorts, the numbers per square meter were tested for association with the chi-square values using Spearman's rank correlation coefficient ( $r_s$ ) (Table 8). Clinotanypus had a highly significant ( $P \leq 0.01$ ) positive correlation at both sample sites for increased dispersal with time, that is, changing from clumped to random distributional pattern with decrease in number, or as a population aged and decreased in size. Chironomus had no significant correlations at either site. Pentaneura also showed a highly significant positive correlation indicating a trend towards dispersal of the population with age.

### Production

Production estimates were calculated for those benthic invertebrates which formed distinguishable cohorts. Two production estimates were used for each taxon (Table 9). The first estimate was calculated according to the Winberg-Edmonson equation and the second by the instantaneous growth equation. A turnover ratio (TR) of net production to mean biomass is shown for each cohort and taxon.

At Site 1, the three generations of Clinotanypus showed that summer was the period of greatest production (Cohort II), followed by the spring (Cohort I), and fall-winter period (Cohort III). At Site 8, the production values for summer (Cohort II) and the fall-winter period (Cohort III) were similar. The spring production of Clinotanypus (Cohort I) was the smallest. Chironomus had a single cohort at Site 1 and made up 37% of the total net benthic production. The combined production of the two generations of Chironomus at Site 8 was markedly less than the single cohort at Site 1.



Table 8. The test for change in dispersal pattern with age (reduced numbers) of a cohort. -- A Spearman ranked correlation coefficient ( $r_s$ ) of the chi-squared test of Morisita's index of aggregation with number per square meter for selected taxa was used. The statistical significance of ( $r_s$ ) appears under P.

Taxa	Site 1		Site 8	
	$r_s$	P	$r_s$	P
<u>Clinotanytus</u>	.54	.01	.56	.01
<u>Chironomus</u>	.49	N.S.	.35	N.S.
<u>Pentaneura</u>			.89	.05

Table 9. Net production (mg ash-free dry weight/m<sup>2</sup>) of the predominant species at Sites 1 and 8.  
 -- The results of the Edmonson-Winberg (EW) are contrasted with estimates using the instantaneous growth method G(B). The turnover rate (TR) is calculated from the Edmonson-Winberg estimates.

Taxa	Cohort	Site 1		Site 8		
		EW	G(B)	EW	G(B)	TR
<u>Clinotanytus</u>	I	614.75	602.17	619.78	621.07	3.85
	II	1018.08	1056.33	816.49	839.53	3.48
	III	475.20	495.38	831.55	842.49	2.17
	Total	2116.11	2153.88	2317.83	2303.09	8.63
<u>Chironomus</u>	I	1250.64	1247.05	513.30	509.35	2.08
	II			383.61	378.53	2.80
	Total	1250.64	1247.05	896.91	887.88	4.80
<u>Pentaneura</u>				467.98	464.62	3.27
	Grand Total	3366.25	3400.93	3682.72	3655.59	2.78

The total net secondary production for both sites showed less than 9% difference. The differences between the two methods of production ranged from 1.0-3.5 percent for the different cohorts, to 1.0 for the total. Although Pentaneura appeared at both sample sites, only samples at Site 8 formed a recognizable cohort. Several generations of Pentaneura probably existed at Site 1, however, the statistical precision of the samples was too poor to delineate cohorts for purposes of calculating production.

In order to see if production of the benthic macrofauna was linearly related to temperature, the instantaneous growth rate, (G), per day was tested for significance of correlation with the mean temperature in each sample interval (Table 10). The correlation values of the individual generations of Clinotanypus, both positive and negative, were not statistically significant. When all temperatures and (G) per day were correlated for Clinotanypus at Site 1, the correlation was positive and statistically significant. Clinotanypus at Site 8 had a highly significant negative correlation in Cohort I and positive but insignificant correlation for Cohorts II and III and the annual overall test. No significant correlations existed for Chironomus and Clinotanypus were negatively correlated with temperature.

#### Utilization

The percent volume of stomach contents comprised of benthic invertebrates was determined for various size classes of three species of fish commonly found in Imperial Reservoir. A similar trend was found in each species (Fig. 25). The smaller fish of each species relied

Table 10. Correlation (r) of temperature with instantaneous growth (G) per day. -- The level of significance (P) and the number of observations (N) is also shown.

Taxa	Site 1			Site 8		
	r	P	N	r	P	N
<u>Clinotanytus</u>						
Cohort I	-.63	N.S.	6	-.94	.01	6
Cohort II	.58	N.S.	10	.42	N.S.	11
Cohort III	.58	N.S.	5	.13	N.S.	4
Total	.48	.05	21	.34	N.S.	21
<u>Chironomus</u>						
Cohort I	.10	N.S.	9	-.55	N.S.	4
Cohort II	-	-	-	.18	N.S.	5
Total				.34	N.S.	9
<u>Pentaneura</u>				.39	N.S.	5

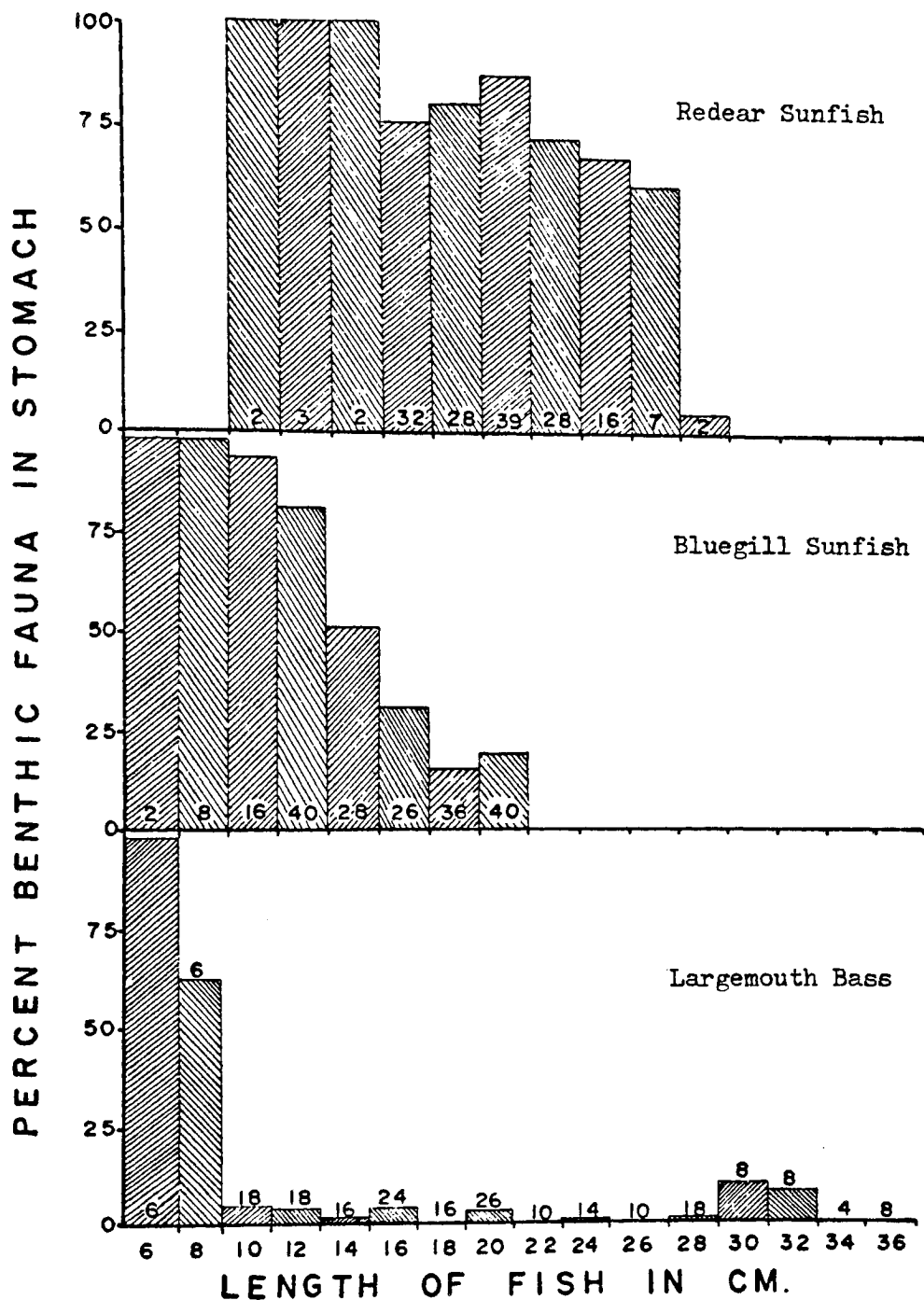


Figure 25. Stomach analysis of three species of fish collected in Imperial Reservoir. -- The value that appears within or above each column represents the number of fish of that size examined.

heavily on benthic invertebrates and dependence was reduced as the fish grew. Redear sunfish consistently had the highest percentage of benthos in their stomachs and it was only in the largest fish that benthic invertebrates were not the predominant food item. Small classes of bluegill sunfish also depended to a large extent on benthic invertebrates. Utilization of invertebrates by bluegill decreased with increasing fish size. Invertebrates made up less than 25% of all food material in the stomachs of the largest size class of bluegill. Only the two smallest sizes of largemouth bass appeared to utilize benthic macroinvertebrates for food. Bass greater than 8 cm had an insignificant amount of benthic fauna in their stomachs.

In order to test if there was prey selection between two of the benthic insects by the three species of fish, a frequency test was performed with a chi-square contingency table (Steel and Torrie 1960). The null hypothesis, that the ratio of the number of insects in each fish is the same within random sample error, was tested against the alternative hypothesis, that there were selective differences in the predation pattern among the three species of fish.

Three paired comparisons using 2 x 2 contingency tests were made on all combinations of the three species of fish (Tables 11-13). An adjusted chi-square was also calculated since there was only one degree of freedom (Steel and Torrie 1960). A coefficient of contingency ranging from 0.0 to 1.0 was determined and interpreted as a relative measure of the difference of the prey selection pattern of the fish taken two species at a time. Significant differences were found between all pairs of fish. The coefficient of contingency showed that

Table 11. Individual chi-square test of prey selection between redear and bluegill sunfish for Chironomid larvae found in stomach analysis.

		<u>Clinotanytus</u>	<u>Chironomus</u>	Total
Redear	Observed	103	694	797
	Expected	140.50	656.50	
	Deviation	- 37.50	+ 37.50	
	$\chi^2$	10.00	2.14	
Bluegill	Observed	157	521	678
	Expected	119.50	558.50	
	Deviation	+ 37.50	- 37.50	
	$\chi^2$	11.76	2.52	
Totals	Observed	260	1215	1475

$$\chi^2 = 26.42$$

Adjusted  $\chi^2 = 25.72$  with 1 d.f. ( $p < 0.001$ )

Coefficient of contingency = 0.179

Table 12. Individual chi-square test of prey selection between redear sunfish and largemouth bass for Chironomid larvae found in stomach analysis.

		<u>Clinotanypus</u>	<u>Chironomus</u>	Total
Redear	Observed	103	694	797
	Expected	326.33	470.67	
	Deviation	-223.33	+223.33	
	$\chi^2$	152.84	105.97	
Bass	Observed	417	56	478
	Expected	193.67	279.33	
	Deviation	+222.33	-222.33	
	$\chi^2$	257.53	178.56	
Totals	Observed	520	750	1270

$$\chi^2 = 694.90$$

$$\text{Adjusted } \chi^2 = 689.67 \text{ with 1 d.f. (p < 0.001)}$$

$$\text{Coefficient of contingency} = .547$$



Table 13. Individual chi-square test of prey selection between bluegill sunfish and largemouth bass for Chironomid larvae found in stomach analysis.

		<u>Clinotanypus</u>	<u>Chironomus</u>	Total
Bluegill	Observed	157	521	678
	Expected	338.12	339.88	
	Deviation	-181.12	+181.12	
	$\chi^2$	97.02	96.52	
Bass	Observed	417	56	473
	Expected	235.88	237.11	
	Deviation	+181.12	-181.12	
	$\chi^2$	139.07	138.35	
Totals		574	577	1151

$$\chi^2 = 470.96$$

$$\text{Adjusted } \chi^2 = 468.40 \text{ with 1 d.f. } (p < 0.001)$$

$$\text{Coefficient of contingency} = .409$$

the redear and bluegill sunfish differed more from the bass than from one another and that the sunfish preferred Chironomus while bass more often selected Clinotanypus.

## DISCUSSION

Two important aspects of this study can be analyzed with respect to other studies. The first is a discussion of the paucity of species in the benthic community in Imperial Reservoir. This will be analyzed under the general topic of limitations to distribution of aquatic invertebrates. The second aspect concerns the secondary benthic production in Imperial Reservoir, the factors that affect it, and the relative importance of benthic production in Imperial Reservoir in relation to other bodies of water.

### Limitation to Distribution

When the number of species of insects, oligochaetes, and molluscs were compared in similar studies of reservoirs, river deltas, flood plain lakes, and natural lakes of differing trophic status, the benthic habitat of Imperial Reservoir had a relatively species poor macroinvertebrate community (Table 14). Only Lake Esrom showed as low a number of benthic taxa as Imperial Reservoir, however, only the data from the profundal zone was presented (Jonasson 1972). The other studies referenced in Table 14 surveyed a more complete range of benthic habitats, as did the present study, and they showed a much higher number of benthic taxa than did Imperial Reservoir. There are a number of factors associated with limitation of benthic macroinvertebrate distribution and a reduction of species number.

Table 14. Comparison of the number of species of insects, annelids and molluscs found in Imperial Reservoir, with numbers found in similar studies.

Type of Body of Water	Insect Species (n)	Annelid Species (n)	Mollusc Species (n)
<b>Reservoirs</b>			
Imperial Reservoir	4	2	1
Lake Kariba (McLachlan and McLachlan 1971)	20	2	0
Slapy Reservoir (Hruska 1968)	20-12	1	1
<b>Rivers, Flood Plain Lake and Deltas</b>			
Lake Matanzas	13	7	2
Lake Chautauqua	29	7	4
Quiver Lake (Paloumpis and Starrett 1960)	17	11	14
Pickereel Slough (Heuschele 1969)	9	3	0
Delta of Rhine, Meuse and Schudt (Parma and Krebs 1977)	12	Not enumerated	Not enumerated
<b>Lakes, Profundal Zone</b>			
Lake Esrom (eutrophic) (Jonasson 1972)	3	3	2
Lake Washington (mesotrophic) (Thut 1969)	15	5	2
Lake Ontario (mesotrophic) (Johnson and Brinkhurst 1971)	43	20	22
Lac la Ronge (oligotrophic) (Oliver 1960)	108	20	23
Banana Lakes (6 lakes ranging from meso to oligotrophic) (Osborne et al. 1976)	18	3	0
Sewage lagoons, Missouri (Fagen and Enns 1966)	12	Not enumerated	Not enumerated

### Physical-chemical Characteristics

Of the chemical-physical data collected in this study, pH was not in the range that would be limiting to benthic macrofauna, except perhaps to organisms requiring a more acid environment as found in soft water lakes. Temperature, while not extreme, was certainly higher than in the north temperate lakes referenced in Table 14. Only the Banana Lakes in Florida had such high temperatures (Osborne, Wanielista and Yousef 1976). Hilsenhoff (1966) found that the life span of chironomid imagos decreased with higher temperature and lower humidity. Imperial Reservoir is subject to tropical desert weather which includes not only high temperatures but low humidity. Dissolved oxygen concentrations were relatively high except for occasional low pre-dawn readings near the bottom (Hallock, personal communication 1975). Low dissolved oxygen concentrations can be limiting to benthic insects as was shown by Fagan and Enns (1966). They found aquatic insect larvae restricted to the margins of sewage lagoons where the water was oxygenated by algae and none were found in the deeper deoxygenated zones. Walshe (1948) showed that chironomid larvae have evolved two independent adaptive lines with regard to high temperature and low oxygen tolerance and these two categories are ecologically restricted to exclusively different habitats. In the summer, Imperial Reservoir has periods of not only occasional low dissolved oxygen concentrations but also relatively high temperatures. All the benthic macrofauna collected possess either physiological (haemoglobin-like respiratory pigments), anatomical (external gill filaments), or behavioral (escaping bottom during the dark) adaptations that strongly suggest some sort of periodic oxygen

deficiency is involved in preventing less tolerant species of benthic macrofauna from inhabiting the reservoir. Corbicula fluminea was found in shallower areas and usually where there were substantial currents and oxygenated waters.

Salinity may also be a factor contributing to the low number of benthic macrofauna in Imperial Reservoir. Specific conductance of water changes proportionately to the amount of dissolved substances and is an index of salinity (Wetzel 1975). Specific conductance in Imperial Reservoir ranged between 1300 to 1600  $\mu\text{mhos/cm}$  (U.S. Geological Survey 1970), placing it approximately 3% as saline as sea water. Some backwaters had  $4 \times 10^4$   $\mu\text{mhos/cm}$  making it nearly as saline as sea water. Remane and Shlieper (1971) found that at 5% salinity the number of freshwater species was drastically reduced and aquatic environments with between 5 and 20 percent had progressively fewer species. Waters with salinities greater than 20 percent had no freshwater species. The only benthic distributional study with conductivity data was from the Florida Banana Lakes and the values ranged from 86 to 169  $\mu\text{mhos/cm}$ , an order of magnitude less than Imperial Reservoir. Parma and Krebs (1977) have shown that salinity, particularly the concentration of the chloride ion, was the limiting factor affecting the colonization and distribution of chironomids in the Delta region of the Netherlands. I compared the concentration of eight common ions in Imperial Reservoir with means for rivers on the major continents and seven north temperate lakes (Table 15). Except for  $\text{SO}_2$  Imperial Reservoir has the highest concentration of all ionic species, especially

Table 15. A comparison of Imperial Reservoir with some rivers and lakes for ionic composition in mg/l. --- Data modified from Benoit 1969.

	Ca <sup>++</sup>	Mg <sup>++</sup>	Na <sup>+</sup>	K <sup>+</sup>	HCO <sub>3</sub> <sup>-</sup>	SO <sub>4</sub> <sup>-</sup>	Cl <sup>-</sup>	SiO <sub>2</sub>
Imperial Reservoir*	96.2	36.5	154.4	148.7	175.1	229.3	139.9	6.7
<u>Rivers</u>								
North America	21	5	9	1.4	68	20	8	9
South America	7.2	1.5	4	2	31	4.8	4.9	11.9
Europe	31.1	5.6	5.4	1.7	95	24	6.9	7.5
Asia	18.4	5.6	6.5	3.8	79	8.4	8.7	11.7
Africa	12.5	3.8	11	-	43	13.5	12.1	23.2
Australia	3.9	2.7	2.9	1.4	31.6	2.6	10	3.9
<u>Lakes</u>								
Superior	12	2.8	1.1	0.6	-	-	-	2.1
Michigan	32	10	3.4	0.9	-	-	-	3.1
Huron	23	6.3	2.3	1.0	-	-	-	2.3
Erie	37	8.0	10	1.4	-	-	-	1.5
Ontario	39	8.2	9.5	1.8	-	-	-	3.0
Sylvan Lake	53	19.5	47	3.4	-	53	-	-
Goose Lake	43	12	72	3	-	13	-	-

\*U.S.G.S. 1970.

chloride. These ions, particularly  $\text{NA}^+$ ,  $\text{K}^+$ ,  $\text{SO}_4^{=}$ , and  $\text{Cl}^-$  could have toxic effects at high concentrations.

### Trophic State

Lakes and reservoirs are classed accordingly to their relative productivity, low to high, as oligotrophic, mesotrophic, or eutrophic (Wetzel 1975). Along with productivity, several other factors such as amount of dissolved substances, particularly nutrients and oxygen, are typical of the various trophic states.

There are four lakes referenced in Table 14 (Esrom, Washington, Ontario, and Lac LaRouge) in the upper half of the north temperate zone which exhibited a range of trophic states. Only waters from the same general latitude were compared because there appears to be a change in the number of species of various groups of organisms from tropic to temperate to arctic zones (Fischer 1960). Lake Esrom is highly eutrophic while Lake Washington and Lake Ontario are both in the mesotrophic range. Lac LaRouge is classified as oligotrophic. Related to the ranking of these four lakes by trophic state was a reduction in the number of kinds of benthic taxa as the lake became more eutrophic. In a review of benthic lake topologies in northern Europe, Brinkhurst (1974) also found that eutrophic lakes supported a simple benthic fauna composed only of a single species of Chironomus and a few oligochaete worms. The TSI of Esrom calculated from data in Jonasson (1972) was in the same range as Imperial Reservoir. Both lakes had very similar benthic faunal assemblages.



### Importance of Detritus

Most benthic invertebrates feed at least partly on organic detrital material (Cummins 1973). Lake Matanzas, Lake Chautaugua, Quiver Lake, and Pickerel Slough were all flood plain lakes on large rivers receiving a relatively large amount of organic detritus, and had a relatively large number of taxa in the benthic community. Hruska (1968) showed that the number of benthic species was reduced from 20 to 12 in Slapy Reservoir after construction of a dam upstream reduced the amount of organic detrital material washed in by the river. Imperial Reservoir is the fifth in a series of major impoundments on the Colorado River. The four upper dams and their reservoirs effectively prevent much of the particulate organic detrital material from the more heavily vegetated headwater regions of the Colorado River from reaching Imperial Reservoir. The watershed between Imperial Reservoir and the next dam upstream is desert and provides relatively little allochthonous organic material. The amount of organic carbon may be an index of the amount of nutrition detrital material in the sediments. In the profundal zone of a newly created African reservoir, a high positive correlation existed between the amount of organic carbon in the hydrosol and benthic faunal biomass (McLachlan and McLachlan 1971). The analysis of benthic hydrosol from three sites in Imperial Reservoir showed a very low nitrogen and carbon fraction indicating that detrital material is low.

### Habitat Characteristics

Habitat diversity was also limited in Imperial Reservoir due to shallowness. Wetzel (1975) lists five generalized benthic zones

present in most lakes. Due to its relative shallowness, Imperial Reservoir possesses only the upper two or possibly three zones. Many other lacustrine benthic zonation classifications were reviewed by Brinkhurst (1974) and it is apparent that there are many types of habitats due to specific substrate types and plant associations which do not occur here.

The most important factor affecting the ecological distribution of benthic macroinvertebrates within Imperial Reservoir was substrate. The heavy current and resulting unstable sandy bottoms prevented the establishment of a benthic community in the channels. Corbicula alone was able to live on shallow sand bars and in shallow areas along the margin of channels. Harman (1972) showed that mollusc species in New York lakes were restricted to specific substrates, and that the number of different kinds of benthic substrate determined the number of species in a lake. Brinkhurst (1974) found that species association of benthic invertebrates were characteristic of certain substrate types in northern European lakes. In an African reservoir where the substrate was made up of greater than 69% sand chironomid larvae were excluded (McLachlan and McLachlan 1971).

The amount, type, and location of vegetation is also a habitat quality. Aquatic macrophytes played a secondary role in limiting benthic macroinvertebrates. Small bodies or ponds of water restricted from the river by beds of T. latifolia acted as evaporating pans and specific conductances of up to  $4 \times 10^4$   $\mu\text{mhos/cm}$  were found (Hallock 1973). These were devoid of benthic fauna. Areas supporting rooted macrophytic vegetation also lacked benthic fauna. Much of the data in

the literature does not distinguish between benthic organisms and those found in the vegetation beds themselves (Andrikovics 1975; McLachlan 1975). Korinkova (1967) found that chironomid larvae greatly increased after removing beds of submersed macrophytes. The soil below T. latifolia beds in Imperial Reservoir was periodically exposed due to fluctuations in the reservoir level, which would be limiting to aquatic fauna. The N. marina beds were thick enough to prevent most eggs laid by aerial insects from reaching the bottom. In addition, N. marina beds contain swarms of young fish which used the cover (Weaver 1971) and other invertebrate predators such as glass shrimp (Palaemonetes kadiakensis) and dragonfly naiads (order Odonata) which were abundant. Such high densities of predators could prevent the development of a benthic community.

The size of the sample site could also be an important factor in determining distribution. Hilsenhoff (1967) reports that newly emerged imagos of Chironomus plumosus are weak fliers and wind direction and velocity during the time of emergence and oviposition are important factors in determining the distribution and abundance of the subsequent crop of larvae on the lake bottom. Imperial Reservoir is located in a desert subject to frequent, persistent, and strong winds. Organisms with this type of life cycle and subject to the vagaries of the winds would have a better chance in larger bodies of water or in an area with many lakes. It would be easier for an organism to remain over a lake with a larger surface area or to colonize and recolonize in areas with many aquatic habitats. The distribution of Chironomus was significantly correlated with size of the sample late in summer.

The food of an organism is often an important factor in determining its ecological distribution. The reported trophic status of an individual benthic taxon varies considerably in the literature (Merritt and Cummins 1978). The oligochaet worms are certainly detritivores, that is they ingest fine particles of dead particulate organic matter and accompanying decomposer microorganisms. In the summer the three chironomid larvae ingested diatoms as well as some detritus (Table 2). The percentage of shorelines having populations of dense stands of rooted aquatic vegetation is a rough measure of the potential for a site to receive local organic detrital material. The ranked correlation of percent vegetation of a shore with the distribution of Pentaneura was significant ( $P \leq 0.05$ ) in the summer (Table 6).

Close association of a sample site with the main river channels which run through Imperial Reservoir may be responsible for bringing increased amounts of fine organic detrital material and inorganic nutrients which are utilized by phytoplankton. Phytoplankton and organic detritus are used as food by benthic invertebrates. In the summer, ranked correlation coefficients were significant ( $P \leq 0.05$ ) and positive for Chironomus, Limnodrilus and Branchiura with sample sites ranked by potential for exchange with the main channels. In the winter, correlations were significantly positive for Branchiura and negative for Chironomus. Thus, of the three variables tested, increased association with the main channel was the factor most associated with the biannual distribution of benthic invertebrates.

### Reduced Invasion Pressure

Barriers to animal dispersal may also contribute to keeping the benthic faunal simple. Imperial Reservoir is in the middle of the driest desert in North America (Shreve and Wiggins 1964). It is several hundred miles from any natural lake. The aerial stages of most benthic insects characteristically last one to several days (Pennak 1953; Usinger 1956) before they breed and die. A fortuitous wind would be necessary before an adult would cross the desert and reach the reservoir. Oligochaet worms and molluscs having no terrestrial or aerial forms would find it even more difficult to reach the reservoir from other watersheds.

### Pesticides

Imperial Reservoir is adjacent to an agricultural area intensely managed with agricultural chemicals, including various pesticides. It also receives irrigation return water from agricultural areas 40-50 river miles upstream. Fish collected in Imperial Reservoir contained variable concentrations of the insecticides DDT and its metabolites DDD and DDE as well as dieldrin (Johnson and Lew 1970; Henderson, Juglis and Johnson 1971). In addition to insecticides, the herbicides 2,4-D, 2,4,5-T and Silvex have been found in water samples taken at Imperial Dam (Schulze, Manigold and Andrews 1973). Therefore, pesticide contamination might be partially responsible for limiting the number of benthic insects in Imperial Reservoir. Routes of dispersion from other bodies of water may also be partially blocked since most of the nearly mesic areas which could serve as corridors or stepping stones for insect migration are also heavily managed with pesticides.

### Community Analysis

The interaction among similar species is also important in determining distribution of biological organisms (Krebs 1972). Taxa may directly interact in several ways: as predator-prey, as competitors, as commensals, or as symbiotics. Brinkhurst (1972) found that one species of oligochaet worm was enhanced by the presence of a second species and that the feces of one was more easily digested than the ambient detritus. Brinkhurst (1974) also found this an important factor in interspecific aggregations of tubficid oligochaetes. Loden (1974) showed that larvae of Chironomus and Pentaneura used oligochaetes as food in both lab experiments and in fishponds. Of all possible pairs of taxa compared in the summer-winter distribution studies, several exhibited an index of affinity of over 0.50 and were formed into recurrent groups. There were no distinct differences among the sites sampled.

Figure 4 shows the arrangement of significantly recurring taxa into recurrent groups. The groups differ only slightly between the summer and winter distribution collections. That so many of the taxa reoccur so often among the seven sample sites with mud bottoms suggests great similarity, or low habitat diversity among the side lakes and furthermore that there may be functional relationships among the macro-invertebrate communities. The low benthic species number supports the contention that there is low habitat diversity in Imperial Reservoir.

### Microdistribution

The determination of annual dispersal pattern, or microdistribution has been presented for the six taxa of Sites 1 and 8. The trend

in chi-square values for both the variance to mean ratio and Morisita's index indicate a microdistribution change from contagious early in the life cycle to random in the later instars for both Clinotanypus and Pentaneura. This trend is also apparent in Chironomus although the correlation was not statistically significant. Other studies have dealt with fewer numbers of samples with both space and time. Thut (1969) described Chironomus sp. as contagiously distributed in Lake Washington in the early life stages. Ricker (1952), Allen and Anderson (1969) and Milbrink, Lundquist and Promsten (1974) used a variety of methods to determine that chironomid larvae were randomly distributed in several north temperate lakes. However, all these studies considered spatial distribution at the family or subfamily level and Paterson and Fernando (1971) have pointed out this could be a mix of contagiously distributed species. A more recent study by Shiozawa and Barnes (1977) showed population trends similar to that found in this present study, that is, a pattern of increased randomization with the age of the population.

Several possible reasons exist for this change in pattern. Edgar and Meadows (1969) artificially clumped an experimental population of Chironomus riparius which became randomly and finally regularly spaced within 100 hrs. This tendency to become more random was predominant among young larvae. One explanation for the oscillations observed in some of the plots of spatial distribution (Figs. 16, 21 and 22) may be the young larvae from different egg masses moving out from their points of initial development. A second cause of the animals distributing themselves in a more random fashion may be found in

a study by Ikeshoji (1974) who extracted growth-retarding and toxic compounds from populations of experimentally overcrowded Chironomus sp. Thus, it may be advantageous for a population to quickly spread out rather than to develop where the egg mass hatches.

### Production

Net production of benthic macroinvertebrates was low in Imperial Reservoir when compared to production estimates from studies in other waters. Table 16 shows the net benthic production, turnover ratio and the general trophic status of a number of different lakes and reservoirs in which similar methods were employed. Production figures were converted to  $\text{Kcal/m}^2$  using information in Cummins and Wuychek (1971) and the trophic state was classified after Carlson (1977).

The highest production measured was in a sewage lagoon (Kimerle and Anderson 1971) where there was both very high primary production induced by high nutrient levels and a large input of organic detrital material. Table 16 shows the dependence of benthic production on primary production in a body of water is apparent within the higher latitudes (Alimov et al. 1972). However, in low nutrient, low productivity oligotrophic lakes the higher temperatures and longer growing season of the temperate region yielded greater production levels of benthos (Alimov et al. 1972; Andronikova et al. 1972). Among lakes in the north temperate region there was no simple association between general trophic state and benthic invertebrate production (Table 16). The Spearman ranked correlation coefficient of annual primary productivity with benthic productivity values from Winberg (1972) and Jonasson (1972) was low ( $r_s = 0.4$ ) and not statistically significant.



Table 16. A comparison of annual benthic macroinvertebrate net production estimates and annual turnover ratios among several different lakes.

	Annual Net Production of Benthic Macroin- Kcal/m <sup>2</sup>	Annual Turn- over Ratio	Lake Classification of Magni- tude of Primary Production
Imperial Reservoir			Shallow eutrophic reservoir
Site 1	20.2	3.39	
Site 8	22.1	2.78	
Kimberle and Anderson (1971)	808	8.49	Shallow margin of sewage lagoon
Alimov et al. (1972)	1.85	1.31	Polar oligotrophic
	4.50	2.1	Polar mesotrophic
Andronikova et al. (1972)	20.4	4.3	Temperate oligotrophic
Kajak et al. (1972)	275.25	13.5	Deep temperate mesotrophic
	82.5	13.2	4 m deep
			8 m deep
	107.25	10.7	Deep temperate eutrophic
	54.75	13.0	4 m deep
			8 m deep
Winberg (1972)	38.25	12.9	Shallow temperate eutrophic
	33.75	14.0	4 m deep
			6 m deep
	19.4	4.3	Temperate mesotrophic
	12.8	3.9	Mesotrophic reservoir
	11.0	0.64	Temperate mesotrophic
	12.3	2.4	Eutrophic temperate
	3.3	4.7	Eutrophic temperate
	11.5	4.8	Eutrophic temperate
	170.4	3.6	Eutrophic reservoir

Table 16--Continued.

	Annual Net Production of Benthic Macroin- Kcal/m <sup>2</sup>	Annual Turn- over Ratio	Lake Classification of Magni- tude of Primary Production
Johnson and Brinkhurst (1971)	74.3 232.7 65.8 50.6	13.6 7.8 2.6 1.3	Lake Ontario
Dermott et al. (1977)	9.5-23.5	3.3-2.8	Temperate mesotrophic
Jonasson (1972)	100	2.4	Temperate eutrophic

Dermott et al. (1977) found that within a mesotrophic lake the difference in the net production of benthic macroinvertebrates was related to increased primary production at different sites.

In addition to the amount of primary production, the other major factors affecting secondary benthic productivity are dissolved oxygen concentration, the amount of allochthonous detrital material brought in, temperature, and fish production.

### Oxygen

In an experimental study of the effect of various oxygen concentrations on Chironomus behavior, Walshe (1948) found that in low concentrations of dissolved oxygen first increased the percent of time a larvae spent in respiratory movements and decreased the amount of time feeding. Further reduction of dissolved oxygen to below 10% saturation caused the larvae to cease feeding. Jonasson (1965, 1972) and Jonasson and Kristianson (1967) found that the rate of benthic production dropped in Lake Esrom and finally stopped during stratification of the lake during the summer when the dissolved oxygen in the hypolimnion reach the lowest point. Daytime dissolved oxygen concentrations in Imperial Reservoir were near and frequently above saturation. Despite the possibility of periodic low concentrations at dawn the production values in Table 9 show no great difference among different generations in different seasons of the year. Therefore the data from Imperial Reservoir do not suggest that low dissolved oxygen concentration was greatly affecting secondary benthic production, even though it does in most stratified eutrophic lakes.

### Detritus

The input of organic detrital material into Imperial Reservoir was not measured in this study, but for reasons already discussed it is presumed to be relatively low when compared to other bodies of water with vegetated watersheds. Kajak (1964a, 1964b, 1965), Kajak and Rybak (1966), Walshe (1951) point out the dependency of certain species of benthos on allochthonous detrital material. Hruska (1968) found that both biomass and number of species was reduced in a reservoir when the input of detritus was reduced. Johnson and Brinkhurst (1971) stated that the decline in macroinvertebrate production in Lake Ontario from inshore to offshore areas was related to decreased sedimentation of detritus and increased settling time. Organic carbon has been shown to be low in hydrosols taken from Imperial Reservoir. Lack of quantity and perhaps lack of different types of organic material were possible reasons for limiting net production.

### Temperature

Net production is equal to gross production, also called assimilation, minus respiration (Ricker 1946). Any environmental factor that increases respiration without increasing assimilation of a population would decrease net production. Berg, Jonasson and Ockelmann (1962) found no fixed relationship between oxygen consumption and temperature but instead found three general response categories: (1) where respiration rate increased less at higher temperatures, indicating some adaptation to temperature stress; (2) a linear increase in respiration with temperature; and (3) where the oxygen

consumption rate increased faster at higher temperatures. In laboratory cultures of bottom cores from Lake Ontario, Johnson and Brinkhurst (1971) showed that, for the ranges of 3° to 21°C, the instantaneous growth rate per day of Oligochaetes and Chironomids was significantly and positively correlated with temperature, indicating a linear response. Walshe (1948) found that a sustained temperature of 29°C had lethal effects on some species of chironomid larvae and that none survived temperatures above 38°C. Several investigations on terrestrial insects have shown that sublethal high temperatures were responsible for slowed growth and delayed development (Fye, Patana and McAda 1969, Fye and Poole 1971, Fye and McAda 1972). This means a slowing of the production rate and implies that the total production would be lowered.

The high summer water temperature, to 30°C in Imperial Reservoir appeared to be a factor contributing to the low benthic productivity. Johnson and Brinkhurst (1971) showed that the predominant benthic production was in the summer months in Lake Ontario. However, in Imperial Reservoir most of the secondary benthic production occurred in the spring and fall (Table 9). Only Cohort II of Clinotanypus was a major producer during the summer months but only comprised 30% of the total at Site 1 and 22% at Site 8. Cohort I and III were also shorter in duration than Cohort II at both Sites 1 and 8. In addition, the correlations of temperature with instantaneous growth rate per day was significant and negative for Cohort I of Clinotanypus at Site 8 (Table 10). The overall correlation of specific growth rate per day with temperature for the three cohorts of Clinotanypus was positive and

significant (Table 10). Cohort I of Clinotanypus and Chironomus at Site 8 were also negatively correlated, although not significantly statistically. Thus, not only is the relationship between temperature and specific growth rate different in magnitude but in the spring the correlation is inverse.

The effect of temperature on productivity over the period of a year was also discussed by Johnson and Brinkhurst (1971). Annual production (P) may be thought of as the mean standing biomass ( $\bar{B}$ ) multiplied by the turnover ratio (TR), or  $P = (\bar{B})TR$ . They found that for several sites in Lake Ontario the mean annual bottom temperature (T) was related to the turnover ratio (TR) by the equation  $TR = T^2/10$ . This relationship does not hold for Imperial Reservoir. If the mean bottom temperature for Site 1, 21.8°C, and Site 8, 21.6°C, are used in the formula, TR's of 47.5 and 46.6 respectively resulted. These values are more than an order of magnitude higher than those for Lake Ontario and three times higher than the highest reported in the literature (Table 16).

### Predation

Finally, one additional factor may be responsible for the relatively low production of benthic macroinvertebrates in Imperial Reservoir. Kajak (1964a, 1966) found that the numbers of aquatic insects increased in benthic areas covered by experimental cages and he stated that the difference may have been due to cropping by small fish. Kajak (1972), in additional experiments, found the exclusion of fish from benthic areas with wire cages also increased benthic net production

over surrounding areas subject to fish predation. Hayne and Ball (1956) showed that experimental introduction or removal of fish from experimental ponds increased both the biomass of numbers of benthic insects. Efford (1972) listed vertebrate predators as the primary factor in limiting net production of benthic herbivore in a small coast lake. He also found predation much higher in the shallower areas where the prey forms could be seen. Site 1 is a typical side lake in Imperial Reservoir. It is euphotic year round allowing predacious fish who hunt by sight to use the entire benthic area. The three species of Centrarchid fish, which were sight feeders, showed heavy utilization of benthic insects relative to other food items (Fig. 25). Weaver (1971) found that distribution of swarms of fish fry was limited to the N. marina beds where there was enough cover to allow them to escape larger fish predators. He also found that these fish had a high occurrence of benthic insects in their stomachs after collections. The smaller-sized fish collected at Site 1 do indeed rely on benthic insects (Fig. 25). Even the larger-sized bluegill and redear sunfish had a large percentage of benthic insects in their stomach contents. Gerking (1962) reported the food habits for larger bluegill (9-17 cm) in a small (3.18 ha) eutrophic Indiana lake similar to the side lakes in Imperial Reservoir in which bluegill was the predominant fish. He found that benthic insects comprised approximately 50% of the dry weight contents of the stomachs which is lower than the mean, 63%, calculated for similar-sized bluegill collected at Site 1. Dipteran larvae comprised between 4 and 80% of redear stomach contents whereas at Site 1 in Imperial Reservoir, redear stomach analysis showed

that 85% of the estimated volume was comprised of Dipteran larvae. It is apparent that the bluegill and redear sunfish in Imperial Reservoir are highly dependent on benthic macroinvertebrates.



## SUMMARY

1. Imperial Reservoir supported a low number of taxa of benthic macroinvertebrates relative to other bodies of water. Reasons for the simple benthic community include high salinity, low habitat diversity, a highly eutrophic condition and the presence of pesticide residue in the water. The remoteness of Imperial Reservoir from other mesic and aquatic habitats was also considered.

2. Benthic invertebrates within Imperial Reservoir were limited to small side lakes. The primary factors limiting distribution were shifting sand substrates, rooted aquatic macrophytes with accompanying swarms of predacious young fish, and high salinity in some of the back-water areas.

3. Potential exchange with the main channels, size of the sample site, and percent of the shoreline with dense vegetation were positively correlated with the distributional pattern of several individual benthic taxa.

4. The dispersion pattern of benthic invertebrates fell into two patterns: taxa which bred continuously, appearing to have no change relative to life history, and taxa which formed recognizable cohorts, appearing to spread out from the initial egg mass and distribution went from clumped to random.

5. Net production of benthic invertebrates in Imperial Reservoir was low relative to values from other studies. High water temperature,

low amount of detrital material, and high predation by fish were considered contributing factors.

6. Stomach analysis of three species of centrarchid fish showed them highly dependent on benthic invertebrates for food. In general, smaller fish were more dependent than larger. There was a difference in the selectivity of prey by the fish.

APPENDIX A

COMPARISON OF TWO INDICES OF DISPERSION  
AND STATISTICAL TESTS

Table A-1. Test of dispersion of Clinotanypus sp. collected in the biweekly samples at Site 1. -- The variance to mean ratio is represented by I followed by its  $X^2$  test. Morisita's index of aggregation ( $I_{\delta}$ ) is followed by a  $X^2$  test and an F statistic,  $X^2$  values greater than 32.8 and F values greater than 1.67 indicated a contagious population.

	I	$X^2$	$I_{\delta}$	$X^2$	F
March 13	1.86	35.34	1.10	35.43	1.86
April 10	4.91	93.29	1.11	93.29	4.91
May 1	0.13	2.46	0.94	2.45	0.13
May 16	4.93	93.71	1.28	93.72	4.93
June 3	4.53	86.13	1.28	86.14	4.53
June 14	3.76	71.51	1.19	71.52	3.76
June 29	3.93	74.59	1.13	74.65	3.93
July 15	4.04	76.78	1.07	76.78	4.04
July 27	7.41	140.87	1.10	140.87	7.41
Aug. 11	3.78	71.90	1.06	71.89	3.78
Aug. 21	5.04	95.67	1.08	95.67	5.04
Sept. 3	4.18	79.48	1.07	79.48	4.18
Sept. 18	6.51	123.65	1.12	123.66	6.51
Oct. 2	3.47	66.02	1.17	66.02	3.47
Oct. 15	1.74	32.97	1.09	32.97	1.74
Oct. 30	2.48	47.11	1.37	47.13	2.48
Nov. 12	1.77	33.66	1.16	33.65	1.77
Dec. 4	3.82	72.59	1.12	72.59	3.82
Dec. 31	1.40	26.57	1.03	26.57	1.40
Jan. 24	3.50	66.52	1.49	66.51	3.50
Feb. 12	1.79	34.07	1.13	34.08	1.79
Feb. 26	5.31	100.93	3.05	100.95	5.31
March 17	11.79	223.98	1.22	223.98	11.79

Table A-2. Test of dispersion of Chironomus plumosus collected in the biweekly samples at Site 1. -- The variance to mean ratio is represented by I followed by its  $X^2$  test. Morisita's index of aggregation ( $I_{\delta}$ ) is followed by a  $X^2$  test and an F statistic,  $X^2$  values greater than 32.8 and F values greater than 1.67 indicated a contagious population.

	I	$X^2$	$I_{\delta}$	$X^2$	F
March 13	3.52	67.03	1.47	67.15	3.53
April 10	3.31	62.98	2.13	63.00	3.32
May 1	2.00	37.95	1.26	37.96	2.00
May 16	9.92	188.55	1.25	189.40	9.97
June 3	1.08	20.54	1.01	20.55	1.08
June 14	5.23	99.30	1.30	99.30	5.23
June 29	3.74	70.97	1.29	70.97	3.74
July 15	3.76	71.45	1.43	71.44	3.76
July 27	4.57	86.77	1.82	86.95	4.58
Aug. 11	2.76	52.47	2.34	52.46	2.76
Aug. 21	2.67	50.81	2.22	50.78	2.67
Sept. 3	1.37	26.06	1.54	26.00	1.37
Sept. 18	1.42	27.07	2.14	27.00	1.42
Oct. 2	-	-	-	-	-
Oct. 15	-	-	-	-	-
Oct. 30	-	-	-	-	-
Nov. 12	-	-	-	-	-
Dec. 4	-	-	-	-	-
Dec. 31	-	-	-	-	-
Jan. 24	-	-	-	-	-
Feb. 12	-	-	-	-	-
Feb. 26	-	-	-	-	-
March 17	-	-	-	-	-

Table A-3. Test of dispersion of Pentaneura sp. collected in the biweekly samples at Site 1. -- The variance to mean ratio is represented by I followed by its  $X^2$  test. Morisita's index of aggregation ( $I_{\delta}$ ) is followed by a  $X^2$  test and an F statistic.  $X^2$  values greater than 32.8 and F values greater than 1.67 indicated a contagious population.

	I	$X^2$	$I_{\delta}$	$X^2$	F
March 13	1.96	37.25	1.36	37.24	1.96
April 10	-	-	-	-	-
May 1	1.41	26.83	1.16	26.80	1.41
May 16	.85	16.24	.87	16.18	.85
June 3	1.20	22.80	2.00	23.00	1.21
June 14	1.04	19.84	1.11	19.89	1.05
June 29	.77	14.57	.61	14.67	.77
July 15	.76	14.44	.00	15.00	.79
July 27	3.15	59.90	3.05	59.95	3.16
Aug. 11	.73	13.93	.00	16.00	.84
Aug. 21	-	-	-	-	-
Sept. 3	-	-	-	-	-
Sept. 18	-	-	-	-	-
Oct. 2	.90	17.10	.71	17.00	.89
Oct. 15	1.05	19.95	1.05	20.00	1.05
Oct. 30	-	-	-	-	-
Nov. 12	.97	18.46	.95	18.71	.98
Dec. 4	-	-	-	-	-
Dec. 31	-	-	-	-	-
Jan. 24	3.46	65.69	3.33	65.67	3.46
Feb. 12	.57	10.84	.68	10.78	.57
Feb. 26	1.21	23.07	1.32	23.14	1.22
March 17	1.64	31.16	4.00	31.00	1.63

Table A-4. Test of dispersion of Branchiura sowerbyi collected in the biweekly samples at Site 1. -- The variance to mean ratio is represented by I followed by its  $X^2$  test. Morisita's index of aggregation ( $I_{\delta}$ ) is followed by a  $X^2$  test and an F statistic.  $X^2$  values greater than 32.8 and F values greater than 1.67 indicated a contagious population.

	I	$X^2$	$I_{\delta}$	$X^2$	F
March 13	1.40	26.56	1.09	26.48	1.39
April 10	3.16	59.96	6.11	59.89	3.15
May 1	1.02	19.45	1.03	19.47	1.02
May 16	1.77	33.54	1.66	33.52	1.76
June 3	1.97	37.46	2.42	37.43	1.97
June 14	3.17	60.29	4.19	63.67	3.35
June 29	2.23	42.30	2.06	42.22	2.22
July 15	3.39	64.42	2.08	64.44	3.39
July 27	1.56	29.70	1.20	29.70	1.56
Aug. 11	1.71	32.47	1.88	39.33	2.07
Aug. 21	-	-	-	-	-
Sept. 3	-	-	-	-	-
Sept. 18	.73	13.96	1.09	22.70	1.26
Oct. 2	1.74	32.98	1.19	33.00	1.74
Oct. 15	3.36	69.55	1.36	69.55	3.66
Oct. 30	2.26	42.89	2.30	46.00	2.30
Nov. 12	1.13	21.46	1.02	21.47	1.13
Dec. 4	2.25	42.67	1.20	42.68	2.25
Dec. 31	1.92	36.40	1.11	36.41	1.92
Jan. 24	1.65	31.30	1.06	26.94	1.42
Feb. 12	2.58	48.97	2.08	53.67	2.82
Feb. 26	3.83	72.83	2.15	72.83	3.83
March 17	1.43	27.23	2.67	27.33	1.44

Table A-5. Test of dispersion of Limnodrilus hoffmeisteri collected in the biweekly samples at Site 1. -- The variance to mean ratio is represented by I followed by its  $X^2$  test. Morisita's index of aggregation ( $I_g$ ) is followed by a  $X^2$  test and an F statistic.  $X^2$  values greater than 1.67 indicated a contagious population.

	I	$X^2$	$I_g$	$X^2$	F
March 13	.86	16.28	.96	16.27	.86
April 10	.50	9.41	.77	9.43	.50
May 1	1.63	31.03	1.52	31.00	1.63
May 16	2.07	39.24	1.45	39.22	2.06
June 3	1.51	28.69	1.14	28.68	1.51
June 14	1.83	34.78	2.31	34.69	1.83
June 29	2.37	45.09	2.86	45.00	2.37
July 15	2.48	47.06	3.33	47.00	2.47
July 27	1.41	26.82	1.07	26.83	1.41
Aug. 11	-	-	-	-	-
Aug. 21	.90	17.10	.71	17.00	.89
Sept. 3	2.03	38.58	1.93	41.40	2.18
Sept. 18	2.32	43.99	1.78	43.97	2.31
Oct. 2	3.36	63.89	4.00	64.00	3.37
Oct. 15	1.39	26.33	1.27	26.29	1.38
Oct. 30	.32	6.09	.84	6.62	.35
Nov. 12	.58	11.09	.78	11.11	.58
Dec. 4	1.58	30.02	2.22	30.00	1.58
Dec. 31	1.24	23.49	1.45	23.55	1.24
Jan. 24	1.51	28.71	2.22	28.78	1.51
Feb. 12	1.07	20.35	1.06	21.45	1.13
Feb. 26	2.04	38.76	6.00	39.00	2.05
March 17	-	-	-	-	-



Table A-6. Test of dispersion of Clinotanypus sp. collected in the biweekly samples at Site 8. -- The variance to mean ratio is represented by I followed by its  $X^2$  test. Morisita's index of aggregation ( $I_g$ ) is followed by a  $X^2$  test and an F statistic.  $X^2$  values greater than 32.8 and F values greater than 1.67 indicated a contagious population.

	I	$X^2$	$I_g$	$X^2$	F
March 20	2.75	52.32	1.05	52.32	2.75
April 10	7.39	140.42	1.14	140.42	7.39
May 1	3.48	66.11	1.11	71.02	3.74
May 16	3.20	60.90	1.18	60.81	3.20
June 3	1.54	29.21	1.07	38.62	2.03
June 14	2.67	50.74	1.06	50.76	2.67
June 29	2.98	56.55	1.08	56.54	2.98
July 15	4.58	87.04	1.10	87.04	4.58
July 27	1.75	33.21	1.02	33.21	1.75
Aug. 11	5.00	95.07	1.12	95.07	5.00
Aug. 21	4.48	85.11	1.09	85.10	4.48
Sept. 3	3.63	69.01	1.13	69.01	3.63
Sept. 18	1.90	36.06	1.04	36.06	1.90
Oct. 2	2.53	48.04	1.08	48.04	2.53
Oct. 15	2.63	49.94	1.11	49.95	2.63
Oct. 30	.98	18.66	1.00	18.67	.98
Nov. 12	1.43	27.09	1.06	27.09	1.43
Dec. 4	3.55	67.51	1.09	70.04	3.69
Dec. 31	3.68	70.00	1.13	70.00	3.68
Jan. 24	2.83	53.86	1.09	53.85	2.83
Feb. 12	2.09	39.69	1.11	39.70	2.09
Feb. 26	1.89	35.83	1.05	35.83	1.89
March 17	3.86	73.36	1.06	73.37	3.86

Table A-7. Test of dispersion of Chironomus plumosus collected in the biweekly samples at Site 8. -- The variance to mean ratio is represented by I followed by its  $X^2$  test. Morisita's index of aggregation ( $I_{\delta}$ ) is followed by a  $X^2$  test and an F statistic.  $X^2$  values greater than 32.8 and F values greater than 1.67 indicated a contagious population.

	I	$X^2$	$I_{\delta}$	$X^2$	F
March 20	1.23	23.45	1.07	25.40	1.34
April 10	4.87	92.48	2.01	92.49	4.87
May 1	.97	18.34	.99	18.35	.97
May 16	4.18	79.39	1.37	104.66	5.51
June 3	1.13	21.46	1.02	21.47	1.13
June 14	1.27	24.16	1.04	24.16	1.27
June 29	3.22	61.10	1.41	61.08	3.21
July 15	1.32	25.12	1.17	25.11	1.32
July 27	-	-	-	-	-
Aug. 11	-	-	-	-	-
Aug. 21	-	-	-	-	-
Sept. 3	-	-	-	-	-
Sept. 18	-	-	-	-	-
Oct. 2	1.71	32.45	1.54	32.46	1.71
Oct. 15	1.23	23.32	1.21	23.45	1.23
Oct. 30	1.44	27.29	1.82	27.18	1.43
Nov. 12	1.20	22.80	2.00	23.00	1.21
Dec. 4	2.71	51.53	1.17	51.53	2.71
Dec. 31	2.10	39.83	1.16	39.84	2.10
Jan. 24	6.01	114.14	2.69	110.45	5.81
Feb. 12	1.39	26.39	1.44	26.44	1.39
Feb. 26	1.19	22.66	1.14	22.63	1.19
March 17	1.14	21.61	1.17	21.50	1.13

Table A-8. Test of dispersion of Pentaneura sp. collected in the biweekly samples at Site 8. -- The variance to mean ratio is represented by I followed by its  $X^2$  test. Morisita's index of aggregation ( $I_{\delta}$ ) is followed by a  $X^2$  test and an F statistic.  $X^2$  values greater than 32.8 and F values greater than 1.67 indicated a contagious population.

	I	$X^2$	$I_{\delta}$	$X^2$	F
March 20	1.05	19.90	1.05	19.95	1.05
April 10	-	-	-	-	-
May 1	-	-	-	-	-
May 16	-	-	-	-	-
June 3	-	-	-	-	-
June 14	-	-	-	-	-
June 29	-	-	-	-	-
July 15	-	-	-	-	-
July 27	-	-	-	-	-
Aug. 11	-	-	-	-	-
Aug. 21	-	-	-	-	-
Sept. 3	-	-	-	-	-
Sept. 18	-	-	-	-	-
Oct. 2	-	-	-	-	-
Oct. 15	-	-	-	-	-
Oct. 30	-	-	-	-	-
Nov. 12	-	-	-	-	-
Dec. 4	1.95	37.07	1.10	37.06	1.95
Dec. 31	.96	18.23	1.03	23.74	1.25
Jan. 24	.85	16.10	.86	16.14	.85
Feb. 12	1.16	22.00	1.17	22.05	1.16
Feb. 26	.95	18.05	.95	18.00	.95
Mar. 17	.82	15.62	.56	15.44	.81

Table A-9. Test of dispersion of Chaoborus punctipennis collected in the biweekly samples at Site 8. -- The variance to mean ratio is represented by I followed by its  $X^2$  test. Morisita's index of aggregation ( $I_g$ ) is followed by a  $X^2$  test and an F statistic.  $X^2$  values greater than 32.8 and F values greater than 1.67 indicated a contagious population.

	I	$X^2$	$I_g$	$X^2$	F
March 20	1.66	31.49	1.16	31.50	1.66
April 10	3.54	67.31	2.42	67.29	3.54
May 1	1.37	26.03	1.37	26.00	1.37
May 16	3.00	57.00	1.97	57.00	3.00
June 3	.87	16.54	.93	16.59	.87
June 14	1.37	26.06	1.54	26.00	1.37
June 29	.85	16.24	.73	16.27	.86
July 15	1.93	36.71	1.26	36.71	1.93
July 27	1.36	25.86	1.17	25.83	1.36
Aug. 11	2.66	50.47	2.02	50.50	2.66
Aug. 21	1.67	31.82	1.28	32.00	1.68
Sept. 3	4.24	80.47	1.36	80.48	4.24
Sept. 18	2.20	41.71	1.10	41.71	2.20
Oct. 2	1.27	24.16	1.04	24.16	1.27
Oct. 15	3.05	57.93	1.16	57.94	3.05
Oct. 30	1.87	35.47	1.05	35.47	1.87
Nov. 12	4.66	88.60	1.17	88.60	4.66
Dec. 4	1.44	27.42	1.04	27.25	1.43
Dec. 31	1.34	25.41	1.04	25.43	1.34
Jan. 24	3.04	57.78	1.17	57.79	3.04
Feb. 12	2.83	53.83	1.22	53.83	2.83
Feb. 26	1.41	26.84	1.03	26.85	1.41
Mar. 17	1.55	29.38	1.10	34.05	1.79

Table A-10. Test of dispersion of Limnodrilus hoffmeisteri collected in the biweekly samples at Site 8. -- The variance to mean ratio is represented by I followed by its  $X^2$  test. Morisita's index of aggregation ( $I_g$ ) is followed by a  $X^2$  test and an F statistic.  $X^2$  values greater than 32.8 and F values greater than 1.67 indicated a contagious population.

	I	$X^2$	$I_g$	$X^2$	F
March 20	-	-	-	-	-
April 10	1.65	31.35	2.12	31.33	1.65
May 1	2.75	52.30	1.81	52.29	2.75
May 16	-	-	-	-	-
June 3	3.43	65.10	2.25	65.16	3.43
June 14	1.89	35.83	3.00	34.00	1.70
June 29	2.00	38.00	1.46	38.00	2.00
July 15	1.60	30.40	1.64	30.47	1.60
July 27	-	-	-	-	-
Aug. 11	.90	17.10	.71	17.00	.89
Aug. 21	1.62	30.74	2.18	30.82	1.62
Sept. 3	-	-	-	-	-
Sept. 18	1.15	21.85	1.43	22.00	1.16
Oct. 2	1.47	27.87	1.82	28.00	1.47
Oct. 15	-	-	-	-	-
Oct. 30	1.29	24.43	1.90	24.43	1.29
Nov. 12	3.04	57.80	3.16	57.84	3.04
Dec. 4	.85	16.08	.77	16.23	.85
Dec. 31	.58	10.98	.52	10.89	.57
Jan. 24	1.62	30.75	2.18	30.82	1.62
Feb. 12	1.43	27.14	1.90	24.43	1.29
Feb. 26	2.72	51.60	2.81	51.53	2.71
Mar. 17	.55	10.39	.38	10.33	.54

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