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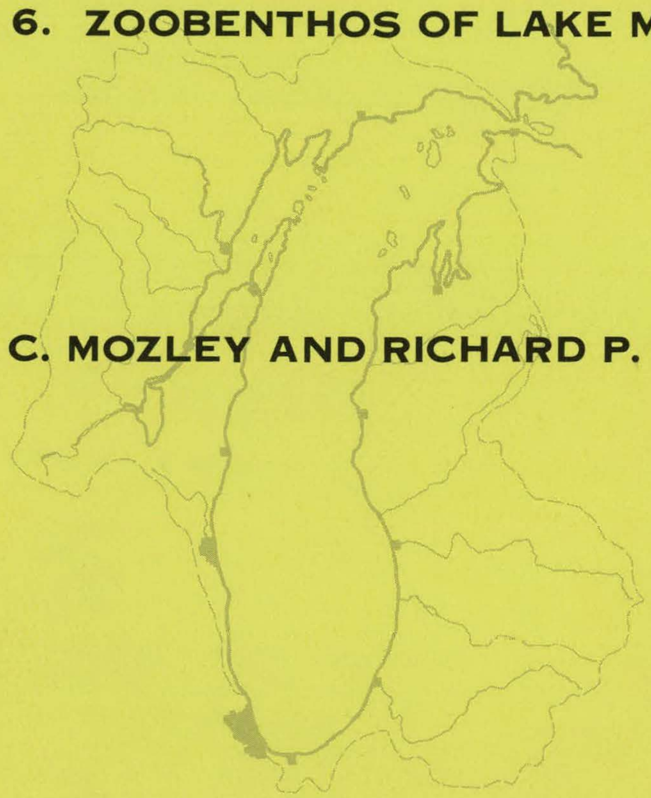
ENVIRONMENTAL STATUS OF THE LAKE MICHIGAN REGION

VOLUME 6. ZOOBENTHOS OF LAKE MICHIGAN



SAMUEL C. MOZLEY AND RICHARD P. HOWMILLER

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ARGONNE NATIONAL LABORATORY, ARGONNE, ILLINOIS

Prepared for the U. S. ENERGY RESEARCH
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Printed in the United States of America
Available from
National Technical Information Service
U. S. Department of Commerce
5285 Port Royal Road
Springfield, Virginia 22161
Price: Printed Copy $8.00; Microfiche $3.00

ANL/ES-40 Vol. 6
Environmental Control Technology
and Earth Sciences (UC-11)

ARGONNE NATIONAL LABORATORY
9700 South Cass Avenue
Argonne, Illinois 60439

ENVIRONMENTAL STATUS OF THE LAKE MICHIGAN REGION

Volume 6. Zoobenthos of Lake Michigan

by

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September 1977

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DEDICATION

This volume is dedicated to my coauthor Dick Howmiller, who died in June 1976 as the result of a traffic accident. Dick was a thorough and thoughtful scientist and he always approached his work with enthusiasm. He was continuing to expand his fields of interest, balancing basic ecological research with an active and responsible involvement in environmental conservation, at the time of his death. His most significant work in the Great Lakes was in refining the tubificid indicator system which is used to assess pollution in many inland waters, and he was in the process of placing the system on a more quantitative basis. He was never hesitant to call scientific and public attention to the progressive deterioration of water quality which his own work in Green Bay and elsewhere had demonstrated. He made several important contributions to the taxonomy of Tubificidae, and worked in the Galapagos Islands and California streams. His outspoken advocacy was a significant factor in the recent expansion of the old Midwest Benthological Society to the North American Benthological Society. I consider myself fortunate to have been his friend, and to have worked with him on this volume.

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PREFACE

Assessments of the environmental impacts of individual nuclear power plants sited on the shores of Lake Michigan have led to increased recognition of the need for regional considerations of the environmental impacts of various human activities, and a compendium of information on the environmental status of the region for use in assessing such impacts. In response to these needs, a report series describing the status of Lake Michigan and its watershed is in preparation. This series is entitled "Environmental Status of the Lake Michigan Region"; this report is part of that series.

The report series provides a reasonably comprehensive descriptive review and analysis of natural features and characteristics, as well as past, present, and proposed natural processes and human activities that influence the environmental conditions of Lake Michigan, its watershed, and certain adjacent metropolitan areas. This series will constitute a regional reference document useful both to scientific investigators and to other persons involved in environmental protection, resource planning, and management. In these regards, the "Environmental Status of the Lake Michigan Region" will serve in part as an adjunct to reports of broader scope, such as the Great Lakes Basin Commission's Framework Study.

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ENVIRONMENTAL STATUS OF THE LAKE MICHIGAN REGION

VOL. 6. ZOOBENTHOS OF LAKE MICHIGAN

by

Samuel C. Mozley and Richard P. Howmiller

ABSTRACT

This report summarizes Lake Michigan zoobenthic studies up to 1974, including reports of power-plant surveys. It describes ecologies of macroinvertebrate species and some microfauna, partly through use of data from other Great Lakes. The following are discussed: methodology of field surveys; zoobenthic indicators of pollution; zoobenthic effects on sediment-water exchanges; and numbers, biomass, and production of total macroinvertebrates. Prominent features of Lake Michigan zoobenthos include predominance of the amphipod Pontoporeia affinis, usefulness of tubificid oligochaetes in mapping environmental quality, and pronounced qualitative gradients in zoobenthos in relation to depth. Further research is needed on sampling methods, energy flow rates and pathways through benthic communities, factors limiting distribution of species near shore, and effects of macroinvertebrates on sediment chemistry and structure.

INTRODUCTION

Benthos are plants and animals that live in or on the substrates of aquatic habitats. A few animals that remain near the bottom during the day, but become planktonic at night, are also included in this report. Hutchinson (1967) applied the term "meroplankton" to this group in fresh water.

Not all organisms which meet the criteria implied in the definition of benthos are included in standard benthic studies; several taxonomic groups (fish and benthic plants) are more in the domain of the ichthyologist and botanist. In Great Lakes benthic studies, primary attention has been devoted to the so-called macroinvertebrates--the larger species of animals, or at least their later life stages--that are readily collected by benthic sampling devices.

Most information about Lake Michigan benthos is based on grab-sampler data, but we have added accounts of qualitative studies employing other techniques to give a more balanced view of the total benthos. Rocky and complex benthic habitats which cannot be sampled with grabs are common near shore where effects of man-induced environmental alterations are greatest.

BENTHIC COMMUNITIES

Most Lake Michigan benthic communities depend to a large extent on organic detritus for food. As organic materials reach bottom, they enter a web of energy transfers that sustain the benthic community. Fungi and bacteria break down and biochemically rearrange these materials to supply their needs for growth and they, in turn, may be eaten by an assortment of consumers in the saprobic food web. Many consumers fall prey to fish, especially if they rise above bottom at times (*e.g.* amphipods), and others are eaten by invertebrate predators (*e.g.* some leeches and chironomids). Insects emerge from the Lake and enter terrestrial communities as adults. Remaining animals die in place and are rapidly recycled by bacteria, fungi, and saprophagous animals. Species composition and primary pathways of energy flow in these communities vary with different kinds and amounts of sedimenting detritus, and with whether or not the detritus tends to remain in place.

On shallow, rocky bottoms or in weedbeds, these stable substrates support dense growths of diatoms and filamentous algae, which are grazed by tiny protozoans, rotifers, and crustaceans or by the larger snails and insects. Larger crustaceans--such as isopods, amphipods, and crayfish--also make extensive use of the periphyton or its symbiotic bacteria and fungi. Semiplanktonic predators hover near the periphyton to feed on the smaller herbivores and are themselves exploited by sessile hydras and ectoprocts. A few animals, notably chironomids, have developed the ability to burrow through the tissue of the larger aquatic plants. The intense concentration of zoobenthic life around rocks, macrophytes, and other stable structures in shallow water (such as water intakes, pilings, wrecks, and buoys) remains among the least studied of the benthic communities. Two types of benthic habitats are diagrammed in Figure 1.

Primary production may be important also in areas of unconsolidated sediments (sands, silts, and clays). Large numbers of diatoms of many species occur in beach and nearshore sands, living between and on the surfaces of sand grains. The depth distribution of benthic diatoms, the rates at which they fix solar energy, and their responses to nutrients in overlying water are so far unexplored in Lake Michigan.

A few benthic animals (*e.g.* clams) or meroplanktonic animals, such as the opossum shrimp (*Mysis relicta*), feed on plankton. Planktivores in the water column increase the rate of energy transfer from plankton to benthos by consolidating partially digested plankton into fecal pellets which settle to the bottom.

EARLY STUDIES

Prior to collections of Eggleton (1936, 1937) in 1931-32, only a few samples of zoobenthos were taken in Lake Michigan, and none permit estimation of composition or abundance for comparison with recent studies. These studies are reviewed by Cook and Johnson (1974).

One of the more thorough studies was that of Ward (1896) and coworkers near Charlevoix, Michigan. Extensive collections were forwarded to experts in each taxon. Results for several taxa--including Turbellaria, Ectoprocta, Rotatoria, Crustacea, and Mollusca--were included in Ward's (1896) report.

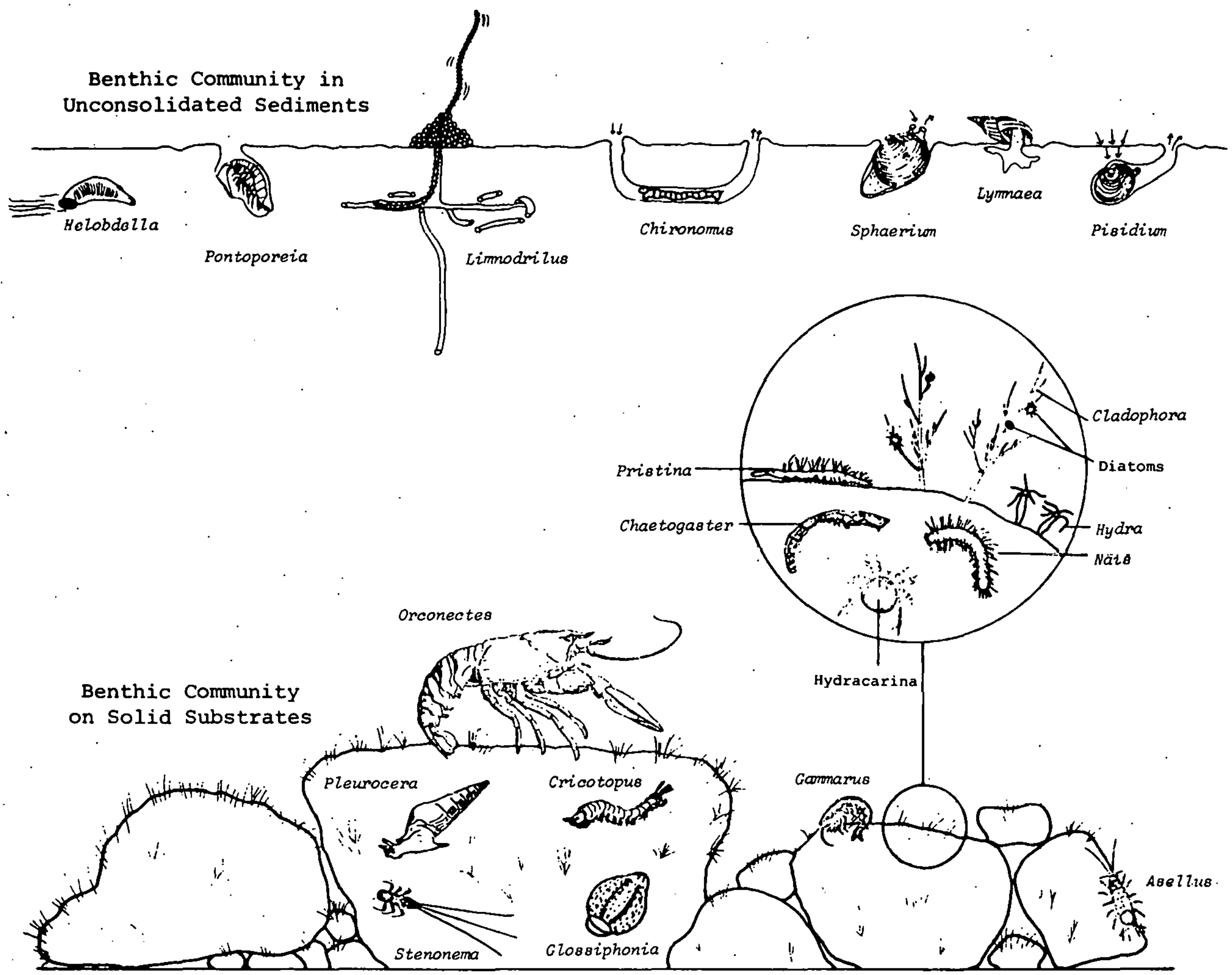


Fig. 1. Diagrammatic Representation of Two Important Types of Benthic Habitats.

Moore (1906) listed a few oligochaetes from that expedition, including a naidid (*Chaetogaster*) and a glossoscolecid (*Sparaganophilus*). Curiously, oligochaetes in the families Lumbriculidae and Tubificidae, which now constitute a large fraction of the Lake Michigan macrobenthos, were not mentioned until the studies of Eggleton (1936, 1937). This may in part be due to the taxonomic difficulty with which this group was burdened until the mid-1960's. Several other, more restricted, historical studies are cited below, *e.g.* Shelford (1913).

METHODS OF INVESTIGATING ZOOBENTHOS

The methods used to study benthos are discussed here to indicate the potential for prejudice and error in the research upon which this review is based, and to emphasize the need for additional research and development of many aspects of methodology.

SAMPLING DEVICES

No single device is completely reliable for collection of all benthic animals. Samples of macroinvertebrates have been obtained with dredges, corers, or grabs. Dredges (*i.e.* bags or scoops that are dragged along the bottom) are seldom used in Great Lakes investigations because they are not quantitative. They may, however, provide qualitative samples of large, thinly dispersed organisms such as unionid clams (Roth and Mozley, 1973--unpublished). Other sampling devices used for studying meroplanktonic animals and those benthos not collected well by grabs include diver-operated airlift pumps, macrophyte boxes, fishing trawls, traps, or simply the hands of divers.

Corers have the advantage of sampling all sediment depths equally, in contrast to most, or possibly all, grabs. Grabs sample different depths within the sediments unequally, and the configuration of the bite is affected by the nature of the sediment (Fig. 2). Furthermore, most conventional grabs are preceded by a *shock wave* (hydraulic disturbance) that blows aside surficial sediments and benthos (Brinkhurst, 1967b; Brinkhurst *et al.*, 1969; Hamilton *et al.*, 1970). Absence of a shock wave may explain the excellence of newer coring devices in parallel trials with commonly used grabs (Brinkhurst *et al.*, 1969; Flannagan, 1970). However, corers have some disadvantages for macroinvertebrate sampling because they cannot be used on hard sands common in many areas of Lake Michigan. Furthermore, corers sample a small surface area, and more casts may be required to obtain an adequate sample of macroinvertebrates at a station. On Lake Michigan, where ship time is expensive and rough weather common, this is a serious drawback. Corers have been used in few Great Lakes benthos investigations (Table 1).

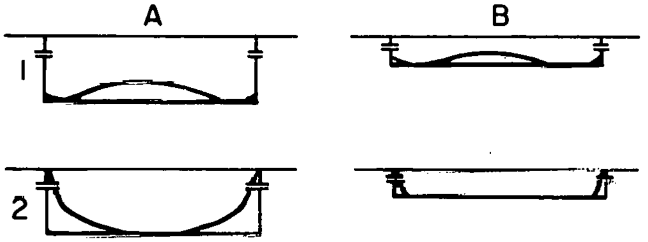


Fig. 2.

Bite Profiles of (1) Petersen and (2) Smith-McIntyre Grabs in (A) Soft and (B) Hard Sediments. Redrawn from Gallardo (1965) (with permission, see credits).

Grabs are devices that scoop or enclose a small area of the upper layer of sediment and carry it more or less intact to the surface. Many animals escape capture by grabs, including epibenthic forms that are blown aside by the shock wave, small individuals that are lost by leakage during retrieval, and large animals that actively avoid the sampler. Moreover, grabs and corers are ineffective on rocky bottoms or in beds of aquatic macrophytes.

Planktonic and meroplanktonic animals often are captured as the open grab descends. Because grabs have relatively small openings and are silhouetted against the surface, however, avoidance is easy for many of these animals, and they are not sampled quantitatively.

Nevertheless, grabs (often erroneously referred to as dredges) have been the favored samplers in benthological investigations of the Great Lakes. Most studies prior to 1965 were conducted with the Foerst Company's modification of the Petersen grab (Petersen and Boysen-Jensen, 1911) (Fig. 3). In a few other studies, the orange-peel (Reish, 1959) and Smith-McIntyre (Smith and McIntyre, 1954) were used. Since 1965, the Ponar (Powers and Robertson, 1967) has become the most widely employed grab. Many studies on bays and harbors have been done with the messenger-triggered modification (Birge, 1922) of the Ekman (1911) grab (Fig. 3).

Table 1. Samplers and Mesh Gauges Used by Investigators of Lake Michigan Benthos

Samplers	*Mesh Gauges*	*Investigators*
Smith-McIntyre; Ponar	0.5-mm sieve	Alley (1968); Alley and Powers (1970); Mozley and Alley (1973); Powers and Alley (1967); Powers *et al.* (1967)
Fager hand-corer	No. 5 bolting cloth	Alley and Anderson (1968)
Ekman; Petersen	No. 35 sieve	Balch *et al.* (1956)
Ponar	No. 30 sieve	Beak Consultants (1973); Industrial Bio-Test (1973); Truchan (1971); Willson (1969)
Petersen	No. 30 sieve	Cook and Powers (1964); Hiltunen (1967); U. S. Dep. Inter. (1968)
Petersen	Fine-mesh grit gauze	Eggleton (1936, 1937)
Orange-peel, Smith McIntyre	No. 32 grit bolting cloth	Henson (1970); Henson and Herrington (1965)
Ponar; Petersen	No. 30 sieve	Limnetics (1973)
Petersen	0.5-mm sieve	Marzolf (1965a)
Free-falling corer	Not stated	Marzolf (1965b)
Orange-peel; Petersen	No. 30 sieve	Merna (1960)
Ponar	0.5-mm sieve	Mozley (1973a); Mozley and Garcia (1972); Ayers and Huang (1967); Copeland and Ayers (1972)
Smith-McIntyre	0.5-mm sieve	Powers and Robertson (1965)
Ponar	No. 35 sieve	Rains (1971)
Petersen	0.5-mm sieve	Robertson and Alley (1966)
Ekman; Petersen	No. 30 sieve	Surber and Cooley (1952)

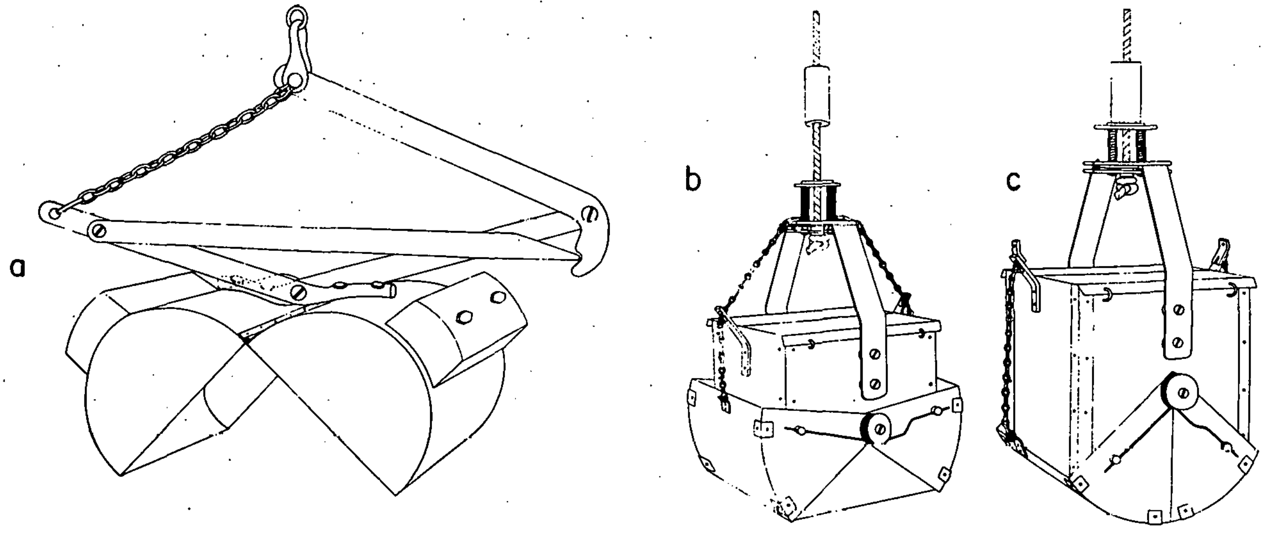


Fig. 3. Two Commonly Used Grab Samplers: (a) the Foerst Petersen in the open position, and (b-c) the Birge Ekman in the (b) open and (c) closed positions. Slightly modified from Welch (1948) (with permission, see credits).

The Foerst modification of the Petersen grab (hereinafter called simply the Petersen) has several deficiencies. Because the jaws have no openings through which water can flow, the grab is undoubtedly preceded by a shock wave. Wigley (1967) showed that a shock wave detracts considerably from the efficiency of the Van Veen grab, which has a jaw design similar to the Petersen. Another disadvantage of the Petersen is that material can be squeezed out the sides as the jaws come together (Orton, 1925). Also, large waves or swells cause the suspending cable to slacken, so that the grab closes prematurely. Casts must often be repeated in heavy weather.

The orange-peel grab (hereinafter called the orange-peel) consists of four sectors designed to take a hemispherical bite of the bottom. It was designed for construction work but has been adapted for biological work with a few simple modifications (Reish, 1959). This grab has been used in Lake Michigan because it obtains samples in hard clay and gravel (Merna, 1960; Henson and Herrington, 1965; Henson, 1970). For scientific work, a canvas shroud is usually placed over the upper portion to minimize washout, but this shroud is open at the top, and its base is not sealed to the jaws. Some loss of sediments is thus unavoidable. Sediment loss also occurs because the jaws of the orange-peel often do not fit together properly and much of the sample can leak out.

The area sampled with the orange-peel varies with the depth of penetration. To estimate the area sampled, it is necessary to measure the volume of each sample and then consult tables that relate sample volume to surface area (Merna, 1962). This is an inconvenience and an additional source of error.

The Smith-McIntyre, or Aberdeen, grab (hereinafter called the Smith-McIntyre) was designed specifically for work in heavy seas (Smith and McIntyre, 1954). It is cocked open against powerful springs and tripped only when two trigger plates on opposite corners of the supporting frame contact the bottom. Thus, the problem of premature tripping in rough weather is eliminated. The spring closure ensures a strong, reproducible bite. The jaws fit together tightly, and an overlapping flange on one jaw reduces the chance of leakage and particle entrapment between the jaws. The large screened opening in the top of each jaw reduces shock-wave effects (Wigley, 1967). The Smith-McIntyre has many features that make it desirable for work on the Great Lakes.

The Petersen, orange-peel, and Smith-McIntyre grabs were compared in parallel trials on Lake Michigan (Beeton *et al.*, 1971--unpublished). Triplicate samples were taken with each grab at five depths (5.5, 18.3, 36.6, 54.9, and 73.2 m) on each of four transects in southern Lake Michigan [stations of Hiltunen (1967)]. In these trials, the Petersen usually caught the fewest animals and the Smith-McIntyre usually caught the most, especially at greater depths (Fig. 4). The average catch with the Smith-McIntyre grab was higher than that of the other two samplers at fourteen of the twenty stations and at eleven of the twelve deepest stations. Yields from the orange-peel grab averaged highest at five of the twenty stations, and those from the Petersen at only one station. Not only was the Smith-McIntyre most effective, but there was considerably less variation between triplicate samples than with the Petersen and orange-peel (Beeton *et al.*, 1971--unpublished).

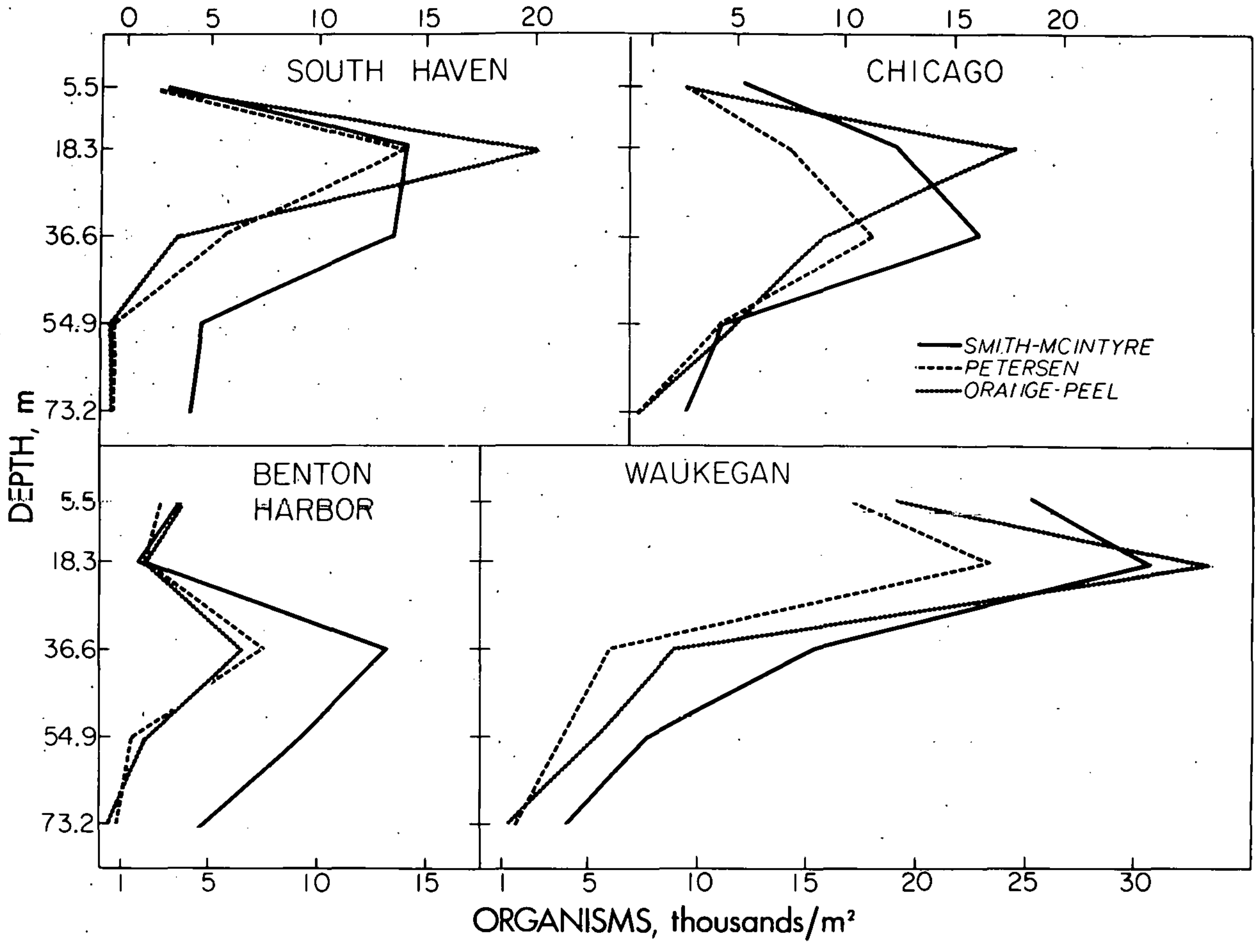


Fig. 4. Depth Distribution of Benthic Macroinvertebrates Determined with Petersen, Orange-peel, and Smith-McIntyre Grab Samplers along Four Transects in Southern Lake Michigan. Each point is based on three replicate samples with each grab. From Beeton *et al.* (1971--unpublished) (with permission, see credits).

Powers and Robertson (1967) also compared Petersen and Smith-McIntyre grabs in southern Lake Michigan. Comparison of means of triplicate samples at each of 12 stations yielded much the same conclusions as the study of Beeton *et al.* (1971--unpublished). On the average, the Petersen captured 0.41 as many macroinvertebrates as the Smith-McIntyre. Though impressed with the sampling efficiency of the Smith-McIntyre, Powers and Robertson (1967) felt that it had several disadvantages for routine work: *"It was large and unwieldy, the mechanism is complicated and subject to failure, and the powerful tripping springs render it somewhat dangerous."*

These drawbacks of the Smith-McIntyre motivated design of a new sampler, the Ponar, which combines the jaw design of the Smith-McIntyre with the Petersen closing mechanism. In many respects, the Ponar is a return to the original Petersen design (Petersen and Boysen-Jensen, 1911), reviving many discarded features. In parallel trials, the Ponar was at least as effective as the Smith-McIntyre (Powers and Robertson, 1967), and has become the most widely used sampling device in Lake Michigan benthic investigations.

The Ekman is another grab sampler of significance in Lake Michigan benthos collections. Comparison of Ekman and Ponar grabs revealed that while the Ponar seemed to be effective on harder sediments, the Ekman was superior on the soft muds of harbors and bays. Flannagan (1970) found that, on mud, the Ekman caught more animals per unit area, with a smaller standard error, than the Ponar. Howmiller (1971a, 1971b) compared Ponar and Ekman grabs at 26 stations in Green Bay. For the Bay as a whole, the Ekman was more effective, but the Ponar sampled better for at least certain organisms on harder substrates along the western side of the Bay. In deep water (over 50 m), the Ekman may not be as effective, even in soft sediments, because of its light weight and high center of gravity.

There appear to be several reasons for greater effectiveness of the Ekman on soft substrates. It no doubt creates less of a shock wave as it descends--doors on the top swing up as the grab falls, permitting water to flow through relatively unimpeded. In contrast, the upper opening of the Ponar grab is covered with fine screening, which has been shown with other grabs to cause a smaller catch of organisms (Dugdale, 1955). In addition, the hinge and screen top of the Ponar retard penetration beyond 10 cm, whereas the Ekman may penetrate with little resistance to at least 20 cm. The greater weight of the Ponar and the lever system for forcing the jaws together make it more effective for biting into harder sediments. Here, its shallow bite is unimportant since neither sampler penetrates well in sand or well-compacted silt.

Howmiller (1971a) proposed that the best features of these two devices be combined for maximum effectiveness over an area with diverse sediment types, such as Green Bay. The proposed design is essentially an Ekman box with heavy Ponar-type jaws and a double lever system. Like the Ekman, it should fall with very little shock wave, and, like the Ponar, should penetrate deeply in hard sediments. An additional feature is that after the grab is tripped, the top doors are held shut to prevent loss of organisms (Flannagan, 1970). A prototype has been built, but results of parallel trials are not available at the time of this writing.

Slack (1972) also published a description of "a lever-operated Ekman grab," a design developed independently but almost identical to that proposed by Howmiller (1971b). In Slack's parallel trials, the new device was not as effective as a standard Ekman, though the difference was probably not significant. As design changes were directed primarily at improving Ekman performance in sand, Slack's soft-mud trials were not an adequate test of its potential.

Two other devices employed in several recent investigations of Great Lakes benthos are the Shipek sampler (Flannagan, 1970) and the Triplex Ponar (Mozley and Chapelsky, 1973). The Shipek sampler is very heavy (70 kg), has a spring-loaded jaw, and will obtain a sample from nearly any substrate. However, its bite is always shallow, and its solid profile should produce an undesirable shock wave as it descends (Wigley, 1967). The Shipek may be acceptable for geological sampling (Sly, 1969) but does not appear to be reliable for biological purposes (Flannagan, 1970).

The Triplex Ponar is divided internally into three chambers, parallel to the closing plan of the jaws, so that three separate samples result from each cast. Samples in end compartments are removed through doors in the sides of the jaws. This design permits study of small-scale variability in density; provides simultaneous, quantitative samples for different types of analysis; and enables adjustment of sample size in accordance with zoobenthic density. The latter capability may increase laboratory efficiency by eliminating the need for picking much larger samples than are necessary for particular purposes.

The great differences in effectiveness of samplers used by Lake Michigan investigators place severe limitations upon data comparability. For example, when recent data from a study done with the Petersen are compared to findings with a Ponar, the Ponar study indicates greater densities of organisms, even though true densities may have undergone no change (Fig. 5). Critical comparison with earlier studies may warrant use of the Petersen, even if we now know it to be relatively ineffective (Robertson and Alley, 1966).

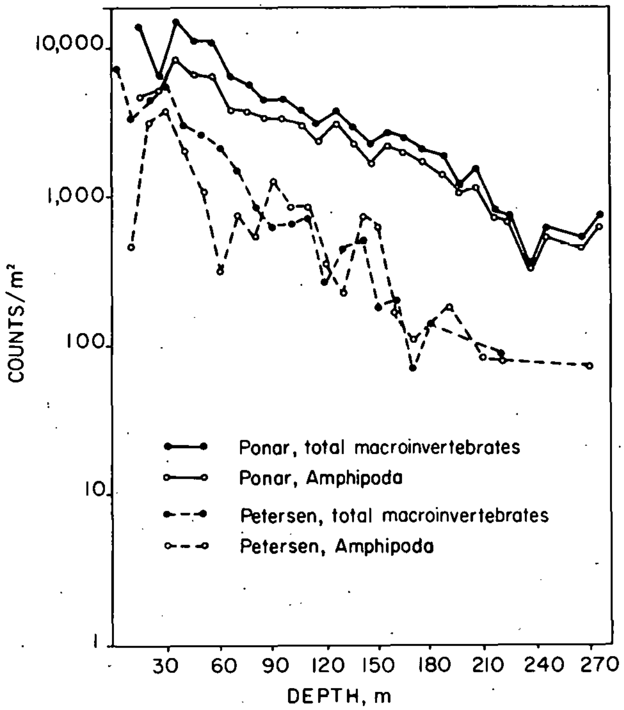


Fig. 5.

Difference in Effectiveness of the Petersen and Ponar Grabs in Lake Michigan. All data were collected between 1962 and 1967. Sources of data: Ponar (Powers *et al.*, 1967; Petersen, total macroinvertebrates (U. S. Dep. Inter., 1968); Petersen, Amphipoda (Robertson and Alley, 1966).

SCREENING AND SORTING SCREEN RESIDUES

The usual procedure in benthos investigations involves screening fresh samples to remove macroinvertebrates from fine sediments. In the United States, a U. S. Standard No. 30 sieve (0.565-mm openings) generally is used (Welch, 1948) (see also Table 1). Jónasson (1955, 1958), after a survey of the (mostly European) literature, concluded that the mesh gauge most commonly used was 0.6 mm. Most investigators apparently consider this size satisfactory, but Jónasson (1955) showed that a change in mesh size from 0.62 to 0.51 mm resulted in a 47% increase in the catch of *Procladius* (as *Tanypus*) larvae from soft gyttja bottoms in a Danish lake. He also found that meshes of 0.51, 0.26, and 0.20 mm were equally effective for cocoons of Oligochaeta, *Chaoborus* (as *Corethra*) larvae and pupae, and *Pisidium*. However, important components of the benthos--tubificid worms and larvae of *Chironomus* *anthracinus*--were represented by very different numbers, depending on the mesh gauge (Table 2).

Table 2. Estimates of Number of Individuals/m^2 Recovered in Samples Processed with Various Mesh Gauges, August 1954*

Type of Individual	*Mesh Gauge* *0.51 mm*	 *0.26 mm*	 *0.20 mm*
Tubificidae	1,564	2,920	3,620
Chironomus anthracinus larvae	3,956	16,072	15,936
Total benthos	9,928	22,476	24,212

**Adapted from Jónasson (1955).*

Relative efficiencies of different mesh gauges were dependent on average sizes of the animals, and varied with season. For example, discrepancies among mesh sizes in estimates for chironomids and tubificids were much greater earlier in the year (Table 3).

Table 3. Estimates of Number of Individuals/m^2 Recovered in Samples Processed with Various Mesh Gauges, July 1954*

Type of Individual	*Mesh Gauge* *0.51 mm*	 *0.26 mm*	 *0.20 mm*
Tubificidae	989	1,885	5,760
Chironomus anthracinus larvae	192	7,984	15,736
Total benthos	7,536	15,906	26,112

**Adapted from Jónasson (1955).*

Hamilton (1965) used an 0.18-mm sieve in conjunction with the standard 0.56-mm mesh. He found that a mesh of 0.56 mm did not adequately sample chironomid larvae less than 9 mm in length. Also, Chironominae and Orthocladiinae tended to pass through the screen more readily than heavier-bodied Tanypodinae of the same length. Even the 0.18-mm mesh may have been too coarse to capture earlier instars of some chironomids (Hamilton, 1965).

These studies show that the U. S. Standard No. 30 sieve (0.565-mm mesh) is neither quantitative for small tubificids and early instars of chironomids, nor effective for studies on secondary production or population dynamics of animals in these groups. Despite its limitations, the No. 30 sieve will probably continue to be used by most investigators to facilitate comparisons with earlier studies (Table 1). It is, and for some years has been, a primary technique in assessment of environmental quality. Use of this mesh size has been recommended by Welch (1948), the American Public Health Association (APHA, 1960), and the Environmental Protection Agency (Weber, 1973).

Use of smaller mesh sizes, a desirable procedure for many kinds of benthic ecological studies, creates other practical difficulties. Sieving time and volume of residue from which animals must be picked increase greatly with smaller mesh sizes, even in fine muds (Jónasson, 1955), as shown in Table 4.

Table 4. Relationship Between Sieving-Residue Volume, Sieving Time, and Mesh Gauge*

Meshes, no./in.	*Wire Size, mm*	*Opening, mm*	*Sieving-Residue Volume from Samples of 9-10 Liters, ml*	*Sieving Time, min*
30	0.25	0.62	-	5
30	0.36	0.51	20-30	5
60	0.17	0.26	60-65	12
80	0.13	0.20	115-140	20

**Adapted from Jóhasson (1955).*

Lake Michigan sediments that contain coarse plant fibers may take hours to screen and may leave large amounts of residue on finer sieves. Since the time required to pick animals from the residue increases greatly with larger volumes, a balancing reduction in the number of samples taken would have to be implemented for field surveys.

Separating Animals from Sieve Residue

Animals are sometimes separated from sieve residue by flotation methods in a solution (sugar, $MgSO_4$, NaCl, CCl_4) with specific gravity intermediate between organisms and sediments. When substantial amounts of organic debris occur in residues, flotation is of little use because the specific gravity of the debris is frequently close to that of the animals. Oligochaetes float only briefly (Anderson, 1959), probably because their highly permeable integument permits rapid uptake of the solute. Fast (1970) found that an average of 76% of total oligochaetes remained in residues after sugar flotation. Moreover, clams and animals that build cases of sediment particles cannot be floated free of inorganic residues. Flotation is generally inappropriate for Lake Michigan benthic studies.

Elutriation is a gentle way to remove most kinds of animals and speed sorting when residues include compacted clay, coarse sand, or gravel. In a device described by Lauff *et al.* (1961), air and water are introduced at the bottom of a column, carrying animals and fine materials into suspension. When animals are well separated from sediments, a side port is opened and suspended animals flow out onto a screen. A modification of this device has been used successfully in separating invertebrates from stiff, lumpy clay with little damage to the organisms (Worswick and Barbour, 1974).

Another elutriation device has been used for several years by the University of Michigan's Great Lakes Research Division (Powers and Robertson, 1965) (Fig. 6). A grab sample is stirred vigorously with a jet of water from a hose in a funnel-shaped tub. Before finer particles settle out of suspension, the slurry is poured through a spout in the side of the funnel and strained in a cylinder of 0.5-mm-gauge screen. When elutriation is complete, the residue in the cylinder is rinsed into an attached jar; the jar is then removed from the device for addition of preservative and replaced with an empty jar for the next sample. Sand and coarser inorganic sediments are rinsed out the bottom of the funnel, directly overboard. While loss of animals may occur in several ways (leeches affixed to internal surfaces, incomplete rinsing, *etc.*), the device is well suited to handling large numbers of samples rapidly without spillage, even in rough weather. The possibility of losing animals with this technique must be balanced against loss of time and efficiency in examining voluminous residues. Samples containing only fine sediments may be washed completely through the screen, and since they are first suspended as a mud-water slurry, sieving proceeds more rapidly and probably with less damage to macroinvertebrates than occurs in ordinary direct sieving.

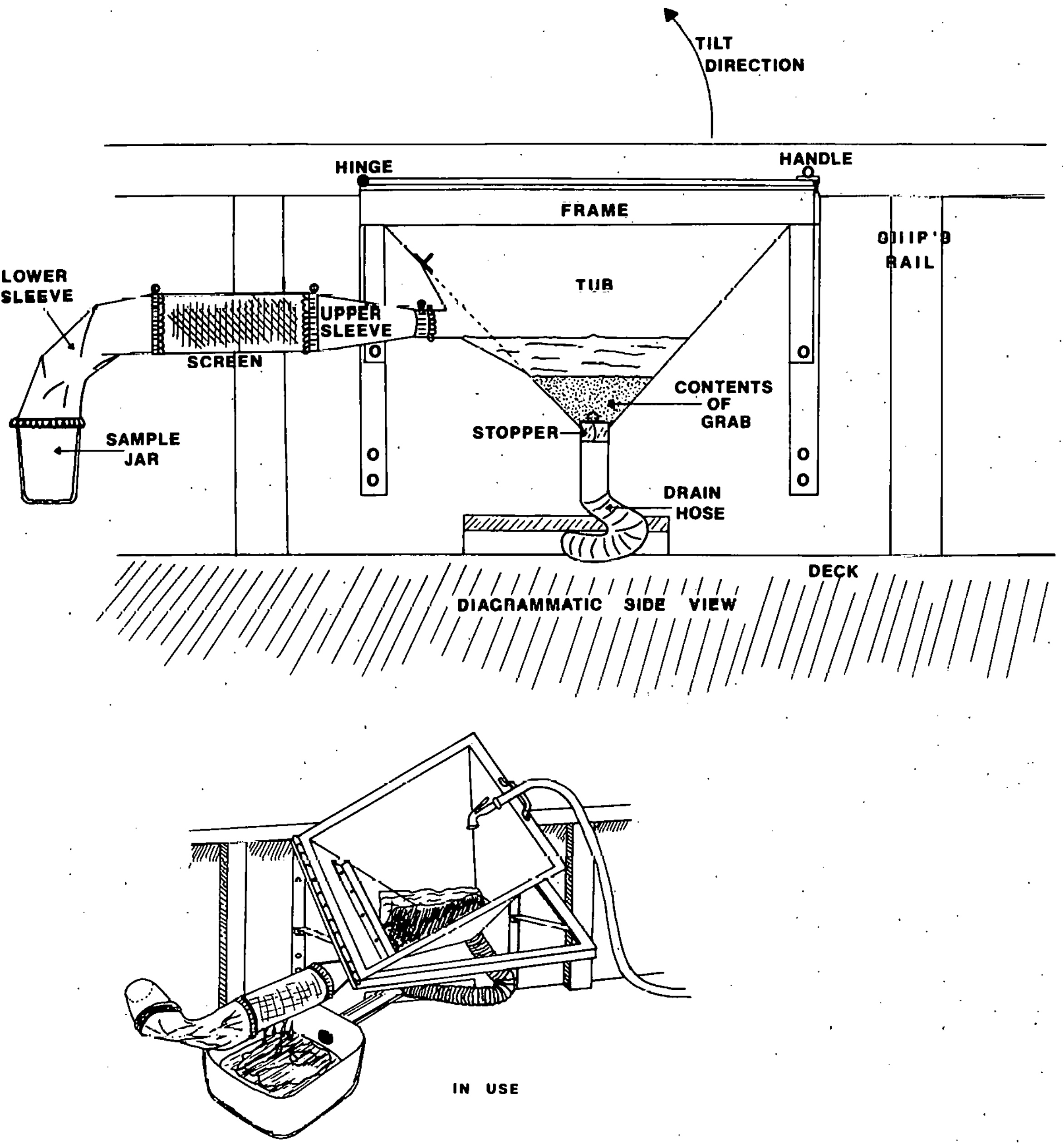


Fig. 6. Shipboard Elutriation Device.

Final Sorting and Weighing of Organisms

In the final stages, animals are picked from residues and sorted to major taxonomic categories for counting. Species identification or weighing of organisms, or both, may follow.

Biomass of benthic animals is a desirable parameter, but it should be noted that both the wet and dry weight of invertebrates decrease greatly during preservation (Howmiller, 1972; Stanford, 1973). Ideally, biomass should be determined from live animals, or estimated from conversion factors based on linear measurements of preserved animals for which actual biomass is known (Johnson and Brinkhurst, 1971b).

Preserving Specimens

Many benthos surveys in Lake Michigan have been concerned solely with *numbers* in four major taxa--amphipods, oligochaetes, sphaeriids, and chironomids--and samples were preserved simply with sufficient formalin (5-10%) to prevent decomposition. However, the increasing capability and necessity to identify *species* dictates more careful preservation, particularly with respect to mollusks. A relatively new preservative, propylene phenoxetol, both narcotizes and preserves invertebrates. Its narcotic effects are especially valuable, because later identification of the Hirudinea, Turbellaria, and Mollusca is much easier with relaxed specimens (McKay and Hartzband, 1970). Unlike formalin, propylene phenoxetol has no tendency to destroy mollusk shells. Carbonated water may also be used as a narcotic agent for invertebrates before preservation of samples.

BENTHIC HABITATS--DISTRIBUTION AND TYPICAL FAUNA

Shelford (1913) recognized zonation of benthic communities in Lake Michigan surprisingly early in the history of limnological studies. He described four distinct zones delimited by wave action and broad thermal fluctuations. The shallowest zone was circumscribed by the maximum depth (8 m) at which waves appeared to move sand. Shelford divided this zone into a variety of substratal habitats, each with unique faunal characteristics. *Eroding* bottoms of exposed bedrock, cobbles, or boulders were inhabited mainly by Trichoptera, Plecoptera, Ephemeroptera (all large aquatic insects), and the amphipod *Hyalella*. *Depositing* bottoms of shifting sand were inhabited by few or no animals to a depth of 4 m; between 4 and 8 m, the bottom was inhabited by *Sphaerium striatinum* (as *S. vermontanum*), two midge larvae, and the pulmonate snail, *Lymnaea woodruffi*. A third substrate, *protected* bottom (presumably embayments or inlets), was said to contain animals similar to those of the next deeper zone and to be very rich in species (21 listed), many of which also occurred in small lakes.

The next distinct zone was delimited at the upper boundary (8 m) by wave action, and at the lower boundary (25 m) by the depth to which broad thermal fluctuations were believed to occur. The lower depth was the deepest from which *Chara* or *Cladophora* had been collected in the Great Lakes. The most abundant animals were said to be *Crangonyx*, *Sphaerium*, *Amnicola*, *Valvata*, and *Lymnaea woodruffi*, and--near Gary, Indiana--oligochaetes, chironomids, and leeches.

The next zone was said to overlap the preceding zone to some extent, but generally was described by depths of 25-54 m and seasonal thermal fluctuations of 3°C or less. Shelford believed this to be the shallowest zone in which *Pontoporeia* or *Mysis* existed, but we now know that these organisms occur at much shallower depths.

In the fourth zone (54-115 m), light was said to be very weak and temperatures were believed to vary only slightly from 4°C. The sediments were described at different locations as reddish-brown sandy mud or dark-colored impalpable mud. Invertebrates were abundant and evenly distributed; the most numerous types were *Pontoporeia, Mysis*, water mites, midge larvae, and *Pisidium*. Although Shelford did not mention oligochaetes in describing the zones, it is unlikely that they were absent or unimportant.

At depths greater than 115 m, light, primary producers, and temperature fluctuations were described as lacking or negligible, and there were no unique faunal characteristics.

The differing viewpoints of benthologists then and now are illustrated by Shelford's table of species. This table included large numbers of mollusks and several species of ectoprocts that few current authors mention, but had only a single tubificid representing the Oligochaeta and one chironomid generic name (*Metriocnemus*, possibly a misnomer for *Heterotrissocladius*). Nowhere did he estimate the numbers of invertebrates present. The distribution of Shelford's designated zones in the southern half of Lake Michigan are depicted in Shelford (1913).

The most extensive recent description of sedimentary features with reference to the requirements of benthos was developed by Powers and Robertson (1968) from visual-analysis survey data of Ayers (1967), and from their notes on benthos stations in the southern two-thirds of the Lake. The boundaries in the resulting map (Fig. 7) are based on predominating or average sediment types. Powers and Robertson separated five generalized textural types: sand, silty sand-sandy silt, silt-clayey silt layered over stiff clay, silt-clayey silt, and hard bottom. Hard bottom was either rock or highly compacted stiff clay from which no grab samples could be obtained. Finer sediments had more organic carbon, and silt and clay-sized sediments increased in average carbon content with increasing depth (Fig. 8). Overlapping depth ranges of different sediment types indicated the heterogeneity of the benthic environment in certain depth zones. In general, boundaries between sediment types occurred at about the same depths as proposed by Shelford (1913).

Shallow areas with rocky bottoms are widespread in the Chicago area and along promontories of the western and northern shores of the Lake (Ayers, 1967). Groins, jetties, rip-rap, and other artificial structures extend the associated benthic community throughout the Lake, even in regions without naturally rocky bottoms (Herbst, 1969). Besides the forms listed by Shelford, one would expect to find *Gammarus* (an amphipod), *Asellus* (an isopod), several kinds of chironomid larvae, gastropods, water mites, naidid oligochaetes, *Hydra*, and crayfish in rocky habitats. Quantitative studies of this environment have been initiated only recently in Lake Michigan (Industrial Bio-Test, 1974). Bocsor and Judd (1972) provided additional qualitative information for a Lake Ontario rocky habitat.

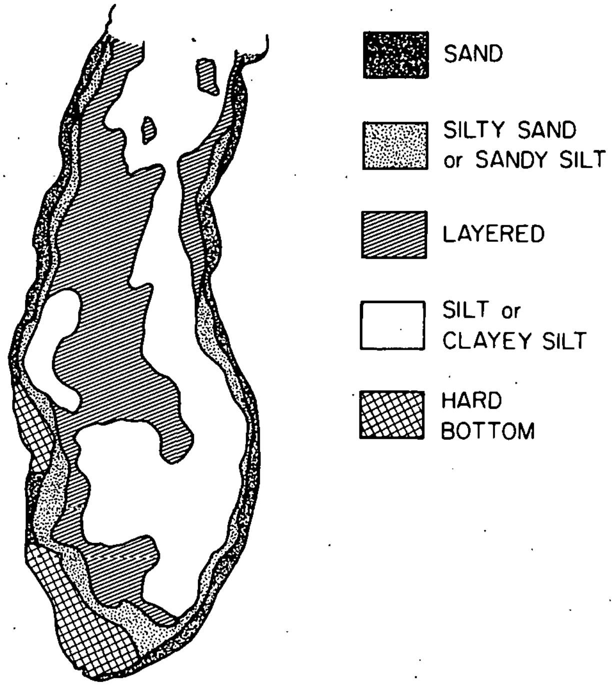


Fig. 7.

Distribution of Sediment Types in Lake Michigan. Slightly modified from Powers and Robertson (1968) (with permission, see credits).

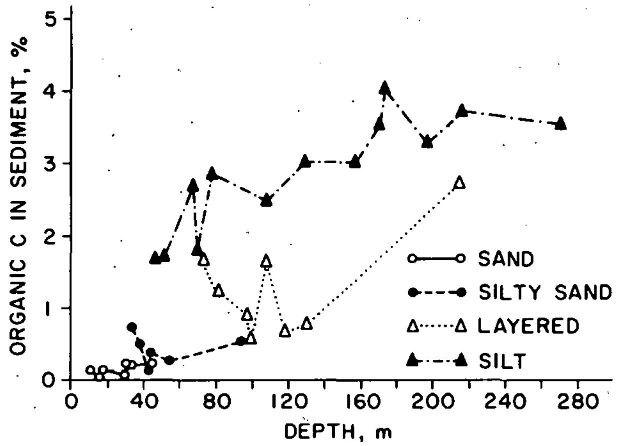


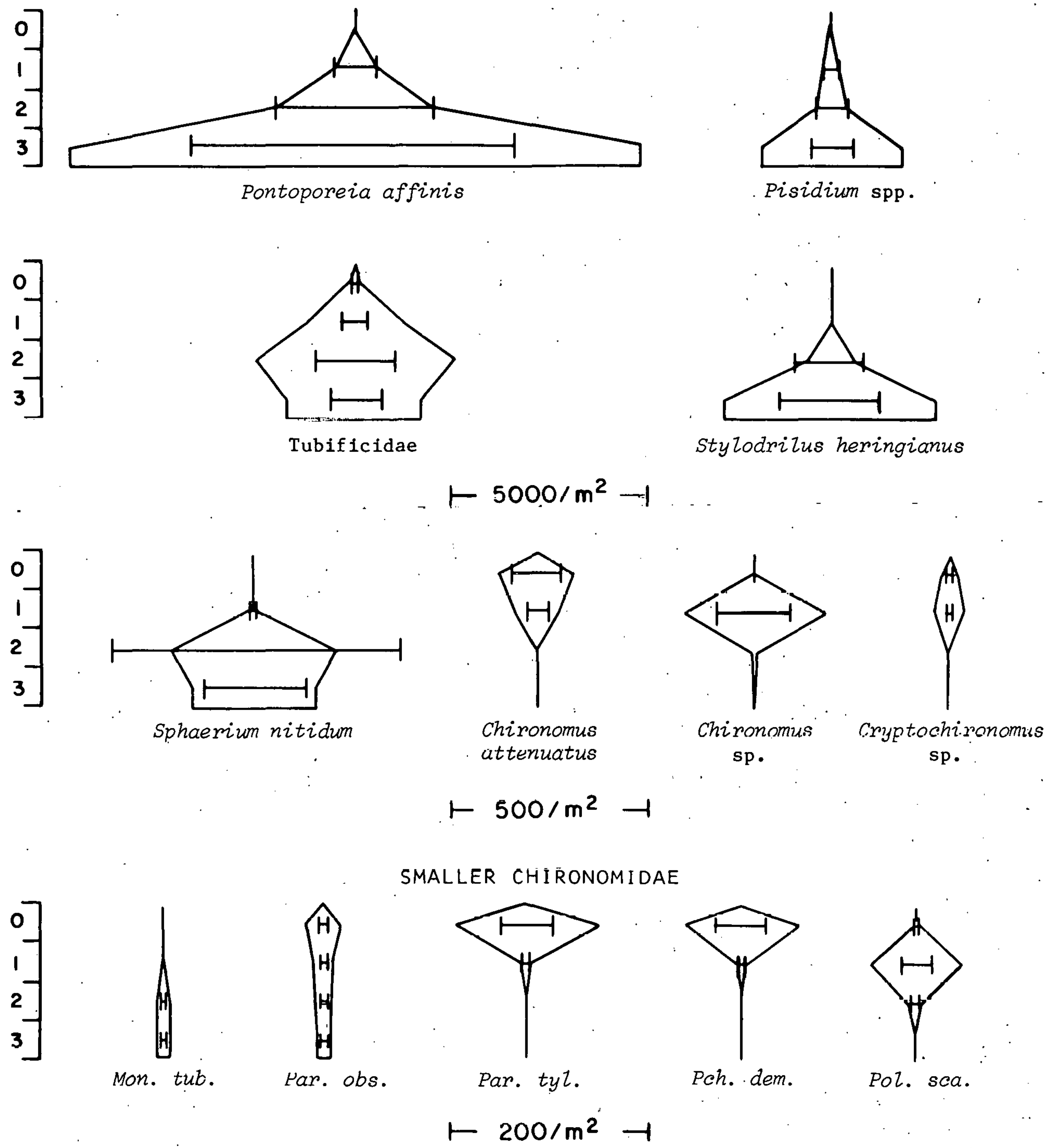
Fig. 8.

Interrelations of Sediment Type, Carbon, and Depth in Lake Michigan. Slightly modified from Powers and Robertson (1968) (with permission, see credits).

We are unaware of any benthological studies of vascular macrophyte beds in the Great Lakes, but this habitat has been observed by divers in parts of Green Bay, Grand Traverse Bay, and northeastern island and shore areas.

Unconsolidated sediments cover most of the bottom of Lake Michigan. They grade from coarse and medium sands near the beach to silt and clay at depths of 30 m or more. Thickness of recent sediments differs considerably from place to place in the Lake; maximum accumulations occur in a band between 30- and about 100-m depths from Benton Harbor to Muskegon, Michigan (Lineback and Gross, 1972). The western half and much of the deeper parts of the Lake are covered with thin, flocculent layers of fine material over cohesive clay or rocky till.

Shoreward of the 30-m depth, there are several faunal zones defined approximately by depth and sediment type (Mozley and Garcia, 1972; Mozley 1973a) (Fig. 9). The first zone, 0 to 8 m, is populated largely by several Chironomidae and Naididae, with occasional patches of tubificid oligochaetes



Mon. tub. = *Monodiamesa tuberculata*; *Par. obs.* = *Paracladopelma* cf. *obscura*; *Par. tyl.* = *Paracladopelma tylus*; *Pch. dem.* = *Parachironomus* cf. *demeijerei*; *Pol. sca.* = *Polypedilum scalaenum*.

Fig. 9. Mean Numbers with Standard Errors for Dominant Zoobenthic Taxa in Southeastern Lake Michigan in July 1971. The vertical scales indicate depth intervals: 0 = 0-8 m; 1 = 8.1-16 m; 2 = 16.1-24 m; 3 = depth > 24 m.

in localized accumulations of mud or detritus. The next deeper zone, about 8 to 16 m, is characterized by fine sands with variable but usually minor fractions of silt. Many species of chironomids, oligochaetes, and sphaeriid clams inhabit this zone, together with variable numbers of *Pontoporeia* and a few leeches and snails.

Between 16 and 40 m, a transition takes place from shallow-water assemblages to the typical profundal community of Great Lakes benthos. *Pontoporeia affinis,* the lumbriculid oligochaete *Stylodrilus heringianus*, and *Pisidium conventus* become very abundant and are supplemented by a few species which occur almost exclusively in this interval--the clam *Sphaerium nitidum*, and the chironomid *Procladius* (not illustrated). Tubificidae reach their highest abundances in this interval.

Total animal density increases to the maximum, but the number of species is quite low, by a depth of 35 or 40 m. The widespread Great Lakes chironomid *Heterotrissocladius* cf. *subpilosus* is lacking in shallower areas and *Mysis relicta* occurs in grab samples with increasing frequency at greater depths, but the many species typical of nearshore areas drop out of the benthic fauna at depths over 40 m.

As Shelford recognized, the protection afforded by embayments and harbors may permit development of species associations similar to those in smaller lakes. However, environmental deterioration associated with urban effluents has eliminated many naturally occurring species from these habitats around Lake Michigan, and has fostered dense assemblages of pollution-tollerant Tubificidae and Chironomidae.

Animals which inhabit sandy beaches (psammon) are usually overlooked in benthic surveys because they are so small. Factors such as sand-grain size, location with respect to water level, grinding action of the waves, and content of organic material are probably important, just as they are in beaches of small lakes (Pennak, 1940). Pennak (1940) showed that total numbers of invertebrates in a Milwaukee beach are much less than in small-lake beaches, and several taxa typical of small lakes are very rare (*e.g.* Acarina, Ostracoda, Nematoda, and Tardigrada). The most numerous kinds of animals are rotifers, flatworms (Platyhelminthes and Turbellaria), and small chironomid larvae (Seibel *et al.*, 1973). Protozoa may be important members of the fauna, but techniques necessary to collect and identify fragile ciliates have not yet been applied to Lake Michigan.

AUTECOLOGY OF ZOOBENTHIC SPECIES

The following sections* review much of the information available on individual taxa of zoobenthos in Lake Michigan. Discussions of *Pontoporeia affinis, Mysis relicta,* and Oligochaeta are more detailed, for these are the most numerous macroinvertebrates over much of the Lake (Fig. 10). However, other groups contain species that are more numerous locally than most species of these major taxa. For example, the leech *Helobdella stagnalis* and certain

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In these sections, the underlining of taxonomic designations such as class, order, and scientific name is solely for the editorial purpose of format.

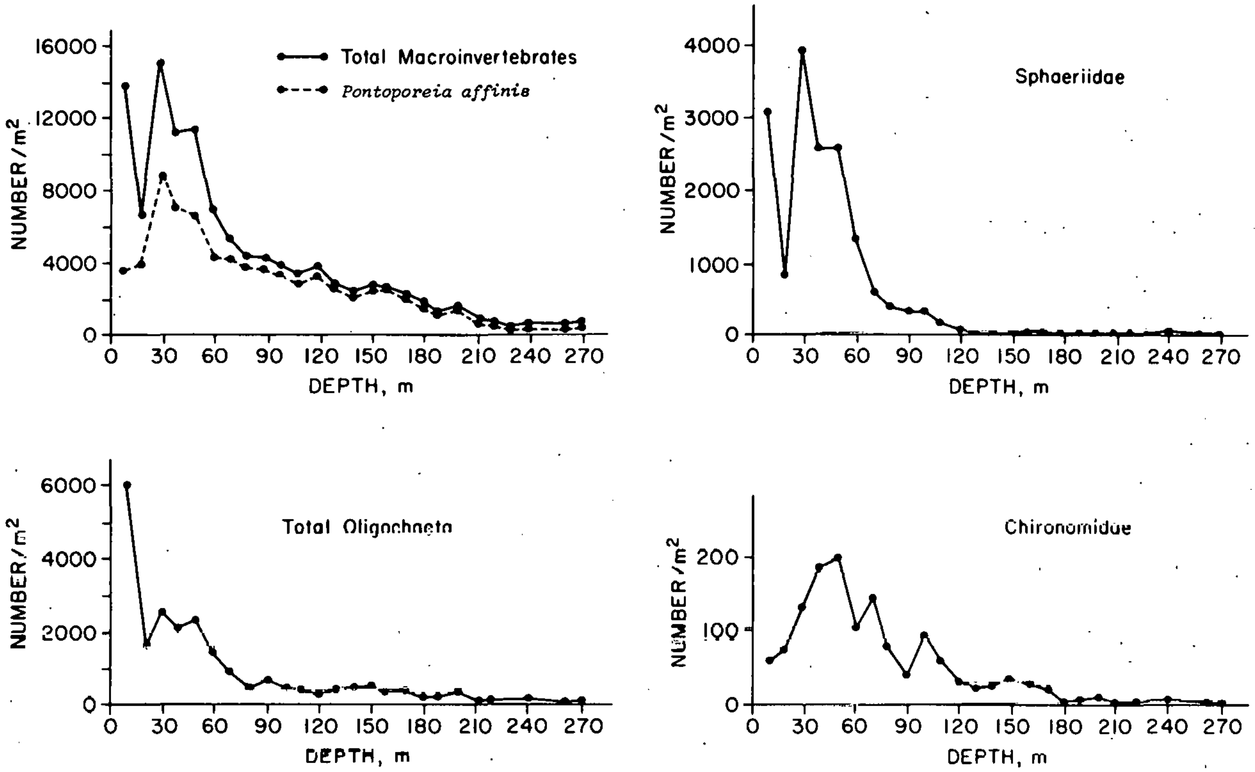

Fig. 10. Depth Distribution of Major Taxa of Zoobenthos in the Main Basin of Lake Michigan 1964-1966. Modified from Powers and Alley (1967) (with permission, see credits).

species of Gastropoda in the genera *Amnicola*, *Valvata*, and *Lymnaea* occur in moderate abundances in many parts of the Lake.

Hirudinea, Gastropoda, and most species of Sphaeriidae, Chironomidae, and Oligochaeta are numerically important only near shore at depths less than 30 or 40 m. The percentage of the amphipod *Pontoporeia* in Lake Michigan macrobenthos (estimates vary around 60-80%) completely overshadows that of any other single genus of zoobenthos (Fig. 10). This is largely because the profundal zone (depths of about 40 m and deeper), where *Pontoporeia* is especially suited to live, comprises most of the area of the Lake. (The effects of man, however, occur mostly along the shore, as do our uses of lake water.) The numerical preponderance of *Pontoporeia* should not be allowed to obscure importance and distinctiveness of benthos near shore. Unfortunately, available information on shallow-water communities is fragmentary and characterizes only a small fraction of the shore area or types of benthic communities there. Several investigations of inshore habitats have begun recently around the Lake (Mozley, 1974; Industrial Bio-Test, 1974; Limnetics, 1974b), and knowledge of those areas should expand rapidly in the next few years.

ARTHROPODA

Most bottom animals in Lake Michigan fall into two orders of arthropods: Amphipoda (Crustacea) and Diptera (Insecta). Several other crustacean and insect groups may be common locally. The next sections summarize information on the more common species in taxonomic arrangement.

Crustacea

Amphipoda

Sometimes called scuds or sideswimmers, these animals range from 2- to 15-mm long and are flattened from side to side. They have the usual crustacean mouthparts and 13 sets of paired body appendages adapted in series for handling food, walking, and swimming. Amphipods swim rapidly but remain close to the substrate most of the time. A representative form, *Pontoporeia affinis*, is pictured in Figure 11.

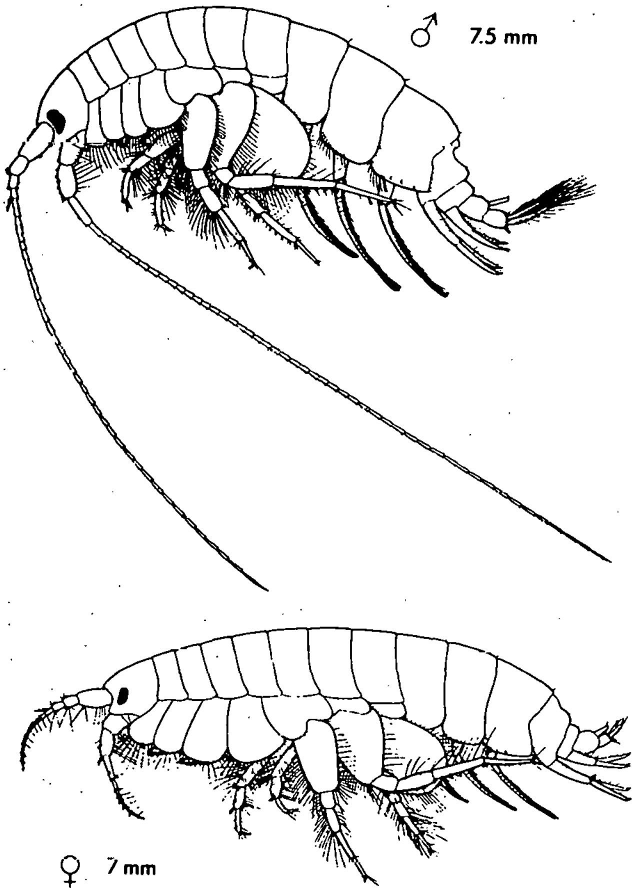

Fig. 11.

Mature Male and Mature Female *Pontoporeia affinis*. Slightly modified from Segerstråle (1937) (with permission, see credits).

Pontoporeia accounts for nearly all Lake Michigan amphipods, but *Hyalella azteca*, *Crangonyx*, and several species of *Gammarus* occur near shore and in harbors and bays. These genera are easily distinguished (Pennak, 1953), and recent keys to species of *Gammarus* (*e.g.* Holsinger, 1972) simplify identification of the several Lake Michigan forms.

Pontoporeia affinis Lindstroem. *Pontoporeia* is a northern element in the fauna, reaching its southernmost limit in Lake Michigan. Its distribution in deep lakes with well-oxygenated hypolimnia follows the farthest extent of glacial advance and indicates that *Pontoporeia*, like *Mysis relicta*, is a glacial relict (Ricker, 1959).

The first specimens of *Pontoporeia* collected from the Great Lakes were described as two new species, *P. hoyi* and *P. filicornis*, by Smith (1874).

Less than 20 years later, *P. hoyi* was synonymized with European *P. affinis*, and *P. filicornis* was recognized to be the mature male form of the same species (Segerstråle, 1937). Subsequently, Segerstråle (1971a) has concluded that three forms of mature males occur within North American *P. affinis* populations: *P. affinis* f. *filicornis*, *P. affinis* f. *brevicornis*, and *P. affinis* f. *intermedia*. This differentiation and other morphological features indicate that nearctic *Pontoporeia* should be placed in one or more new species. Dr. E. L. Bousfield (National Museum of Natural Sciences, Zoology Division, Ottawa, Canada) is currently reconsidering the genus.

Pontoporeia matures at the last molt, which brings pronounced morphological changes in both sexes (Segerstråle, 1937) (Fig. 11). Males develop longer antennae, a slenderer abdomen, and more setae and spines on legs and uropods, which seem to increase swimming ability. In females, a marsupial chamber is formed by plates (oostegites) that issue from the bases of walking legs and interlock beneath the thorax. Eggs are laid into the marsupium and fertilized at the molt. Embryos are brooded for several months until they reach a length of about 2 mm. Males die after mating, thus spending only a short time in the mature state. Females die soon after broods are released.

Pontoporeia begins releasing young in late spring. Populations deeper than 16 m continue to drop broods later in the year, or irregularly throughout the year (Alley, 1968; Segerstråle, 1971b; Mozley, 1974) (Fig. 12). Shallower populations mature in one year, but deeper populations require two years or more (Alley, 1968; Mozley, 1974). At depths from 10 (Alley, 1968) or 16 (Mozley, 1974) to 35 m, *Pontoporeia* has two separate size classes representing populations that breed in alternate years (Fig. 12). Mating is synchronized in late autumn by decreasing photoperiod (Segerstråle, 1971c). Segerstråle (1971b) believed that year-round breeding, which occurs deeper than 60 m, results from lack of sufficient light to trigger synchronous development.

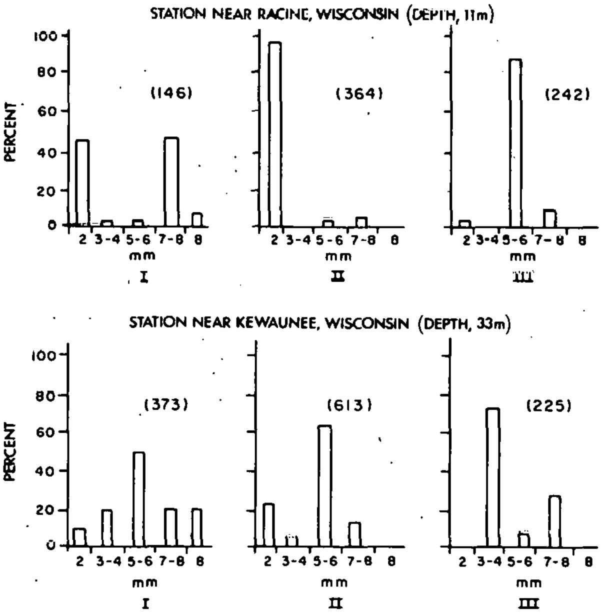

Fig. 12.

Size Frequency Histograms of *Pontoporeia* Populations at Two Stations in Three Sampling Periods: (I) late April-early May; (II) late May-early June; and (III) early October of 1965. Numbers in parentheses are sample sizes. Modified from Alley (1968) (with permission, see credits).

Reproductive synchrony causes *Pontoporeia* abundances to fluctuate in a seasonal cycle. Near shore, newly released young swell the population rapidly in summer, but mortality and emigration cut numbers almost back to April levels by November (Industrial Bio-Test, 1973; Mozley, 1974) (Fig. 13). Fluctuations range over a factor of 10 at depths of 8 to 16 m, but only over a factor of 2 at 40 m (Mozley, 1974). Little or no seasonal variation in abundance occurs deeper than 66 m (Alley, 1968).

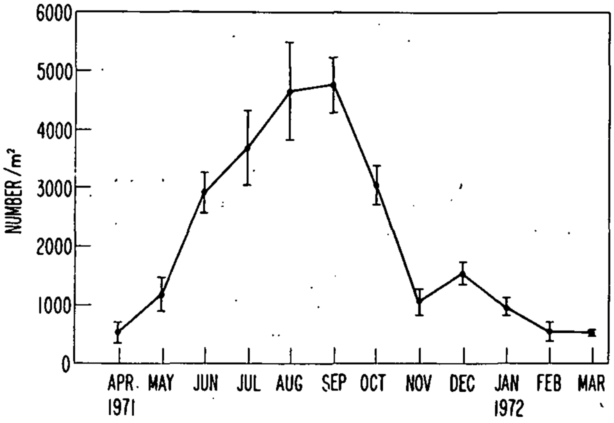

Fig. 13.

Monthly Mean Abundances of *Pontoporeia affinis* at Depths of 3 to 18 m near Waukegan, Illinois. Data from Industrial Bio-Test (1973).

Nearshore densities of *Pontoporeia* are highest in summer. Representative numbers for southeastern Lake Michigan populations in July would be 100/m^2 at 8 m, 1000/m^2 at 12 m, and 5000/m^2 at 24 m (Beak Consultants, 1973; Industrial Bio-Test, 1973; Mozley, 1974). In early April, corresponding densities would be 30, 100 and 500/m^2.

An epiprofundal maximum and declining abundances with increments in depth, both shallower and deeper, have been observed in several lakewide surveys (Eggleton, 1936, 1937; Merna, 1960; Alley, 1968), but the pattern can be modified locally by substratal or topographic features. *Pontoporeia* prefers sediments with mean grain size less than 0.5 mm (Marzolf, 1965b), and in the Lake, greater densities occur in silt-sand mixtures than in pure sand or silty clay (Alley, 1968; Henson, 1970; Mozley and Alley, 1973). Moreover, this amphipod selects microbially active sediments rather than sterile ones with the same grain size (Marzolf, 1965b; Kidd, 1970). Mozley and Alley (1973) showed that densities of *Pontoporeia* are low in hard clay and gravel. A band of these substrates beyond the 10-m contour corresponded to a dip in *Pontoporeia* abundance in southwestern Lake Michigan (Lamble, 1971--unpublished).

Henson (1970) noted an interruption in the depth/amphipod curve between 25 and 40 m in the Straits of Mackinac (Fig. 14). A decrease within that interval was attributed to the steep slope of the bottom and lesser accumulations of fine sediments.

Marzolf (1965b) was unable to find any relationship between depth and abundance (Fig. 15). His study area outside Grand Traverse Bay, like Henson's, had a relatively steep angle of slope, perhaps steep enough to alter sedimentation patterns and completely disrupt the typical depth/abundance relationship.

Many of these substrate effects are apparently due to the fact that *Pontoporeia* derives most of its nourishment from bacteria. Amphipod abundance did prove to be correlated with numbers of bacteria in Marzolf's (1965b)

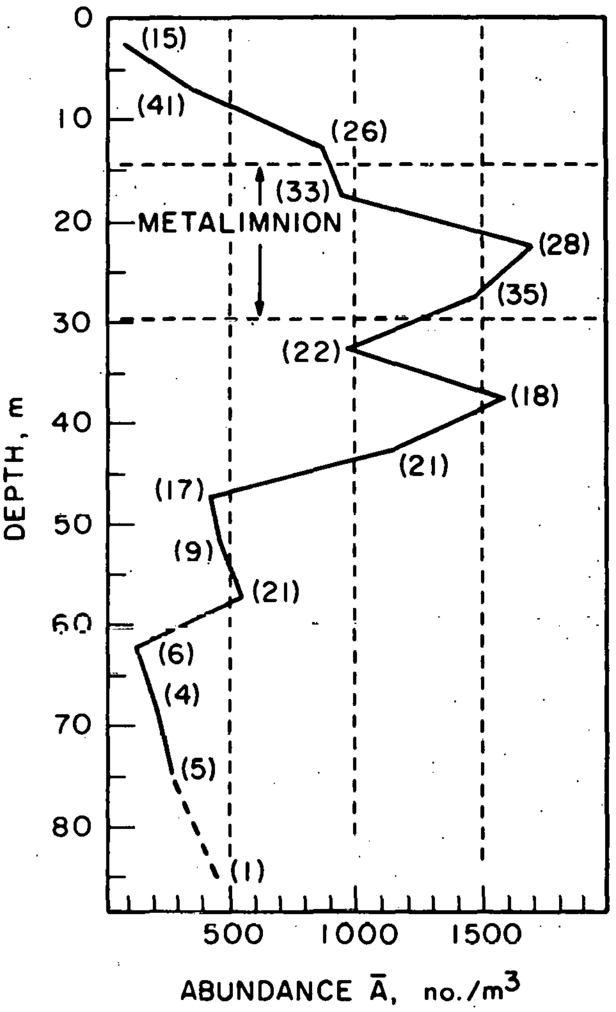

Fig. 14.

Relationship of the Mean Abundance (Ā) of *Pontoporeia* to 5-m Depth Intervals. The numbers in parentheses are the number of samples collected in each stratum. Modified from Henson (1970) (with permission, see credits).

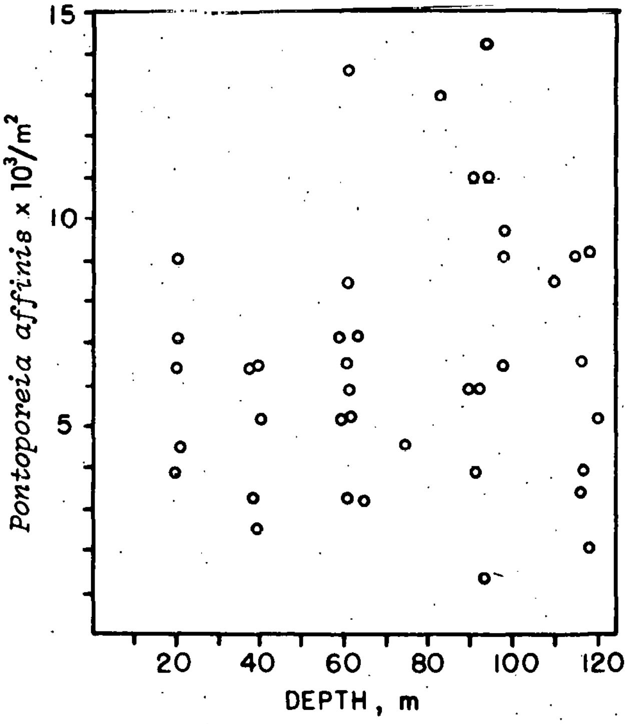

Fig. 15.

Scatter Diagram of the Number of *Pontoporeia affinis* vs. Depth of Sampling. Slightly modified from Marzolf (1965b) (with permission, see credits).

study, and in his selectivity experiments, *Pontoporeia* chose substrates in which bacteria were growing rather than substrates comprised of sterile materials. Although *Pontoporeia* could ingest live algae, it was unable to digest them. Decaying algae were readily utilized, as Kidd (1970) showed in experiments on the role of feeding in radionuclide uptake. Interestingly, *Pontoporeia* did not feed when insufficient sediment was provided for burrowing (Marzolf, 1965b); it preferred its food as a thin surficial layer rather than mixed into the sediments (Marzolf, 1965b).

Maximum growth of *Pontoporeia* occurs in seasons when detrital sedimentation is greatest. In spring, terrigenous organic materials and nutrients introduced into nearshore habitats promote and supplement increased algal productivity, which rapidly increases the food available to amphipods (Johnson and Brinkhurst, 1971b). *Pontoporeia* grows to adulthood by late October of the first year of life at depths shallower than 16 m, and in one section of Lake Ontario contributes almost 90% of total macroinvertebrate production (Johnson and Brinkhurst, 1971b), a proportion that probably applies to much of Lake Michigan.

Production (Johnson and Brinkhurst, 1971b) and abundance of *Pontoporeia* can vary widely in consecutive years (Powers *et al.*, 1967; Alley, 1968; Mozley, 1974). Interannual variations may even exceed magnitudes that have been used as evidence of enrichment of Lake Michigan over a 30-year period (Robertson and Alley, 1966). However, these variations are probably less dramatic offshore where most of Robertson and Alley's stations were located. The point is that abundance of *Pontoporeia* at a given place and time may not be representative of the population, and must be used with caution in assessing nearshore benthic environmental quality.

Temperature of the bottom water is commonly assumed to be one of the primary factors controlling the occurrence of *Pontoporeia*, since glacial relicts by definition characterize residual islands of cold aquatic climates in generally warmer temperate zones (Ricker, 1959). Smith (1972) obtained thermal-tolerance data on populations from Lake Superior which appear to confirm that summer bottom temperatures limit shoreward occurrence of *Pontoporeia* in Lake Michigan. *Pontoporeia* acclimated at 6°C had an LD-50 (24 hr) of 12°C and an LD-50 (96 hr) of 10.8°C. Stocks acclimated at 9°C had an LD-50 (30 day) of 10.4°C, which presumably represents the upper limiting temperature for *Pontoporeia* on a continual basis. In contrast, large numbers of *Pontoporeia* have been encountered in Lake Michigan at stations where temperatures were as high as 19°C (Alley, 1968). At a depth of 12 m, summer temperatures reach 23°C and frequently exhibit fluctuations of more than 5°C within a few hours (Ayers, 1973), but young *Pontoporeia* persist in densities of 100/m^2 or more from June to September (Mozley, 1974).

One is forced to conclude that the importance of thermal factors in shoreward limitation of *Pontoporeia* occurrence is less than would be expected. Other potentially limiting factors include fish predation and coarse-grained, unstable sediments, which occur commonly at depths less than 20 m (Mozley and Alley, 1973).

Many kinds of fish feed on *Pontoporeia* but the most important in terms of predation pressure (number of predators) are alewives (Morsell and Norden, 1968) and smelt (Anderson and Smith, 1971; Mozley, 1975b--unpublished data).

The primary impact of these fish on *Pontoporeia* populations may be highly seasonal, as both have pronounced seasonal onshore migrations. Rare, but perhaps more effective predators inshore, are carp, white and longnose suckers, and bullheads.

In addition, many smaller species--which serve as forage for the large, salmonid piscivores--feed primarily on *Pontoporeia*, including trout-perch, spottail shiners, slimy sculpin, and sticklebacks (Anderson and Smith, 1971; Industrial Bio-Test, 1974; Mozley, 1975b--unpublished data). These fish occur primarily in shallow water, and feed most heavily on amphipods in late summer and fall. A similar seasonal pattern is characteristic of the feeding habits of yellow perch on *Pontoporeia*; they shift from chironomids and fish eggs to amphipods in August and September (Industrial Bio-Test, 1974; Mozley, 1975b--unpublished data).

While probably unimportant in terms of impact on amphipod populations, a number of valuable game fish utilize *Pontoporeia* heavily during part or all of their life cycles, including lake trout and burbot (Van Oosten and Deason, 1938), bloaters (Wells and Beeton, 1963), whitefish (Ward, 1896) and coregonids (Anderson and Smith, 1971). Conclusive demonstration of a limiting effect of fish predation on *Pontoporeia* density, however, awaits more careful study of feeding rates and population densities of the predominant species.

Oldsquaw ducks may also be important predators on *Pontoporeia* in some parts of the Lake (Hickey *et al.*, 1966). Overwintering flocks along the Wisconsin shore dive to considerable depths to feed on amphipods.

There is no evidence that *Pontoporeia* competes with other macroinvertebrates for food or space. Positive correlations with abundances of other taxa, particularly sphaeriid clams, occur over much of Lake Michigan (Alley, 1968). It is generally assumed that densities of amphipods and oligochaetes are inversely related (Powers and Robertson, 1965; Ayers and Huang, 1967; Cook and Powers, 1964), but this is probably true only when tubificid oligochaetes alone are compared with amphipods, and when enrichment levels are high in nearshore areas. In such situations, differing tolerance to sediment factors is more likely causal than is competition between the two taxa (Gannon and Beeton, 1969). Alternatively, vertical mixing of surficial sediments by the worms may decrease availability of fresh sediments to the amphipods. *Mysis relicta* is another potential competitor, for it, too, feeds on detritus in surficial sediments. *Pontoporeia* density decreases as *Mysis* density increases with increasing depth offshore in Lake Michigan (Reynolds and DeGraeve, 1972; Powers and Alley, 1967), perhaps because of interspecific competition for food or predation of *Mysis* on young *Pontoporeia* (Lasenby and Langford, 1973).

Pontoporeia probably carries a number of intermediate stages of parasites. The only confirmed one is the acanthocephalan *Echinorhynchus salmonis*, for which several coregonids and salmonids are definitive hosts (Scott and Crossman, 1973). Frequencies of infection have not been documented for either the amphipod or fish hosts.

A small proportion of *Pontoporeia* migrates vertically. This behavior is largely nocturnal (Wells, 1960; Marzolf, 1965a; McNaught and Hasler, 1966), but may occur in the daytime as well (McNaught and Hasler, 1966; Wells, 1968). Light does not exercise as much control over migration of *Pontoporeia* as over that of *Mysis* (McNaught and Hasler, 1966).

Segerstråle (1937) proposed that vertical migration was related to mating, and Marzolf (1965a) primarily found adults and preadults in his samples. Wells (1968) observed a lakeward shift in daytime catches of *Pontoporeia* above bottom from late spring into summer, which would correspond to a progression of breeding activity from inshore areas in winter to offshore areas in summer (Segerstråle, 1971b). Marzolf's (1965a) net was coarse enough (1-mm openings), however, to allow young *Pontoporeia* to escape. Studies with a finer net, 0.35 mm, have shown no tendency for mature or submature specimens to be overrepresented in samples of migrating amphipods (Mozley, 1974).

An alternative impetus for swimming behavior might be instinctive, seasonal migrations toward or away from shore. European *Pontoporeia* migrate shoreward in late autumn to breed, and young move offshore as surface waters warm in spring (Samter and Weltner, 1904). One group of investigators (Limnetics, 1974a, 1974b) reported a similar sequence in Lake Michigan, but Mozley (1974) observed an increase in *Pontoporeia* young at depths less than 16 m in early summer, and a sudden decrease in autumn for several consecutive years. In one year, at least, the summer increase exceeded the reproductive potential of adults present at those depths earlier in the spring, and necessarily involved some migration shoreward from deeper areas. Merna (1960) also concluded that young released offshore migrated to shallower areas in summer. Only a small fraction of the young migrate, however, for total numbers and proportion of young individuals in offshore populations increase at about the same time as in nearshore ones. Perhaps the apparent migration is simply a passive, general dispersal of young over wide areas, and is more evident near shore where ambient populations are much smaller. Autumnal decreases may also involve some movement away from shore, for Mozley (1974) observed an increase in the number of *Pontoporeia* in nocturnal plankton samples in shallow water at the time benthic populations were rapidly declining there.

Pontoporeia concentrates sublethal quantities of toxic materials and radionuclides from its environment. Wisconsin nearshore populations accumulated pesticides from mud by a factor of about 50 and thereby contributed to tenfold greater concentrations of DDT and its derivatives in alewives, whitefish, and oldsquaw ducks which fed on the amphipods (Hickey *et al.*, 1966). *Pontoporeia* accumulated radioactive isotopes of zinc, manganese, barium, and cesium from sediments or water in laboratory experiments (Kidd, 1970; Mozley, 1973b).

Mass deaths of unknown cause occurred in a population of *Pontoporeia* 10 km southwest of Benton Harbor, Michigan, in early May 1971. Most specimens retrieved in an epibenthic sled towed at 25 m were dead and decaying (Mozley, 1975b--unpublished data). Samples from depths of 31 and 40 m contained somewhat larger proportions of live animals, most of which were in smaller size classes. Heavy coats of fungus made it difficult to determine age and sex of dead specimens, but at least a few were juveniles. This is the only incident of its kind reported to date.

Other Amphipoda. *Hyalella azteca*, a common amphipod in smaller bodies of water (Bousfield, 1958; Pennak, 1953), occurs sparsely in shallow areas of Lake Michigan near Chicago (Shelford, 1913), Grand Traverse Bay (Mozley, 1975b--unpublished data), Green Bay (Howmiller and Beeton, 1971), Little Traverse Bay (Evans, 1973), Port Sheldon (Truchan, 1971), and in northwestern shore areas (Limnetics, 1974b). In accordance with its shallow occurrence, *Hyalella* is more tolerant of high water temperatures than *Pontoporeia*. Specimens from Lake Ontario acclimated at 10°C had an LD-50 (96 hr) of 31.5°C (Sprague, 1963). *Hyalella*'s thermal tolerance was not affected by oxygen concentrations as low as 1.7 mg/1. Tests at 20°C indicated an LD-50 (24 hr) of 0.7 mg oxygen/1 for this hardy amphipod (Sprague, 1963).

Gammarus species are more diverse, and probably more abundant, than *Hyalella* in Lake Michigan. *Gammarus fasciatus* has been found in the northeast (Ward, 1896), southeast (Mozley, 1975b--unpublished data), Ludington (Olson, 1974), and Green Bay areas (Howmiller and Beeton, 1971). Merna (1960) found *G. fasciatus* together with *Pontoporeia* at depths as great as 24 m near Beaver Island. *Gammarus pseudolimnaeus* inhabits rocky substrates near Ludington (Olson, 1974) and in western shore areas (Limnetics, 1974b). *Gammarus lacustris* is distributed near many streams entering the northern part of the Lake (Bousfield, 1958). Unidentified *Gammarus* species have also been collected near Port Sheldon (Truchan, 1971) and Beaver Island (Merna, 1960). Both *Gammarus* spp. and *Hyalella* are more common on breakwalls, pilings, and rocks than in unconsolidated sediments, and neither organism burrows well. Both occur in the water column at night.

Gammarus fasciatus is more tolerant than *Hyalella* of high temperatures, but less tolerant of low oxygen concentrations (Sprague, 1963). Specimens of *G. fasciatus* acclimated at 10°C had an LD-50 (24 hr) of about 30°C, and others acclimated at 20°C had an LD-50 (24 hr) of 32°C. The lower lethal oxygen concentration for this species at 20°C (LD-50, 24 hr) was 4.3 mg/1. Sprague also tested tolerances of *Gammarus pseudolimnaeus*, but his stocks came from a small stream rather than Lake Ontario, as in the case of *Hyalella* and *G. fasciatus*. At the maximum acclimation temperature (29°C), *G. pseudolimnaeus* had an LD-50 (48 hr) of 29.3°C. It appears, therefore, that both *Gammarus* spp. and *Hyalella* are physiologically better equipped than *Pontoporeia* to persist in warm, enriched nearshore areas with some oxygen depletion (see also Smith, 1973).

The only other amphipod genus reported from Lake Michigan is *Crangonyx*. It was represented by a few specimens from Green Bay tentatively identified as *C. gracilis* (Howmiller, 1971a). This species was said by Holsinger (1972) to find a "favored habitat" in the Great Lakes.

Mysidacea

Mysis relicta Lovén. The common name of *Mysis relicta* is opossum shrimp, which derives from both a shrimp-like appearance (Fig. 16) and the habit of carrying young in a pouch beneath the thorax until they are ready for independent life. Free-living individuals range from about 2.4 to 26 mm in length. *Mysis* is transparent in life, except for large, stalked eyes and scattered chromatophores. It swims smoothly forward by paddling with thoracic legs, but to escape harm can also jump quickly backwards by contracting powerful abdominal muscles in the manner of a crayfish. *Mysis* feeds by

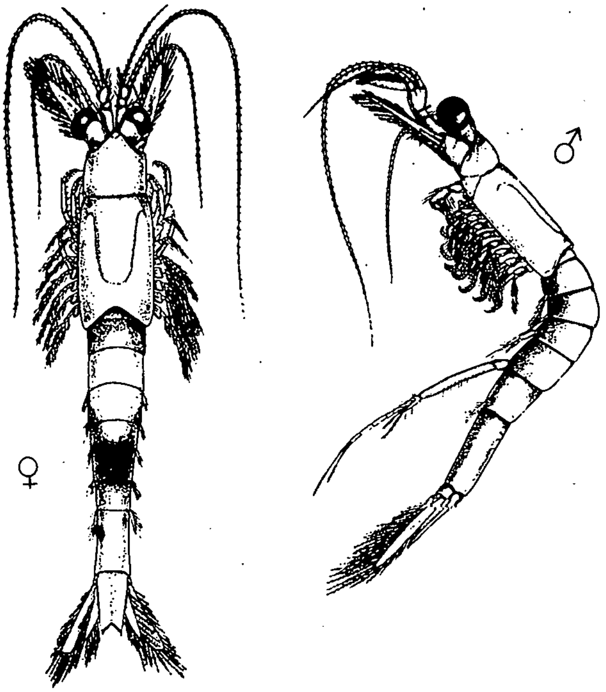

Fig. 16.

Adult Female (not breeding) and Adult Male *Mysis relicta* Lovén. From Tattersall and Tattersall (1951) (with permission, see credits).

filtering suspended particles from the water with its inner thoracic appendages, or possibly by seizing zooplankton. When feeding on the bottom of the lake, *Mysis* stirs sedimented particles into the water in order to use its filtering apparatus.

The taxonomy and identification of *Mysis* was most recently presented by Holmquist (1972). *Mysis relicta* is distinct from the marine *Mysis oculata* and is the only recognized representative of the Mysidacea genus *Mysis* in the Great Lakes, contrary to some published reports. *Mysis* occurs in deep, freshwater lakes throughout the formerly glaciated portions of the northern hemisphere, and has been successfully introduced into a number of lakes that were not affected by the Ice Age (Ricker, 1959).

In southeastern Lake Michigan, offshore *Mysis* live about one year and mate and shed young in all seasons (Reynolds and DeGraeve, 1972). In the shallowest areas, the adults move inshore and mate from winter (December) through early spring, shed their young in April and May, and move offshore as the water warms. Seasonality begins to disappear from *Mysis* reproduction at a depth of about 54 m. Upon reaching a length of about 16 mm, females begin to deposit eggs into the marsupium (abdominal pouch) and simultaneously breed with the males (Reynolds and DeGraeve, 1972). They continue to grow as the embryos and larvae develop. After about five months, the young mysids are shed from the marsupium, at which time the spent female is about 22 mm long. Adults whose breeding function is finished die during the late summer and autumn.

In the deepest parts of the southern and northern parts of the Lake, *Mysis* appears to live slightly longer, and individuals in all life stages are continually present in the population (McWilliam, 1970). Due to the prominence of certain size classes, however, McWilliam was able to detect an intensification of reproduction in late autumn in the southern basin (depth, 152 m) and during winter in the northern basin (depth, 260 m). Further, she found that in the southern basin brooding females were larger and carried larger broods than those in the north. Apparently, a few females continue to grow and molt following the release of their first brood, and may breed a second time. In deeper parts of the northern basin, females were thought to have lifespans approaching two years. This seems likely in view of the findings of Lasenby (1971), who showed that *Mysis* had a one-year life cycle in a productive temperate lake, but a two-year life cycle in an unproductive arctic lake.

Mysis grows about 1 mm per month or faster in the slope region of the southern basin (Reynolds and DeGraeve, 1972), and at about the same rate in the center of that basin (McWilliam, 1970), but individuals in the northern basin apparently grow at a rate of 0.8 mm per month or less (McWilliam, 1970). By applying the relationship between size and weight to their field data on size distributions, Reynolds and DeGraeve (1972) showed the annual cycle of population biomass for *Mysis* at depths less than 72 m (Fig. 17). A large increase in the standing crop occurred in the spring. While length increases at a constant rate, biomass increases as the cube of length, so population production appears to be maximal when the population age structure is dominated by the older individuals. An abrupt decline in standing crop in autumn was said to result from the mortality of postreproductive adults. Ayers *et al.* (1967) reported the occurrence of dead *Mysis* in benthos, zooplankton, and sled-net samples from the central part of the Lake in late summer and autumn. This was probably due to normal mortality following reproduction, but detailed examination of a few samples indicated that immature individuals might also have been dying. The occurrence of seasonal mortalities needs further investigation.

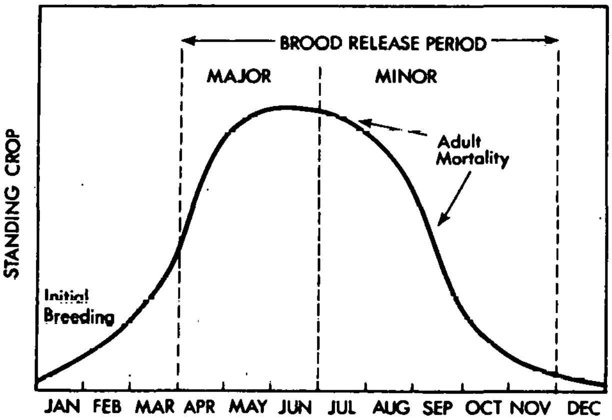

Fig. 17.

Conceptual Annual Cycle of Mysid Biomass in Southeastern Lake Michigan. Redrawn from Reynolds and DeGraeve (1972) (with permission, see credits).

The distribution of *Mysis* in Lake Michigan is primarily oriented according to depth. They are present all year at depths over 30 m. Their geographical range includes the entire Basin and Grand Traverse Bay (Powers *et al.*, 1967). The shoreward movement of populations in winter brings large numbers into depths at least as shallow as 18 m (Reynolds and DeGraeve, 1972), and probably much shallower. Mozley (1973a) collected a few specimens at 6 m in April 1972 in the southeastern part of the Lake, and, by using an epibenthic sled that samples the surficial sediments, found considerable numbers at 12 m. During summer upwellings *Mysis* follows cold water inshore, so it may be found in the shallowest areas any time of the year (Reynolds and DeGraeve, 1972).

One of the most interesting characteristics of *Mysis* is its nocturnal migration habit. Beeton (1960) demonstrated the typical diurnal cycle in Lake Michigan. In daytime, at depths as great as 90 m (Robertson *et al.*, 1968), *Mysis* remains near bottom and probably burrows into the sediments in the shallower parts of its range. At about 100 m, *Mysis* may occasionally range up to 7 m above bottom (Beeton, 1960). At depths over 150 m, mysids probably remain planktonic all day (Robertson *et al.*, 1968). There is evidence in McWilliam's (1970) data that younger individuals range farther above bottom in daytime than mature ones, at least in the deeper parts of the Lake.

When the light intensity in the appropriate wavelength (515 nm) falls below 10^{-1} lux, *Mysis* begins rising toward the surface (McNaught and Hasler, 1966). Beeton (1960) measured a vertical movement speed of 40-80 cm/min, but McNaught and Hasler (1966) found a slower rate of ∿25 cm/min at shallower depths. If *Mysis* encounters higher light intensities near the surface, *e.g.* when the moon is full, the ascent is slowed or reversed. If a sharp thermocline (temperature change rate of 1.7°C/m or more) or high temperature (11°C or over) is encountered, *Mysis* will also stop or slow its ascent. Gradually, most of the population comes to lie near the lower limit of the thermocline in the middle of the night. Shortly before sunrise, descent begins and continues rapidly until the whole population has returned to daytime habitats. While a large part of the population appears to make the nightly journey upward, stragglers are spread throughout the water column, and some may remain close to bottom all night. Swain *et al.* (1970) occasionally collected *Mysis* in summer at 10 m below the surface in midlake, but always at night. They caught many more specimens by the same technique in Lake Superior than in Lake Michigan.

Mysis relicta feeds freely on suspended materials. McWilliam (1970) found amorphous material in the stomachs of most specimens, together with a few recognizable remains of planktonic organisms--the sort of particles that make up surficial sediments. On one occasion, however, she observed individuals which had fed solely on fresh diatoms. Ward (1896), without indicating the basis for his statement, reported that *Mysis* fed mostly on copepods. Diet analysis of European *M. relicta* is similarly ambiguous (Tattersall and Tattersall, 1951). Lasenby (1971) and Lasenby and Langford (1973) demonstrated that *Mysis* is opportunistic and will ingest *immobilized* chironomid larvae, zooplankton, suspended organic particles, or algae growing on submerged moss. The possible connection between migration and feeding is still unresolved.

Virtually every kind of fish that occupies the deeper parts of the Lake includes *Mysis* in its diet (Anderson and Smith, 1971). Reynolds and DeGraeve (1972) listed extensive recent literature that establishes it as a major food item of smelt, adult bloaters, juvenile lake trout, burbot, and four-horned sculpin. In addition, Morsell and Norden (1968) found *Mysis* to be an important component in the diet of the alewife. However, the impact of fish predation on *Mysis* populations has not been determined.

Present-day geographical distributions of *Mysis relicta* indicate that this species is dependent on a cold, well-oxygenated hypolimnion for survival in temperate-zone lakes (Ricker, 1959); distributional data from Lake Michigan also suggest a preference for cold water. Studies of the thermal tolerance of *Mysis* from Trout Lake in northern Wisconsin (Smith, 1970) showed that it can readily tolerate temperatures below 10°C, but begins to suffer some mortality at higher temperatures. Half a group of experimental animals kept under low-light intensity died in four days when subjected to 16-18°C. No animals survived exposure to 20°C for longer than a few days. In the absence of light, however, *Mysis* from Great Slave Lake, Canada, tolerated temperatures of 16-18°C for long periods (Ricker, 1959), and after a sudden thermal shock (10°C increase), *Mysis* acclimated to 9°C exhibited a significantly higher survivorship than those acclimated to 7°C. Most field records suggest that *Mysis* is seldom abundant in water warmer than 14°C.

Smith (1970) also demonstrated the effects of light on survival. *Mysis* in a darkened aquarium survived for 12 weeks at 7.5°C with only minor mortality, but of those animals exposed to laboratory room light during the day at the same temperature, 82% died. The mechanism of injurious effect of light on *Mysis* was not apparent.

Tolerance of *Mysis* to low oxygen concentrations can only be deduced from field measurements. Juday and Birge (1927) trapped some *Mysis* in water strata with oxygen concentrations below 1 ppm in Green Lake, Wisconsin. Most of the populations were in water with higher oxygen concentrations. *Mysis* has the ability to move up near the thermocline when deeper parts of the lake become deoxygenated, but *Mysis* is not known to occur in any lakes in which there is complete depletion of oxygen in the hypolimnion.

Present information suggests that this species is one of the most important biotic components in Lake Michigan's pathways of energy flow, especially in offshore areas. Minimum estimates of population density obtained from vertical zooplankton tows, which miss the epibenthic portion of the population, show that *Mysis* populations in the deepest parts of Lake Michigan have standing crops (ash-free dry weight per unit area) approaching or exceeding those of all other macrobenthic animals combined (Table 5).

Table 5. Average Biomass (Dry Weight) of *Mysis relicta* in Deep Vertical-Haul Samples Collected from the Northern and Southern Basins Compared to Average Biomass of Benthos and Zooplankton Taken over the Same Period*

	Average Biomass, g/m² Lake Surface		
Year	*Benthos*	*Zooplankton*	*Mysis*
		Southern Deep (150 m)	
1964	-	0.93	0.47
1965	1.67	0.74	1.01
1966	1.34	0.40	1.01
1967	-	-	1.51
		Northern Deep (260 m)	
1964	-	1.23	3.72
1965	0.27	1.17	3.68
1966	0.16	0.59	4.46
1967	-	-	3.81

**Data from McWilliam (1970, 1972--personal communication).*

The greatest need for research on *Mysis relicta* is a means of obtaining quantitative samples that include all segments of the population. Gear selectivity has, to date, hindered attempts to work out details of mysid distribution over the Lake and to obtain estimates of its absolute abundance and production. Lasenby (1971) used SCUBA to count *Mysis* in bottom quadrats along a transect in Char Lake (North West Territory, Canada) and was able to get good quantitative abundance data and an estimate of production. This technique may have utility in small areas of Lake Michigan, but until a suitable method is found for sampling *Mysis* in deep water over large areas of the Lake, it will be impossible to accurately assess this organism's role in the energy flow of Lake Michigan.

Isopoda

Isopoda are dorsoventrally flattened relatives of the amphipods. Aquatic species have the appearance of the familiar terrestrial sowbugs (Fig. 18); they are similar in size, also, but have somewhat longer legs. Sometimes the animals are taken in benthos samples, but they seem to prefer hard substrates in Lake Michigan. No quantitative studies have been published. The genus *Asellus* is reported by Willson (1969), Evans (1973), and Limnetics (1973). Surber and Cooley (1952) identified specimens from Green Bay as *Asellus communis*, but Balch *et al.* (1956) and Howmiller and Beeton (1971) found *Asellus militaris* there. Merna (1960) found *Lirceus lineatus* as deep as 27 m on shoals near Beaver Island, and there is a single record of *Lirceus* from Green Bay (Howmiller, 1971a).

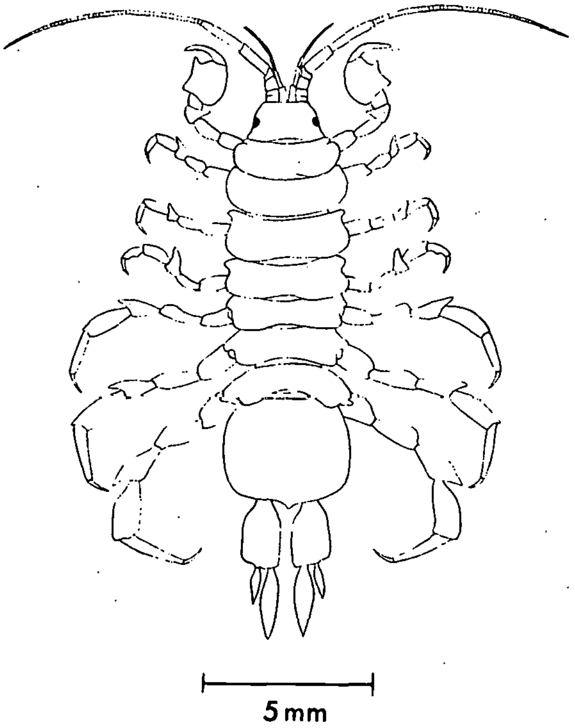

Fig. 18.

Adult *Asellus* sp. From Pennak (1953) (with permission, see credits).

Williams (1972), in a recent review of the taxonomy of *Asellus*, reported that the most common isopod in the Great Lakes proper is *Asellus racovitzai*. Although this species has not been recorded from Lake Michigan, many reports of isopods may be attributable to it. Records noted above indicate that isopods occur from Milwaukee, Wisconsin, around the northern part of the Lake to Grand Haven, Michigan--wherever there are shoals or hard substrata in shallow water. Since the identity of the species is in question, no purpose would be served here in describing biological characteristics in detail.

Decapoda

The occurrence of crayfish in Lake Michigan is sometimes overlooked because of their ability to avoid capture in grab samplers, and their comparatively low numbers per unit area. They also tend to be most numerous on rocky bottoms where they hide in crevices and beneath the stones and easily avoid sampling devices. These animals appear frequently in fish trawls, however, and are presumably common over most of the shallow areas of Lake Michigan. Depth limits of their distribution are unknown. Miscellaneous specimens collected in northern areas of Lake Michigan by divers (and curated at the Great Lakes Research Division, University of Michigan) include two species, *Orconectes virilis* and *Orconectes propinquus*. They often occur at the same location, but *O. virilis* is probably collected more frequently by divers because of its larger size.

Large populations have been observed (Mozley, 1975b--unpublished data) in several parts of Grand Traverse Bay. In the outer part of Little Traverse Bay, these animals have been used as monitoring organisms in a study of radionuclide accumulation and distribution in Lake Michigan biota (Nelson *et al.*, 1971). Stomachs of Grand Traverse Bay specimens were full of algae, but crayfish are known to feed on a wide variety of plants, animals, and detritus. Night observations (Mozley, 1975b--unpublished data) indicated that crayfish were more active and less secretive than in the day. Some females were carrying young on abdominal pleopods in late May in Grand Traverse Bay, and most males were in the Form I life stage [sexually mature and capable of breeding (Crocker and Barr, 1968)] at that time.

Green Bay once supported a commercial fishery for *Orconectes virilis*. Boiled crayfish are said to have been a regular feature at many local taverns, and, according to Creaser (1932), large numbers were shipped to the Chicago market in certain seasons. The current status of the fishery is unknown, but it is apparently much diminished in importance.

Ostracoda

These tiny crustaceans, with carapaces shaped rather like clamshells, have been the subject of a recent qualitative study in Lake Michigan (Avcin and Collinson, 1973--unpublished). In the southern two-thirds of the Lake, they found live specimens of 11 species and two more represented by empty valves. Some species occurred mainly in samples from depths over 35 m: *Candona subtriangularis*, *Candona crogmaniana*, and *Limnocythere friabilis*. Others were found primarily in samples from shallower depths: *Cypridopsis vidua*, *Cyclocypris* sp., *Candona faba*, and *Candona* cf. *rawsoni*. The remaining species were found too seldom to show any depth-related trends in distribution. There were no reliable indications of differences in abundance or species composition in different areas of the Lake. Few other investigators have given data on ostracods due to their generally small size, which usually excludes them from the operational category *macroinvertebrates*.

Insecta

Diptera

Chironomidae. Chironomids--or midgeflies--are holometabolous insects, which means that larval, pupal, and adult stages each have different and characteristic forms (Oliver, 1971) (Fig. 19). The larval stages occur throughout Lake Michigan; they range in length from 1 mm or less when hatched from the egg to 20 mm or longer during prepupal phases of the largest species. Body widths range from less than 0.1 mm to about 2 mm. Some species are brilliant red (giving rise to a common name "bloodworms"), while others are orange, white, yellow, translucent, brown, or pink and green.

At the end of the larval instars (almost always four in number), chironomids transform into pupae (Fig. 19). A few days after pupation, they swim to the surface, where adults (imagoes) emerge from the pupal case and fly away. Adults do not feed, but use stored energy to complete their reproductive functions (Oliver, 1971). Males typically form swarms near the Lake; females fly into the swarms, mate, and fly out over the Lake to drop their egg masses. The eggs are usually encased in a gelatinous sheath in masses of a few hundred to a thousand or more. The first larval stage, or larvula,

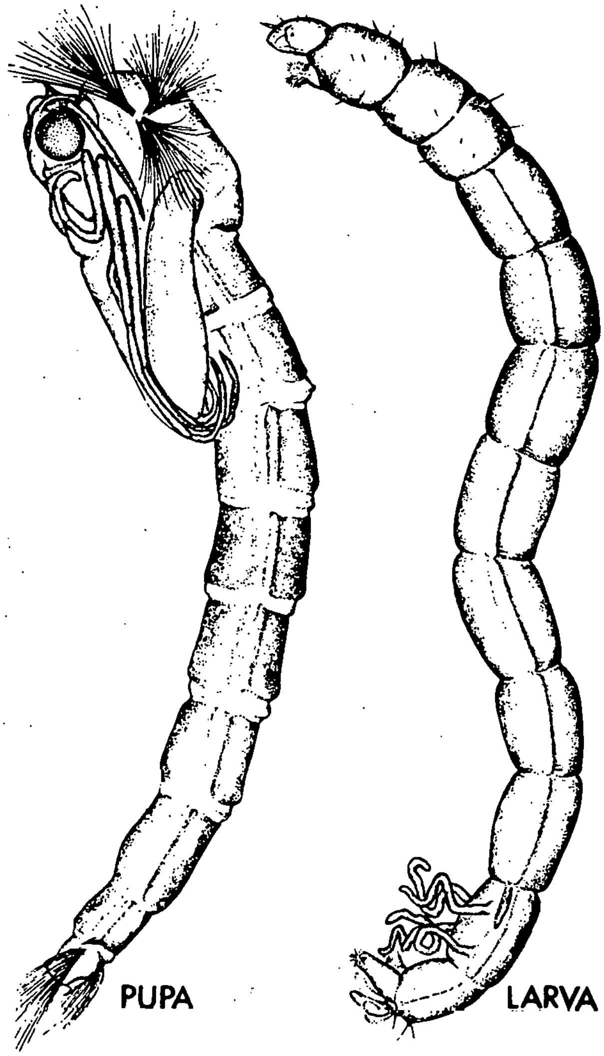

Fig. 19.

Pupa and Larva of *Chironomus* sp. From Johannsen (1937) (with permission, see credits).

digs out of the jelly and becomes planktonic for a few days. Eventually, it settles to the bottom, builds a shallow tube, and molts to the next instar. The remainder of the larval stage may last from a few months to two years, depending on the species of chironomid and the ambient temperature and food supply (Jónasson, 1972).

Many chironomids occur in benthic samples in only one or a few seasons each year. A survey conducted in spring often yields a different assortment of species and relative abundances from one conducted in the fall. Some species emerge in springtime, others in midsummer, and still others in autumn; and from the time of emergence until larvae of the next generation grow to the third--or sometimes even the fourth--instar, each species will be absent or underrepresented in ordinary, sieved collections of zoobenthos.

Larvae possess a number of taxonomically useful body structures, and genera and subgenera can usually be determined from larval morphology. Species-level identification, however, necessitates rearing adult males from the larvae. Species names based only on unreared larvae must be qualified by "cf.", "nr.", or "-group", with rare exceptions [*e.g. Monodiamesa* (see Saether, 1973)]. Recent work has expanded the feasibility of species identification markedly (see Acknowledgements).

Chironomidae larvae recorded from Lake Michigan are listed in Table 6; the study locations are presented in Figure 20. The most abundant or widespread genera in Lake Michigan on sandy or silty bottoms are *Heterotrissocladius, Chironomus, Cryptochironomus, Polypedilum, Procladius, Paracladopelma, Monodiamesa, Potthastia, Micropsectra,** and *Tanytarsus*.* In some areas, *Phaenopsectra (= Sergentia ?), Stictochironomus, Dicrotendipes, Parachironomus, Demicryptochironomus, Cryptotendipes, Protanypus, Trissocladius,* and miscellaneous additional Orthocladiinae are common.

Shallow, rocky substrates on the western shore are colonized by *Cricotopus* spp., *Thienemannimyia*-group (several genera of pentaneurine Tanypodinae indistinguishable as larvae), *Tanytarsus*, *Parakiefferiella*, and *Microcricotopus* (Limnetics, 1974b; Industrial Bio-Test, 1974). In addition, some genera inhabit both sands and silts, and rocky substrates. These genera include *Parachironomus, Chironomus, Monodiamesa, Cryptochironomus, Psectrocladius,* and *Polypedilum*. Chironomid abundances average 1000/m^2, or about 20% of the macroinvertebrates, among rocks near Kewaunee (Industrial Bio-Test, 1974).

Several different systems of generic nomenclature have been used by investigators of Great Lakes chironomids, and comparison of records is difficult or impossible. The typical larva of the profundal zone is an apt example (Henson, 1966). It has been listed as *Spaniotoma, Hydrobaenus*, and *Metriocnemus*, of which the last two are valid names and quite distinct from *Heterotrissocladius*. In recent years, decisions by the International Commission on Zoological Nomenclature have facilitated construction of a widely recognized system of names (Hamilton *et al.*, 1969; Oliver, 1971).

**The genera Micropsectra and Tanytarsus are taxonomically very close and according to Reiss and Fittkau (1971) are inadequately defined for taxonomic discrimination of larvae. We use the names in reference to larvae with (Micropsectra) or without (Tanytarsus) small spurs on the antennal tubercles.*

Table 6. Chironomidae Larvae Recorded from Lake Michigan through 1973*

*Species***	*Study Location*†
Tanypodinae	
Tanypus stellata Coquillet	9
Procladius cf. *culiciformis* (Linnaeus)	1-3,8,10,13
Procladius sp.	5,8-10
Psectrotanypus ? sp.	2
Arctopelopia sp.	7,8,10
Ablabesmyia sp.	1
Pentaneura sp.	1?,2,4,10-12
Diamesinae	
Diamesa cf. *fulva* Johannsen	2
Diamesa sp.	1,7
Potthastia cf. *longimanus* Kieffer	5,7,8,10
Potthastia sp.	13
Protanypus cf. *morio* (Zetterstedt)	5
Monodiamesa cf. *bathyphila* (Kieffer)	3,5,7,8,10
Monodiamesa tuberculata Saether	8-10
Monodiamesa depectinata Saether	5
Monodiamesa sp.	13
Orthocladiinae	
Brillia sp.	10,12
Cricotopus cf. *sylvestris* (Fabricius)	8
Cricotopus sp.	4,7,9,10,12
Heterotrissocladius cf. *grimshawi* Edwards	5,8
Heterotrissocladius cf. *subpilosus* (Kieffer)	3,5
Heterotrissocladius sp.	7,9,10
Psectrocladius cf. *simulans* (Johannsen)	6,8,9
Psectrocladius spp.	4,8,10,11
Diplocladius sp.	8
Smittia sp.	4
Trissocladius cf. *distylus* Goetghebuer	5
Trichocladius sp.	13
Chironominae	
Chironomus cf. *plumosus* (Linnaeus)	1,2,5,12
Chironomus cf. *attenuatus* Walker	1,2,3,8,13
Chironomus cf. *tentans* Fabricius	1,10
Chironomus cf. *riparius* Meigen	10
Chironomus cf. *staegeri* Lundbeck	10
Chrionomus cf. *anthracinus* Zetterstedt	5,8
Chironomus fluviatilis-group	6,8
Chironomus sp.	1,2,4,6,7,10,11
Cryptochironomus cf. *digitatus* (Malloch)	1,2,3,10
Cryptochironomus cf. *blarina* Townes	10
Cryptochironomus spp.	1-3,5-12,13
Cryptotendipes sp.	7,10
Demicryptochironomus cf. *vulneratus* Zetterstedt	8,9
Dicrotendipes cf. *fumidus* (Johannsen)	2,11
Dicrotendipes cf. *nervosus* (Staeger)	6
Dicrotendipes sp.	6,8,9
Endochironomus cf. *nigricans* (Johannsen)	3
Endochironomus sp.	6
Glyptotendipes sp.	1,4,5,10,11
Harnischia cf. *amachaerus* Townes	1-3
Harnischia spp.	2,6-8,10,11

Table 6. contd.

*Species***	*Study Location*†
Chironominae (contd.)	
Kiefferulus cf. *tendipediformis* Goetghebuer	10
Kiefferulus sp.	8
Microtendipes	4,11
Parachironomus cf. *demeijerei* Kruseman [= *P. claviger* (Townes) ?]	6?,8,9
Parachironomus cf. *abortivus* (Malloch)	6
Parachironomus cf. *pectinatellae* (Dendy and Sublette)	6
Parachironomus sp.	7,10,13
Paracladopelma cf. *obscura* Brundin	5,8,9
Paracladopelma tylus†† (Townes)	6,8,9
Paracladopelma nereis†† (Townes)	8
Paracladopelma cf. *naic* (Townes)	7,10,13
Paracladopelma cf. *rolli* (Kirpitshenko)	6,8
Paracladopelma sp.	7,8,10
Paralauterborniella sp.	3,5,7,10
Phaenopsectra sp.	3,5,8
Polypedilum cf. *fallax* (Johannsen)	7,8,10
Polypedilum cf. *halterale* (Coquillet)	7,10
Polypedilum scalaenum (Shrank)	7,8,10
Polypedilum cf. *illinoense* (Malloch)	6
Polypedilum sp.	3,8,12,13
Pseudochironomus sp.	2,12
Stictochironomus spp.	1,2,3,5-7,10
Paratanytarsus sp.	1
Stempellina cf. *bausei* Kieffer	1,3
Rheotanytarsus sp.	8
Tanytarsus-Micropsectra spp.	1-8,10,12,13
Cladotanytarsus spp.	5,8

**For additional records, see Mozley (1974); Limnetics (1974b); Industrial Bio-Test (1974).*

***Nomenclature and order of listing follow Hamilton et al. (1969).*

†*Study locations from which the larvae were taken are shown in Figure 20. Reference sources for study locations are:*

1-3 - Howmiller (1971a)
4 - Evans (1973)
5 - Mozley (1975b--unpublished data)
6 - Truchan (1971)
7 - Beak Consultants (1973)
8 - Mozley (1973a, 1975b--unpublished data); Mozley and Garcia (1972)
9 - Gurney (1973--personal communication); Saether (1973)
10 - Industrial Bio-Test (1973); Saether (1973)
11 - Limnetics (1973)
12 - Merna (1960) (whole Lake)
13 - Rains (1971) (locations same as no. 9).

††*Although P. nereis has been recorded at the Donald C. Cook Nuclear Power Plant, its larval stage is unknown. References to larvae by the name P. nereis prior to 1974 pertain to P. tylus.*

Vascular macrophytes will probably prove to harbor *Cricotopus*, as well as the genera *Glyptotendipes*, *Endochironomus*, *Stenochironomus*, *Polypedilum*, and many kinds of Tanytarsini. Ectoprocts, freshwater sponges, gastropods, and ephemeropterans may also host commensal chironomids (Oliver, 1971).

Species composition of chironomids changes with depth in nearshore areas of southeastern Lake Michigan. The most common forms at depths less than

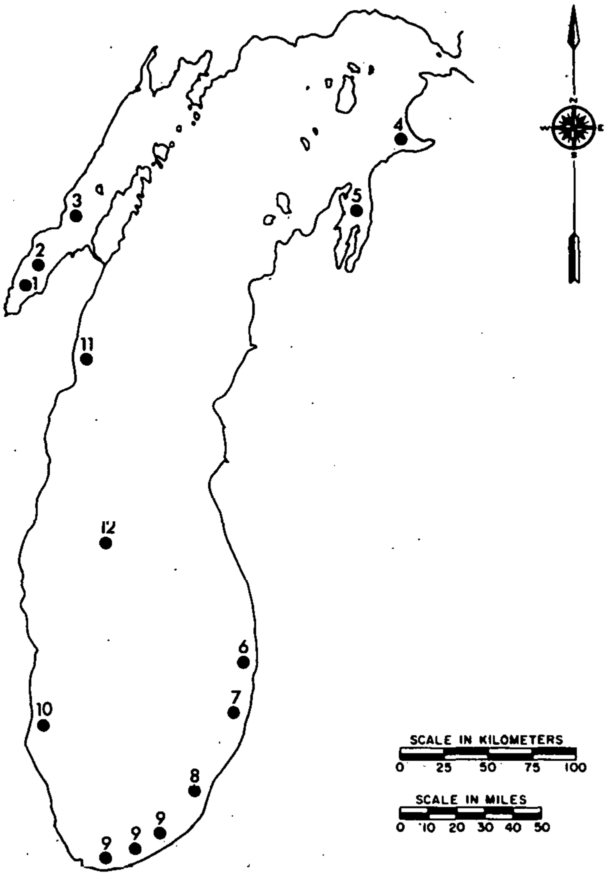

Fig. 20.

Study Locations for Reference Sources on Chironomidae Species Records in Lake Michigan as Presented in Table 6.

8 m are *Chironomus* (two or more species), *Cryptochironomus* sp., *Paracladopelma tylus*, *Paracladopelma* sp., *Psectrocladius* cf. *simulans*, and *Parachironomus* cf. *demeijerei* (Rains, 1971; Truchan, 1971;* Mozley, 1973a, 1974). *Paracladopelma* cf. *obscura* has been collected in this zone occasionally (Mozley, 1973a; Rains, 1971) under the name *P.* nr. *nais*. *Dicrotendipes*, *Endochironomus*, *Stictochironomus*, and *Glyptotendipes* are somewhat rarer, and *Parachironomus* cf. *abortiva*, *Parachironomus* cf. *pectinatellae* (commensal on the ectoproct *Pectinatella*), and *Polypedilum* cf. *illinoense* were found only by Truchan (1971).*

Chironomids comprise nearly all benthic macroinvertebrates (80%) in this shallowest interval (depths <8 m) in spring and summer (Rains, 1971; Truchan, 1971; Mozley, 1973a), but their importance diminishes after July when many species emerge and Naididae, Amphipoda, and Tubificidae increase. Both maximum numbers of chironomids and their proportion in the benthos decrease with increasing depth beyond 16 m in Lake Michigan (Mozley, 1973a) (Fig. 10).

At depths from 8 to 16 m, *Chironomus* spp., *Cryptochironomus* spp., and *Polypedilum scalaenum* are the more common forms. *Micropsectra, Monodiamesa tuberculata, Potthastia longimanus*, and *Paracladopelma* cf. *obscura* occur frequently. From 16 to 25 or 30 m, the most numerous chironomids are

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**Mr. Truchan's collections at the Michigan Water Resources Commission in Lansing were reviewed by S. Mozley to clarify midge identities.*

Procladius and *Chironomus*, accompanied by *Micropsectra*, *Heterotrissocladius* spp., and occasional representatives of genera that are most common in shallow areas. From 30 to 50 m, chironomids are largely composed of *Heterotrissocladius* cf. *subpilosus* and *Procladius*. Beyond 50 m, *H.* cf. *subpilosus* is virtually the only midge present.

Merna (1960) was the first to report generic identities of Lake Michigan chironomids in offshore areas. His findings contrast with those of more recent investigators in the greater variety and different composition he obtained for the upper profundal zone. *Pseudochironomus*, for example, ranged from 9 to 72 m. *Cricotopus*, *Cryptochironomus* and a Pentaneurini species occurred as deep as 54 m. Merna's data on *Brillia*, which was present at his deepest station, probably refer to *Heterotrissocladius* (Henson, 1966).

Industrial Bio-Test (1973) gave seasonal data on chironomid species at depths up to 18 m near Waukegan. *Monodiamesa tuberculata* was the most abundant chironomid, and many of the forms found in the southeast were rare or absent. Total chironomid numbers followed no seasonal pattern, but *Monodiamesa* reached a maximum in August and September, which suggests an autumn emergence (see also Limnetics, 1974a). In contrast, Mozley (1973a) concluded that *Monodiamesa tuberculata* emerged in early spring south of Benton Harbor. Evidently chironomid composition, abundance, and seasonal variations may vary from one part of Lake Michigan to another in nearshore areas.

Several other chironomids exhibited concentrated emergence periods south of Benton Harbor (Mozley, 1973a). *Paracladopelma tylus* has emerged en masse during July for three successive years. This small species passes through meshes of standard sieves in its first three instars, and appears in survey samples only just prior to pupation. *Chironomus* sp., *Polypedilum scalaenum*, *Paracladopelma* sp., and *Parachironomus* cf. *demeijerei* also occurred primarily in summer samples and emerged prior to September. *Potthastia longimanus*, like *Monodiamesa*, emerged in spring and appeared mainly in spring or fall grab surveys. *Procladius*, *Paracladopelma* cf. *obscura*, and *Heterotrissocladius* were autumn emergers. Most chironomids reproduced in months between April and October.

In Green Bay, chironomid larvae occurred at 27 of 28 stations in the southern end, and averaged 1418/m^2 in October 1966 (Howmiller, 1971a; Howmiller and Maass, 1973--unpublished). Dominant forms were *Chironomus attenuatus*, *Chironomus plumosus*, and *Procladius*, which comprised 54%, 26%, and 14% of the total numbers collected, respectively. Seven other taxa made up the remaining 6%. In May 1967, the mean chironomid abundance was 590/m^2, and the two *Chironomus* forms combined contributed only 43% of the total. Either a mass emergence in spring or heavy mortality due to anoxia beneath the winter ice could account for the decrease in *Chironomus*. The May collections in 1967 and 1969 both contained substantial proportions (13-16%) of *Tanytarsus* sp. In October, however, they contributed only 0.3%. In the middle part of the Bay, farther from the Fox River, *Cryptochironomus* cf. *digitatus* appeared in the fauna (8% in May 1969), but composition was otherwise similar to the lower Bay. In the upper Bay around Chamber's Island, an additional ten taxa were collected from only six stations. There, chironomid composition was similar to that found in the open Lake, including *Heterotrissocladius* and *Monodiamesa*. Southern bay elements remained in the fauna, indicating that the area was transitional between the Bay and open Lake.

Henson (1966) reported *Chironomus* cf. *anthracinus* in the southern end of the east arm of Grand Traverse Bay. Other collections have added many genera in the outer parts of the Bay [Mozley, 1975b--unpublished data (study location no. 5 in Table 6)].

Chironomid larvae are known to have a wide variety of feeding habits, but laboratory studies of diets have been infrequent and cursory. *Procladius* feeds on Oligochaeta, copepods, other chironomids, and Protozoa (*Difflugia*), but occasionally ingests diatoms or desmids as well. Positive correlations between numbers of Oligochaeta and numbers of *Procladius* (Rains, 1971) may indicate a feeding preference for worms by Lake Michigan representatives of the genus. *Cryptochironomus* from Lake Michigan have been found several times with stomachs full of oligochaete setae (Mozley, 1975b--unpublished data). Most other chironomids have miscellaneous sediment and detrital particles in their stomachs.

Chironomus from other habitats have been observed to build mucus nets across the lumen of their burrows and pump water through them to strain out suspended particles (Jónasson, 1972). Other species of *Chironomus* may cast threads of sticky mucus over the sediment surface and reel them in to obtain freshly deposited material (Jónasson, 1972). Tanytarsini build elongated, cohesive tubes on or just below the sediment surface, and scrape food particles from the interiors or surrounding mud surfaces. Some *Cricotopus* excavate tunnels in submerged plants, but it is not known whether they do this for food or for shelter. Many chironomid genera that are ordinarily considered to be detrivorous attack and eat tubificids when the opportunity is offered (Loden, 1974).

The combination of filtration and surface-scraping would appear to place chironomids in competition with Sphaeriidae and *Pontoporeia*, but instances of direct competition have not been documented. Alley (1968) found positive statistical correlations between numbers of *Pontoporeia* and total chironomids in Lake Michigan. The literature contains a number of reports of inimical effects of chironomids upon tubificids (Brinkhurst and Kennedy, 1965; Jónasson and Thorhauge, 1972; Loden, 1974), but it is unlikely that the adverse effects are the result of competition for food as the chironomids involved generally feed at the mud surface (Walshe, 1947; Jónasson, 1972) while the tubificids do most of their feeding at depths of several centimeters in the mud (Sorokin, 1966; Davis, 1974a). Observations by Loden (1974) strongly suggest that these adverse effects consist of predation by chironomids upon worms.

Predators of chironomid larvae (other than chironomids themselves) include mites, leeches, and benthophagic fish such as yellow perch, sculpins, trout-perch, sticklebacks, spottail shiners, longnose and common suckers, carp, and bullheads (Anderson and Smith, 1971; Industrial Bio-Test 1974; Mozley, 1975b--unpublished data). Fish that feed mainly on *Pontoporeia* and *Mysis* also take chironomids occasionally. Yellow perch probably feed heavily on pupal stages of chironomids during emergence periods in summer (Tharratt, 1959). Chironomids have not been identified beyond family in fish diet studies in the Great Lakes.

Chironomid larvae undergo nocturnal, vertical migrations. Reports from an increasing variety of habitats--including Lac la Ronge, Saskatchewan

(Mundie, 1959)--list chironomids in nocturnal plankton. Mozley (1974) observed relatively large numbers of several kinds of chironomids in plankton samples near the Donald C. Cook Nuclear Power Plant (hereinafter called the Cook nuclear plant), and Hiltunen (1969a) found larvae in plankton samples from Lake Superior. In many chironomid species, the brief larvula phase just after hatching is planktonic, apparently ensuring dispersal over the available habitat, but larvae in all stages of development swim up from the bottom. Although migration occurs regularly each night and species composition of migrating forms is similar all year, only a few percent of benthic populations are above bottom at a given time (Mozley, 1975b--unpublished data).

Thermal tolerances and preferences of even the dominant species of chironomids in Lake Michigan are unknown. Curry (1965) has compiled field-observation data on temperature tolerances for many species from a wide range of habitats. *Chironomus* species are among the more tolerant members of the family, withstanding natural temperatures of 33°C or higher. One species in Europe, *Chironomus thummi*, has a 22-hr LD-50 of 34.5°C (Walshe, 1948). Since the species identity of *Chironomus* and other chironomids in Lake Michigan is not certain, generalizations on thermal tolerances and preferences derived from literature reports may be invalid.

Trichoptera

The greater portion of the life cycle of Trichoptera is spent as aquatic larvae; the adults are flying terrestrial insects that live about a month. Larvae, the focus of our main concern, range from a few millimeters to about 3 cm in length. They construct cases of detritus or sand grains and move about over the bottom foraging for algal, detrital, or sometimes animal food, or spread mucus nets to trap suspended organic particles. Members of this group are commonly referred to as caddis flies.

Scattered records of unspecified caddis-fly larvae and pupae, as well as a few identifications to genus or species, indicate that caddis flies are usually present in small numbers in all shallow areas of Lake Michigan. They seem to occur with higher frequency and in greater densities in the northern regions of the Lake. Trichoptera were recorded from near the Campbell power plant (Truchan, 1971), near the mouth of the Manistique River (Willson, 1969), at depths to 45 m on shoals near Marquette and to 26 m near Grand Haven (Merna, 1960), on the western shore (Limnetics, 1973), near shore in Little Traverse Bay (Evans, 1973), and in Green Bay (Wis. State Comm. Water Pollut., 1939; Surber and Cooley, 1952). A list of those Trichoptera identified below order is presented in Table 7. Additional records are given by Mozley (1974), Limnetics (1974b), and Industrial Bio-Test (1974). Limnetics (1974b) reported large numbers of *Hydropsyche* in the vicinity of a power-plant discharge, and Mozley (1975b--unpublished data) has encountered large numbers of this genus in coarse terrigenous detritus in the southeastern part of Lake Michigan.

Ephemeroptera

Ephemeroptera, commonly called mayflies, spend most of their life cycle as aquatic immature stages referred to as nymphs. After one or two years, nymphs transform into an aerial immature stage, the subimago. The subimago stage lasts only about a day and the adult imago stage only a few days, existing solely to reproduce and disperse eggs. Like caddis flies, aquatic immature

Table 7. Trichoptera Recorded from Lake Michigan through 1973

Species	*Location*	*Reference*
Helicopsyche borealis	Little Traverse Bay	Evans (1973)
Hydropsyche sp.	Little Traverse Bay Milwaukee	Evans (1973) Limnetics (1973)
Oecetis avara	Little Traverse Bay	Evans (1973)
Athripsodes sp.	Little Traverse Bay Milwaukee	Evans (1973) Limnetics (1973)
Hydroptilidae sp.	Little Traverse Bay	Evans (1973)
Lepidostoma sp.	Beaver Island Shoals	Merna (1960)
Molanna sp.	Beaver Island Shoals	Merna (1960)

stages of mayflies have been found on rocky substrates at shallow depths throughout Lake Michigan. In Green Bay, Grand Traverse Bay,* and the Straits of Mackinac,* they also occur in sand and mud. Scattered records are summarized in Table 8.

Table 8. Ephemeroptera Recorded from Lake Michigan through 1973

Species	*Location*	*Reference*
Baetidae sp.	Green Bay	Wis. State Comm. Water Pollut. (1939)
Baetis sp.	Little Traverse Bay	Evans (1973)
Baetisca sp.	Green Bay	Gannon (1972--personal communication)
Brachycercus sp.	Green Bay	Howmiller (1971a)
Caenis sp.	Green Bay	Howmiller (1971a)
?Centroptilum sp.	Green Bay	Howmiller (1971a)
Ephemera simulans	Chicago	Burks (1953)
Ephemerella sp.	Green Bay	Howmiller (1971a)
Heptagenia lucidipennis	Little Traverse Bay	Evans (1973)
Heptagenia maculipennis	Little Traverse Bay	Evans (1973)
Hexagenia limbata	Green Bay	Surber and Cooley (1952)
Hexagenia sp.	Beaver Island Shoals Green Bay	Merna (1960) Wis. State Comm. Water Pollut. (1939)
Stenonema bipunctatum-group	Little Traverse Bay	Evans (1973)
Stenonema sp.	Milwaukee Little Traverse Bay	Limnetics (1973) Evans (1973)
Tricorythodes sp.	Milwaukee Little Traverse Bay	Limnetics (1973) Evans (1973)

Disappearance of *Hexagenia*, known locally as the "Green Bay fly," from most or all of lower Green Bay is one of the most marked effects of deterioration of the benthic environment there. In 1938-1939, this genus occurred in almost a third of the samples from the lower Bay (Wis. State Comm. Water

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* *Samples stored at the Great Lakes Research Division, University of Michigan Ann Arbor.*

Pollut., 1939) (Fig. 21). In 1952, nymphs were found at only one of 27 stations in the same area (Surber and Cooley, 1952). In 1955, a specimen was noted near the mouth of the Oconto River (Balch *et al.*, 1956). None was found in surveys in 1966 and 1967 (Howmiller 1971a), or in 1969 (Howmiller and Beeton, 1971). Low dissolved oxygen concentrations in large areas of bottom with substrates suitable for this burrowing animal (Fig. 22) is the most probable cause of its disappearance there, as it was in Lake Erie (Britt, 1955).

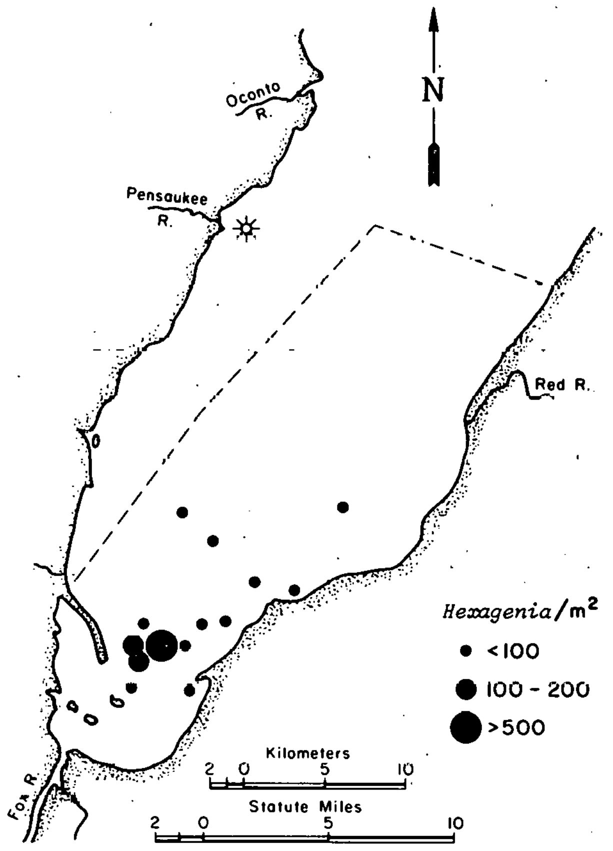


Fig. 21. Distribution and Abundance of *Hexagenia* Nymphs in 1938-1939. Dashed line indicates approximate limits of the area sampled. Redrawn from Wisconsin State Committee on Water Pollution (1939).

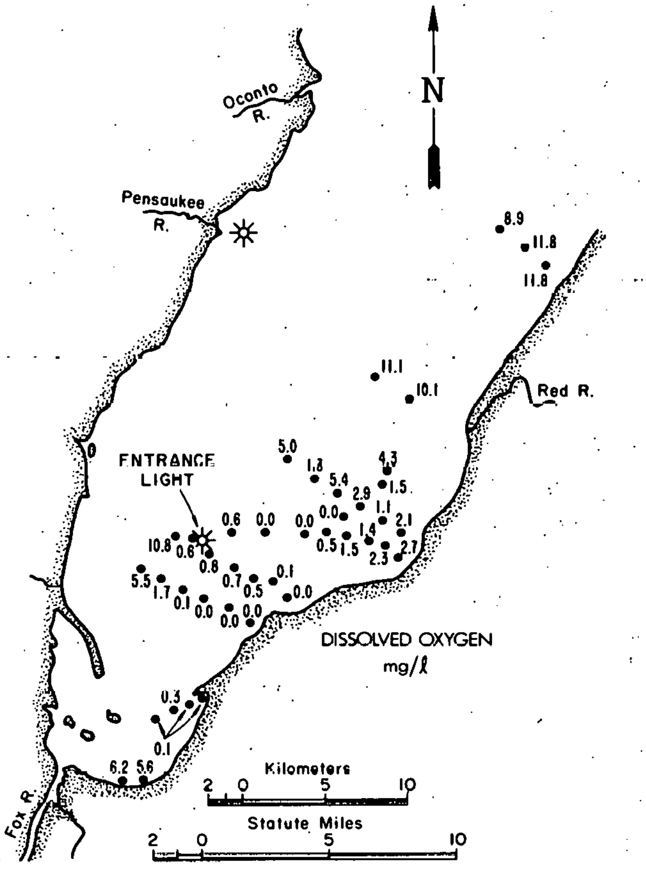


Fig. 22. Dissolved Oxygen Concentrations near Bottom in a Portion of Green Bay, 8-10 February 1967. Data from Schraufnagel *et al.* (1968).

Other Insecta

Larvae of the dipteran families Simuliidae and Ceratopogonidae have been collected near shore in several parts of the Lake (Wis. State Comm. Water Pollut., 1939; Howmiller, 1971a; Mozley, 1975b--unpublished data; Limnetics, 1973; Truchan, 1971). The dipteran *Sephedon* was mentioned by Evans (1973). *Chaoborus* (Diptera, Chaoboridae) have been collected on the southeastern and southwestern sides of the Lake at depths to 15 m (Mozley, 1975b--unpublished data; Limnetics, 1973). Damselflies (order Odonata) occurred in Merna's (1960) samples near Grand Haven at a depth of 45 m, and in earlier surveys of Green Bay (Wis. State Comm. Water Pollut., 1939). These and other records of miscellaneous additional insects give no indication that any of them play a major role in benthic communities of Lake Michigan.

MOLLUSCA

Snails, clams, and mussels comprise the molluscan populations of the Lake Michigan benthos. These animals represent the classes Gastropoda and Pelecypoda. For taxonomic clarity the two classes are treated separately and separate sections are devoted to the two families of pelecypods.

Gastropoda

Most aquatic snails of Lake Michigan have shells rarely exceeding a height of 15 mm. The number of identified species is 45 (Table 9), which is about the same as Oligochaeta, but none of the species are nearly as abundant as the worms. The shells (Fig. 23) of some groups are high and smoothly tapered (Pleuroceridae), while others are coiled in one plane (Valvatidae, Planorbidae). About half are gill breathers (Prosobranchia) with an operculum to close the shell, whereas others respire using modified, lung-like structures (Pulmonata). However, both kinds may live well below the surface. One genus of pulmonates, *Ferissia*, mimics marine limpets in having shells shaped like flattened, uncoiled cones.

Table 9. Gastropoda Recorded from Lake Michigan through 1973*

Species	*Location***	*Reference***
Prosobranchia		
Hydrobiidae		
Bythinia tentaculata	LM,GB,SB	1,2
Amnicola limosa	LM,SB	1,2,3,4
Amnicola lustrica	LM,SB	1,3,4
Amnicola walkeri	LM	1,4
Amnicola integra	LM (abundant)	2
Amnicola binneyana	LM	2,3,4
Amnicola sp.	GB	3,8
Hoyia sheldoni	LM	1
Somatogyrus subglobosus	LM	1,2
Viviparidae		
Viviparus sp.	GB	7,8
Campeloma decisa	LM	3
Campeloma rufum	LM	2
Campeloma sp.	GB	7,8
Valvatidae		
Valvata tricarinata	LM,GB	1,2,3,4,7
Valvata perdepressa	LM,SB	1,2,4,6
Valvata sincera	LM	1,2,3,4
Valvata bicarinata	LM	9
Pleuroceridae		
Pleurocera acuta	LM (abundant)	2
Goniobasis livescens	LM	1,2,3

Table 9. (contd.)

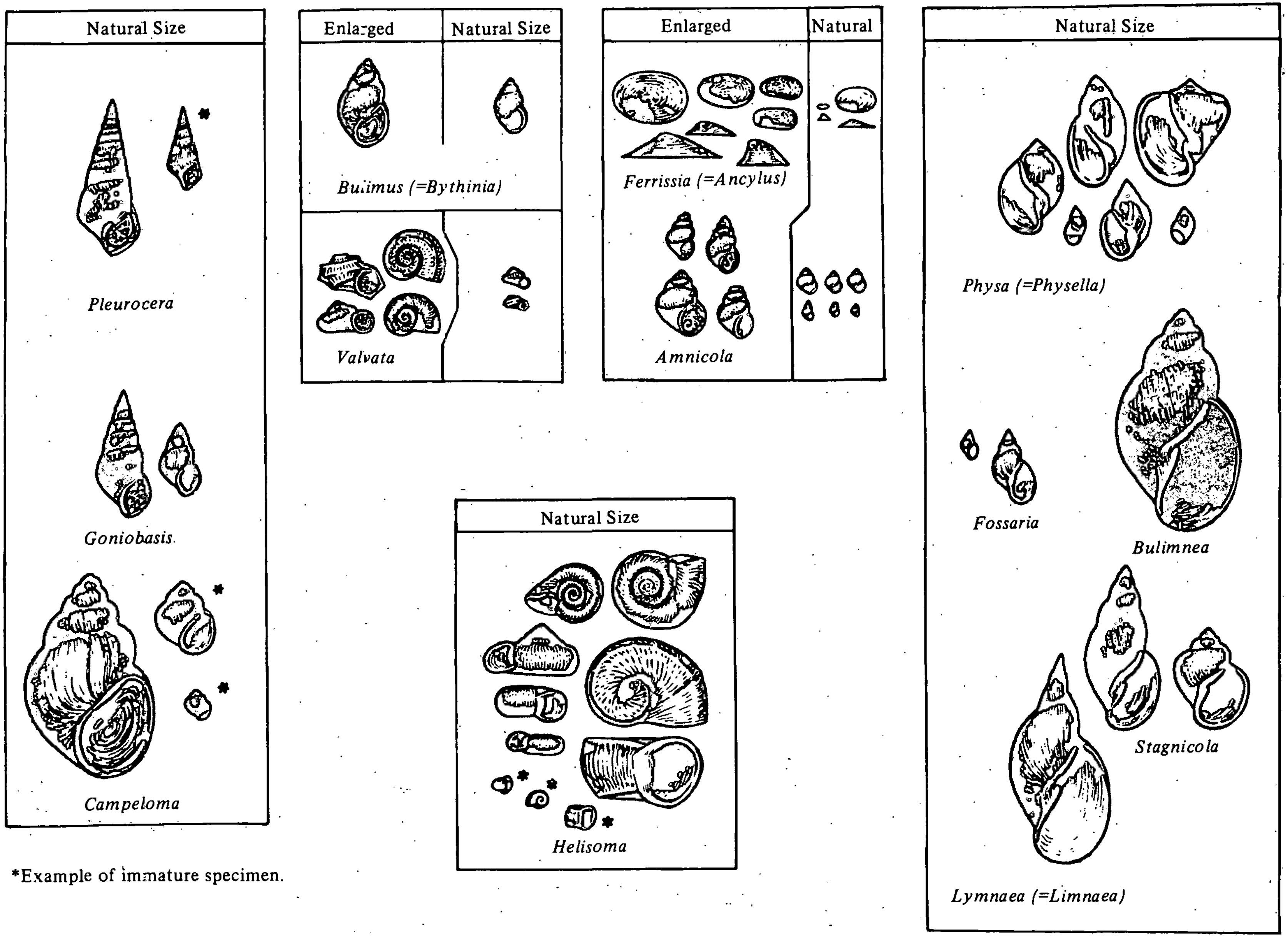
Species	*Location***	*Reference***
Pulmonata		
Lymnaeidae		
Lymnaea (Stagincola) exilis	GB	1
Lymnaea (Stagnicola) lanceata	SB	1
Lymnaea (Stagnicola) emarginata	SB,LM	1,3
Lymnaea (Stagnicola) walkeriana	LM,SB	1
Lymnaea (Stagnicola) woodruffi	LM	1,2,4
Lymnaea (Stagnicola) caperata	LM	5
Lymnaea (Stagnicola) catascopium	LM	3
Lymnaea (Stagnicola) decidiosa	LM	3
Lymnaea (Bulimnea) megasoma	GB	1
Lymnaea (Fossaria) humilis	SB,GB	1
Lymnaea (Lymnaea) stagnalis	LM	3,4
Planorbidae		
Helisoma anceps	SB,LM	1,3,4
Helisoma truncata	SB	1
Helisoma sp.	GB	7
Gyraulus deflectus	SB	1
Gyraulus arcticus	LM	2
Gyraulus parvus	LM	3
?Planorbis exacutus	LM	3,4
Ancylidae		
Ferrissia parallela	?SB	1
Ferrissia tarda	SB	1
Ferrissia kirklandi	SB	1
Physidae		
Physa sayii	LM,GB,SB	1,2
Physa magnalacustris	LM	1
Physa integra	LM	2,3,5
Physa ancillaria	LM	3
Physa gyrina	LM	3

**Generic nomenclature and some synonymies follow Harman and Berg (1971); other synonymies follow LaRocque (1953).*

***Locations:*
LM - Lake Michigan, main basin
GB - Green Bay, excluding tributaries
SB - Sturgeon Bay, including a few peripheral habitats.

References:
1 - Baker (1928a)
2 - Baker (1930)
3 - Ward (1896)
4 - Shelford (1913)
5 - Limnetics (1973)
6 - Industrial Bio-Test (1973)
7 - Surber and Cooley (1952)
8 - Howmiller and Beeton (1971)
9 - LaRocque (1953).

Most species occur on rocks and among attached algae in the upper few meters of water, but *Valvata, Amnicola, Bythinia,* and some Lymnaeidae and Physidae occur as deep as 30 or 35 m. Ward (1896) found *Lymnaea lanceata* as deep as 54 m. Total Gastropoda occasionally exceed 400/m^2 on fine-grained sediments, but concentrations at depths between 4 and 30 m are usually much less than the 100/m^2 recently found near the Cook nuclear plant (Mozley, 1973a). No quantitative estimates of their abundance on rocky substrates have



*Example of immature specimen.

Fig. 23. Representative Genera of Gastropoda in Lake Michigan. Modified from Walter and Burch (1957) (with permission, see credits).

been reported. *Amnicola binneyana, Amnicola integra, Physa sayii, Lymnaea woodruffi,* and *Pleurocera acuta* were abundant in the 1920's on the beaches of southern Lake Michigan (Baker, 1930). *Valvata perdepressa* comprised 60% of the Gastropoda in depths less than 18 m near Waukegan (Industrial Bio-Test, 1973). *Valvata* was also the most numerous snail near the Cook nuclear plant, except in July 1971 when *Lymnaea* and other pulmonates were dominant (Mozley, 1973a). *Pleurocera acuta* prefers solid substrata and is probably abundant on outcroppings of rock and boulders near Chicago. *Bythinia tentaculata* developed nuisance populations on Chicago city water intakes around the turn of the century (Baker, 1902).

Van der Schalie and Berry (1973) studied the effects of temperature elevation on a variety of snails including four species reported from Lake Michigan: *Lymnaea stagnalis, Amnicola limosa, Physa gyrina,* and *Lymnaea emarginata.* As a general rule, they found that sublethal increases in ambient temperature stimulate snail growth, but inhibit reproduction. *Lymnaea* and *Amnicola* did not tolerate warm water as well as *Physa.* Lethal temperatures for all groups were near 30°C.

Ingram (1957) summarized information on reactions of Gastropoda to pollution, some of which may be applicable to Great Lakes habitats.

Pelecypoda

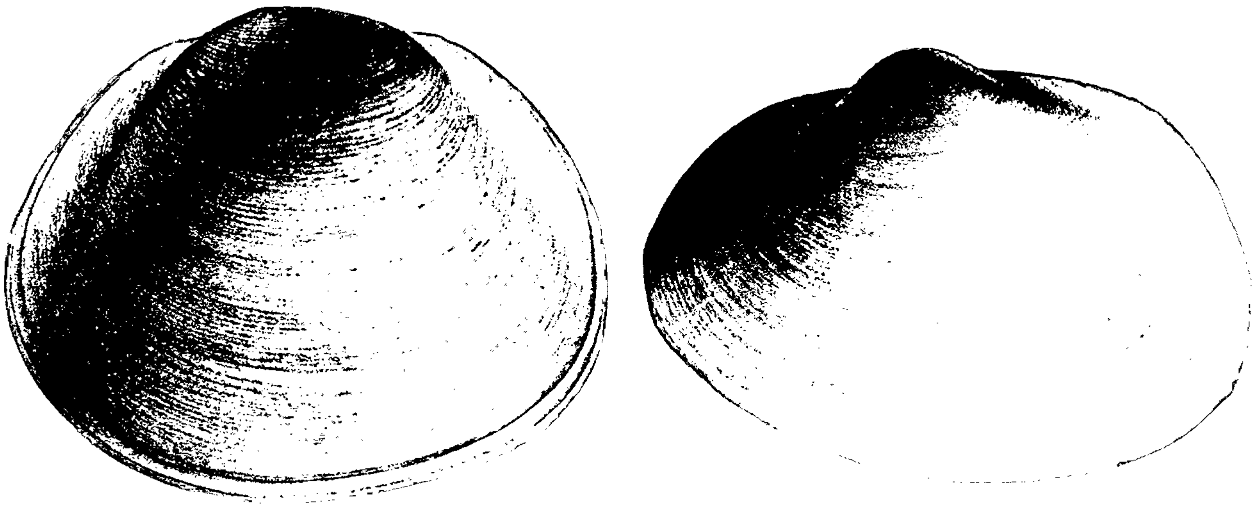
Sphaeriidae

The sphaeriids, or fingernail clams, of Lake Michigan, range from 1 to ∿12 mm in height. Two genera, *Sphaerium* and *Pisidium,* containing 24 species are present (Table 10); representative species are illustrated in Figure 24. The species of *Sphaerium* and *Pisidium dubium, Pisidium amnicum, Pisidium adamsi,* and *Pisidium idahoense* grow longer than 6 mm, while the remaining *Pisidium* are 2 to 4 mm long when full-grown.

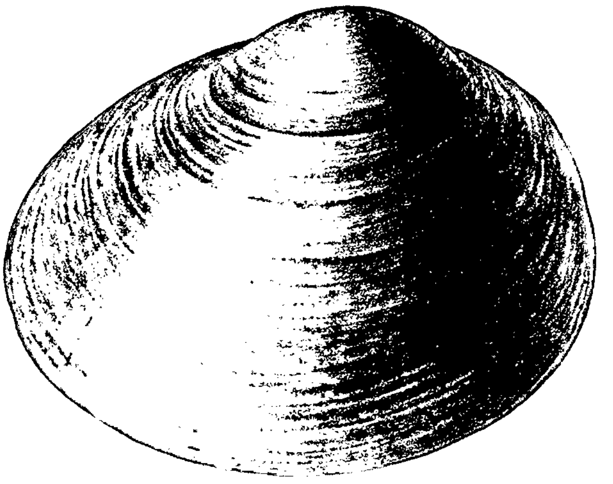
Table 10. Sphaeriidae Recorded from Lake Michigan through 1973

Species	*Reference**	*Species*	*Reference**
Sphaerium corneum	7	*Pisidium fallax*	5,7
Sphaerium lacustre	5,9	*Pisidium ferrugineum*	3,5,7
Sphaerium nitidum	5-9	*Pisidium henslowanum*	5,7,9
Sphaerium simile	1,3,5	*Pisidium idahoense*	1,2,4-6
Sphaerium striatinum	1-8	*Pisidium lilljeborgi*	2-7
Sphaerium transversum	2,3,5,8	*Pisidium nitidum*	5-7
Pisidium adamsi	5	*Pisidium obtusale*	1
Pisidium amnicum	7	*Pisidium punctatum*	1,2,5,6,9
Pisidium casertanum	1,4-7,9	*Pisidium subtruncatum*	5,6,9
Pisidium compressum	1,2,4-7	*Pisidium variabile*	1,2,5,6
Pisidium conventus	3,5-7	*Pisidium ventricosum*	2,5,6
Pisidium dubium	4-6	*Pisidium walkeri*	4,5,6

**References: 1 - Ward (1896)*
2 - Shelford (1913)
3 - Baker (1928b)
4 - Baker (1930)
5 - Heard (1962)
6 - Henson and Herrington (1965) (Lake Michigan samples only)
7 - Robertson (1967)
8 - Mozley and Garcia (1972)
9 - Howmiller (1971a)



Sphaerium nitidum　　*Shaerium transversum*



Pisidium casertanum

Fig. 24.

Representative Species of *Sphaerium* and *Pisidium* in Lake Michigan. Modified from Burch (1972).

Identification of the species of *Sphaerium* is not difficult, particularly with reliably identified reference specimens at hand. Many species of *Pisidium*, however, can be distinguished only by minor features of the shells, many of which are internal, not well developed in young individuals, and variable depending upon habitat. Complete keys to *Pisidium* exist (Burch, 1972; Herrington 1962), but are difficult to use with confidence. Over the last 40 years, almost all identifications of Lake Michigan *Pisidium* species were made or confirmed by the late Rev. H. B. Herrington.

The biology of the most common species in the Lake, *Pisidium conventus*, was reviewed by Heard (1963). This is one of the smallest sphaeriids, and occurs throughout the Lake, mostly at depths over 30 m, though it was taken at depths as shallow as 2 m by Henson and Herrington (1965). Greatest concentrations occur between 30 and 50 m (Robertson, 1967; Henson and Herrington, 1965). Since the sediments at these depths are usually silts or silty clays, this appears to be its preferred substrate, but in the Straits of Mackinac

P. conventus was abundant in silty sand (Henson and Herrington, 1965). Other species of mollusks are only rarely collected at depths greater than 50 m, but *P. conventus* occurs in the deepest parts of Lake Michigan.

Reproduction of *Pisidium conventus* may occur by cross-fertilization or self-fertilization, since each individual produces both sperm and ova simultaneously. The young are brooded inside the parent's shell for about six months, and may be half the length of the adult when released. Production of gametes is continuous, but Heard (1963) observed peak sizes of brooded embryos in May and October, indicating that population increases could be expected in midsummer and midwinter. The relationship between depth and seasonal reproduction was not analyzed. The length of life and number of broods a single individual can produce are unknown, but gametes ready for fertilization were present in specimens with large embryos. The average adult carried six embryos; maximum brood size was 10 in Lake Michigan specimens.

Diatoms appeared to be the most important source of food (Heard, 1963). *Amphora ovalis* var. *pediculus* and *A. ovalis* var. *lybica* were reported to be the most common of 14 diatoms identified in the guts of *Pisidium conventus*.

Pisidium conventus has been observed in the stomachs of the bloater, *Coregonus hoyi*, in Lake Michigan (Heard, 1963). This species was accompanied by *Pisidium lilljeborgi*, *Pisidium nitidum*, and *Sphaerium nitidum* in fish taken at a depth of 26 m, but it was the only clam present in the fish collected at 60 m. Fish diets apparently reflect the composition of available sphaeriids; there is no evidence of selection for particular species. In other lakes, the common white sucker, longnose sucker, and lake trout have been found with sphaeriids in their stomachs. Predation by invertebrates is not documented, but is probably common.

Abundances of Sphaeriidae generally increase with increasing depth from the surf out to ∿40 m (Rains, 1971; Mozley and Garcia, 1972; Mozley, 1974). The large numbers indicated for the shallowest interval in Figure 10 are due to the dominant influence of a single station near Waukegan (Powers and Robertson, 1967). Abundances decline with increasing depth beyond 50 or 60 m (Robertson, 1967) (Fig. 10). Near shore, sphaeriids are distributed in an extremely patchy fashion (Mozley, 1974), and available data are not sufficient to distinguish seasonal variations from sampling error (Rains, 1971).

Most sphaeriid species in the Straits of Mackinac prefer epilimnetic depths and sandy substrates, although they occur sporadically as deep as 50 m (Henson and Herrington, 1965) (Fig. 25). The most numerous species (those accounting for 5% or more of total Sphaeriidae) are *Pisidium conventus*, *Pisidium lilljeborgi*, *Pisidium casertanum*, *Sphaerium striatinum*, *Sphaerium nitidum*, and *Pisidium nitidum* (not shown in Fig. 25)--in that order. In Robertson's (1967) samples from the southern two-thirds of the Lake, these same species were ranked in about the same order, but locally high abundances of *Pisidium henslowanum* and *Sphaerium corneum* were found near Waukegan. Mozley and Garcia (1972) found unusually large numbers, over 400/m^2, of *S. nitidum* in a narrow depth interval between 20 and 25 m. Like *P. conventus*, *S. nitidum* is believed to require a continually cold environment, but this species does not occur in the deeper parts of Lake Michigan.

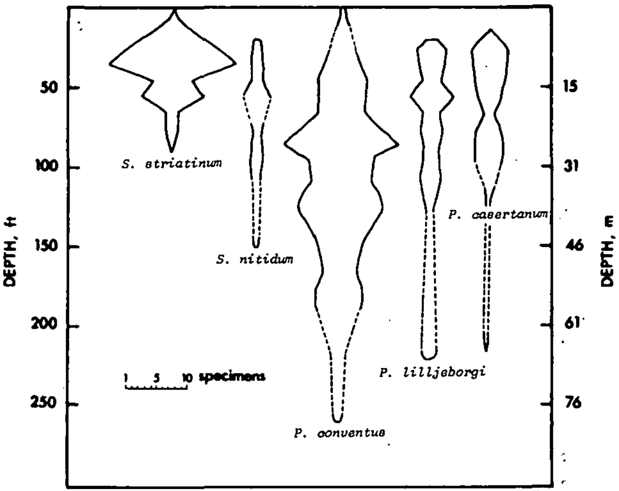


Fig. 25.

Relative Abundance with Respect to Depth of the Five Most Common Species of Sphaeriidae Found in the Vicinity of the Straits of Mackinac. The widths of the polygons are proportionate to the total number of specimens collected within 10-ft (∿3-m) depth intervals. The dashed lines indicate depths from which no specimens were collected. Slightly modified from Henson and Herrington (1965) (with permission, see credits).

Sphaeriids, like filter-feeding crustaceans, may increase during early stages of eutrophication, but later decrease when deposit-feeders predominate (*e.g.* oligochaetes) (Grimås, 1969). This response pattern agrees with observations from western Lake Erie (Carr and Hiltunen, 1965), which showed increases in sphaeriid abundance in midbasin from 1930 to 1961, but decreases over this period near the Detroit, Maumee, and Raisin rivers. Lower and middle reaches of Green Bay, like Lake Erie river mouths, have undergone decreases in sphaeriid numbers (Howmiller and Beeton, 1971). However, the *Sphaerium* species encountered in Green Bay (Table 10) differed considerably from those in western Lake Erie (Brinkhurst *et al.*, 1968), and species-level responses have few features in common among different parts of the Great Lakes. *Sphaerium transversum* (Ingram, 1957; Brinkhurst *et al.*, 1968) and *Sphaerium corneum*, which is abundant near Waukegan (Robertson, 1967) and in Milwaukee Harbor (Emmling, 1974—unpublished) appear to be among species likely to respond positively to increased organic sedimentation.

Since Baker (1930) found about the same species in the same order of relative abundance as later authors, it seems likely that no major changes in the sphaeriid fauna, other than those already noted, have occurred in the past 40 years. Baker's records cannot serve as an ideal baseline, however, since they are based largely on shells washed ashore. For example, the recent records (Mozley and Garcia, 1972; Mozley, 1974) of high abundance of *Sphaerium nitidum* in the southeastern coastal zone may not represent a real increase in the importance of this species, since based on the preference of *S. nitidum* for deep water, one would expect that its shells would be only infrequently washed ashore.

Unionidae

Mussels, or naiades, are found occasionally in Lake Michigan. They range up to 10 cm or more in length and have dark-colored shells (Fig. 26). Scattered collections by divers and fish trawls, and shells washed up on the beach, indicate that only three species occur in the main basin: *Anodonta grandis*, *Anodonta ferussacianus*, and *Lampsilis siliquoidea*. The only specimens in benthos collections (*L. siliquoidea*, *Amblema* sp.) were taken along the western shore of lower Green Bay by Howmiller (1971a) and Howmiller and Beeton (1971). Baker (1928b) mentioned the occurrence of *A. grandis*, *L. siliquoidea*, and *Quadrula pustulosa* from Green Bay. The record of *A. ferussacianus* comes from Ward (1896).

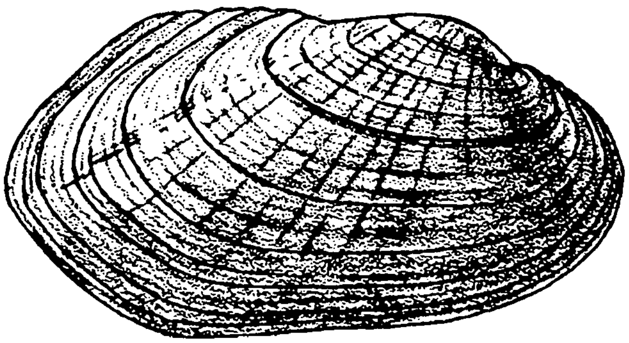


Fig. 26.

Lampsilis siliquoidea × ½. From Heard and Burch (1966) (with permission, see credits).

Unionidae have unique larvae, called glochidia, which must parasitize the epithelium of a fish before completing development into mussels (Baker, 1928b). These larvae are expelled toward a fish through the excurrent siphon of the parent mussel. If the fish is one of a few particular species, glochidia will encyst beneath the fish's skin or upon its gills and accompany it for periods of a week to several months. The glochidia then break out of the cyst and fall to the bottom, where they metamorphose and begin to grow rapidly. The young mature in one to eight years depending on the species, and individuals may survive as long as 20 years.

Their symbiotic dependence on fishes exposes mussels to indirect as well as direct effects of pollution. If the host fish no longer lives in the vicinity of a mussel bed, the population will be unable to reproduce. Siltation or long periods of oxygen depletion may eliminate parent populations. Mussels as a group are not especially sensitive to changes in the benthic environment, for a diverse assemblage persists today in western Lake Erie, despite declining water quality (Roth and Mozley, 1973--unpublished). The few species in Green Bay may also have escaped serious damage from the decline of water quality in the area (Howmiller and Beeton, 1971), though they are apparently absent from the lower Bay and eastern side, the areas most heavily affected by pollution.

Mussels are not usually abundant enough to appear regularly in benthos samples taken with a grab. Absence of species in survey data is not sufficient evidence of their absence from an area. It is necessary to use special methods, such as coarse-meshed dredges or large numbers of grab casts at each station, to obtain representative data on their distribution and composition.

ANNELIDA

The phylum Annelida (segmented worms) includes the class Clitellata, with subclasses Oligochaeta and Hirudinea, and the class Polychaeta. Benthic samples from Lake Michigan generally yield oligochaetes and leeches (Hirudinea). A polychaete, *Manyunkia speciosa*, occurs in some Great Lakes waters but has not been reported in Lake Michigan.

Oligochaeta

The oligochaetes are almost exclusively terrestrial and freshwater in distribution. The aquatic forms look much like the familiar earthworms but generally are much smaller. Hence, they are often referred to as "microdriles," while the term "megadriles" is used in reference to the larger, mostly terrestrial types. A single megadrile, *Sparganophilus tamesis* (family Glossoscolecidae), has been reported in Lake Michigan.

Oligochaetes typically have four bundles of setae* on each segment of the body. The number and shape of the setae are used in the classification and identification of the worms (Fig. 27). Examination of setae generally requires mounting the worms on microscope slides for viewing at a magnification of at least 100×. Identification of some species of tubificids requires examination of special genital setae or penis tubes (Fig. 28) as well as other setae; thus, these types can be recognized only when mature. Some other worms, *e.g.* Enchytraeidae, must be viewed live for examination of minute internal detail, but since this is very nearly impossible in large-scale surveys, these families remain little known.

The common oligochaetes of Lake Michigan belong to the families Lumbriculidae, Naididae, Tubificidae, and Enchytraeidae.

Lumbriculidae

Whereas *Lumbriculus variegatus* has been reported from the shallow littoral of Green Bay (Howmiller, 1971a), *Stylodrilus heringianus* is the only quantitatively important lumbriculid in the Great Lakes. It is probably the most abundant worm in Lake Michigan, occurring in almost all samples from the open Lake and accounting for about 90% of all worms at depths greater than 70 m.

Like the tubificids, this species burrows in and ingests bottom sediments. Nothing is known of its life history in Lake Michigan. Studies done elsewhere (Cook, 1969; Pickavance, 1971) indicate that either a one- or two-year life cycle may occur, but its life cycle may be longer in Lake Michigan where temperatures are lower and food is probably in shorter supply. Data given by Hiltunen (1967) on seasonal fluctuations in abundance at a depth of 46 m reveal no pronounced pattern.

Naididae

In general, species of the family Naididae are smaller and more fragile than the other common worms. Many naidids have numerous long-hair setae and most are capable of swimming, so they are occasionally collected in plankton samples. In inland lakes, naidids are primarily littoral in distribution and are especially abundant in beds of aquatic macrophytes. Since small-lake type littoral habitats are rare in Lake Michigan, and because these fragile worms are easily damaged or lost in processing samples, naidids seldom are recorded in substantial numbers. Nevertheless, at least a dozen species have been found in the Lake (Table 11).

Most naidids can reproduce asexually and may increase in numbers rapidly when conditions are favorable.

Near the Cook nuclear plant from 1970 to 1973, Naididae large enough to be retained in 0.5-mm sieves increased in total abundance, reaching densities of over 1000/m^2 at depths less than 8 m in July 1973 (Mozley, 1974). The most abundant genera were *Chaetogaster, Nais, Stylaria, Uncinais,* and *Piguetiella.*

**Taxonomists differ in opinion as to whether to call these structures setae (as here) or chaetae, in accordance with the class name, Oligochaeta.*

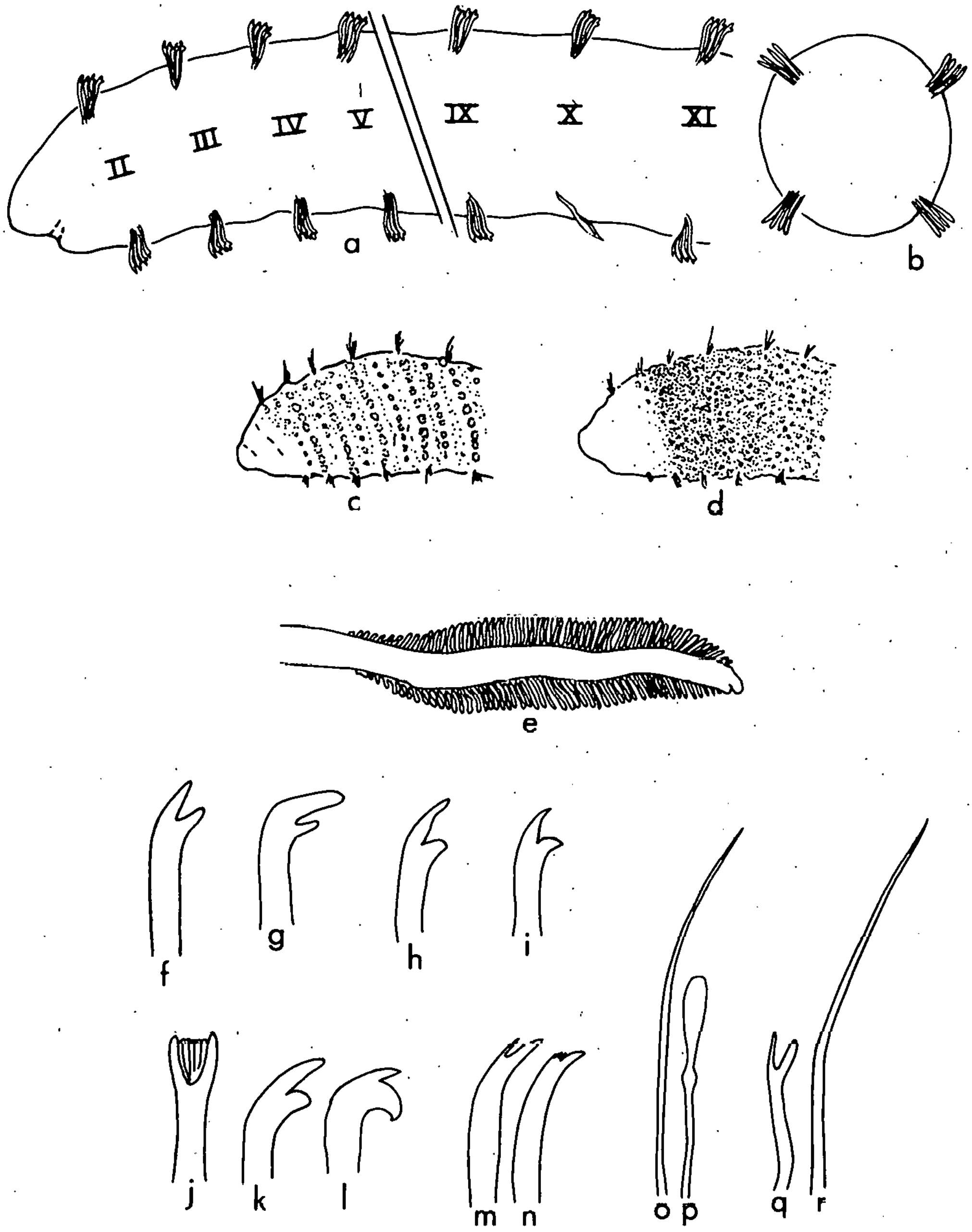


Fig. 27. Some Morphological Characteristics of Tubificid Worms.

(a) Anterior end of generalized tubificid showing system of numbering segments (I lacks setae), dorsal and ventral setal bundles, and ventral spermathecal seta on X; (b) diagrammatic cross section showing arrangement of the four bundles of setae; (c-d) papillation in the body wall of (c) *Peloscolex multisetosus* and (d) *Peloscolex ferox*; (e) gills on posterior end of *Branchiura sowerbyi*; (f) detail of distal end of bifid seta, as of many *Limnodrilus* species; (g-i) anterior ventral setae of (g) *Limnodrilus udekemianus*, (h) *Ilyodrilus templetoni*, and (i) *Tubifex tubifex*; (j-l) setae of *Peloscolex multisetosus multisetosus*--(j) dorsal pectinate, (k) anterior ventral, and (l) posterior ventral; (m-n) setae of *Aulodrilus pluriseta*--(m) anterior and (n) middorsal; (o-p) setae of *Aulodrilus pigueti*--(o) dorsal hair and (p) dorsal oar-shaped; (q-r) setae of *Potamothrix vejdovskyi*--(q) dorsal bifid and (r) hair. Drawings are not all to the same magnification.

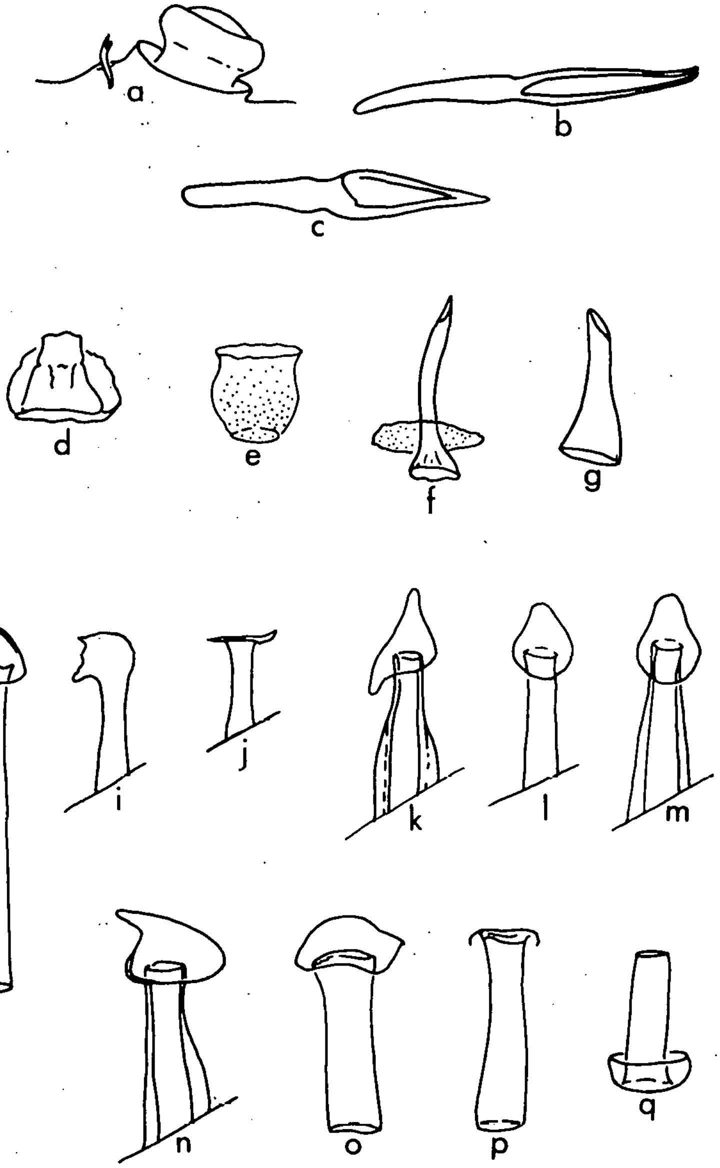


Fig. 28. Genital Structures Used in the Identification of Some Tubificid Worms.

(a) Penis and accessory penial seta of *Potamothrix moldaviensis*; (b-c) spermathecal seta of (b) *Potamothrix moldaviensis* and (c) *Potamothrix bavaricus* (? = *P. bedoti*); (d-q) penis sheaths of (d) *Peloscolex freyi*, (e) *Tubifex tubifex*, (f) *Tubifex kessleri*, (g) *Ilyodrilus templetoni*, (h) *Limnodrilus hoffmeisteri*, (i) *L. hoffmeisteri* in side view, (j) "*spiralis* type" *L. hoffmeisteri* in side view, (k) *Limnodrilus cervix*, (l) *Limnodrilus claparedianus*, (m) form intermediate between *L. cervix* and *L. claparedianus*, (n) *Limnodrilus maumeensis*, (o) *Limnodrilus udekemianus*, (p) *Limnodrilus profundicola*, and (q) *Peloscolex superiorensis*. Drawings are not all to the same magnification.

Table 11. Oligochaeta Reported from Lake Michigan and Green Bay through 1973*

Species	*Lake Michigan*	*Green Bay*
Glossoscolecidae		
Sparganophilus tamesis Benham	x	
Enchytraeidae**	x	
Lumbriculidae		
Lumbriculus variegatus (Müller)		x
Stylodrilus heringianus Claparède	x	x
Naididae		
Amphichaeta sp.	x	
Arcteonais lomondi (Martin)	x	x
Chaetogaster sp.	x	x
Dero digitata (Müller)	x	x
Nais sp.	x	x
Nais elinguis (Müller)		x
Ophidonais serpentina (Müller)	x	x
Piguetiella michiganensis Hiltunen	x	x
Slavina appendiculata (d'Udekem)	x	x
Specaria josinae (Vejdovský)	x	x
Stylaria lacustris (Linnaeus)	x	x
Uncinais uncinata (Ørsted)	x	x
Vejdovskyella intermedia (Bretscher)	x	
Tubificidae		
Aulodrilus americanus Brinkhurst & Cook	x	
Aulodrilus limnobius Bretscher	x	x
Aulodrilus pigueti Kowalewski	x	x
Aulodrilus pluriseta (Piguet)	x	x
Ilyodrilus templetoni (Southern)	x	x
Limnodrilus angustipenis (Brinkhurst & Cook)	x	
Limnodrilus cervix Brinkhurst	x	x
Limnodrilus claparedianus Ratzel	x	x
Limnodrilus hoffmeisteri Claparède	x	x
Limnodrilus maumeensis Brinkhurst & Cook	x	x
Limnodrilus profundicola (Verrill)	x	
Limnodrilus udekemianus Claparède	x	x
Peloscolex ferox (Eisen)	x	x
Peloscolex freyi Brinkhurst	x	x
Peloscolex multisetosus multisetosus (Smith)	x	x
Peloscolex multisetosus longidentus Brinkhurst & Cook	x	x
Peloscolex superiorensis Brinkhurst & Cook	x	
Peloscolex variegatus Leidy	x	
Potamothrix bavaricus (Oschmann)†	x	?
Potamothrix hammoniensis (Michaelsen)		x
Potamothrix moldaviensis (Vejdovský & Mrázek)	x	x
Potamothrix vejdovskyi (Hrabe)	x	x
Rhyacodrilus coccineus (Vejdovský)	x	
Rhyacodrilus montana (Brinkhurst)	x	
Tubifex ignotus (Stolc)	x	
Tubifex kessleri americanus Brinkhurst & Cook	x	x
Tubifex tubifex (Müller)	x	x

**Data from Hiltunen (1967), Howmiller (1974b), Howmiller and Beeton (1970), and Merna (1960).*

***At least two species are present (Howmiller, 1974b).*

†*This should perhaps be P. bedoti (Timm, 1972; Hiltunen, 1973--personal communication).*

The latter two are larger forms and are less seasonal in occurrence. They occupy greater depths than the others. At the same time, plankton tows have revealed large numbers of *Nais* and *Stylaria* in the water column, especially at night. Whether Naididae undergo such population explosions every few years or whether these observations represent changes in the ecology of the Lake is not yet clear. The phenomenon merits considerable attention, since it is occurring in an area of great environmental concern. Had the changes not been observed before operation of the plant, and in reference areas as well as near the plant site, they might have been attributed to the plant.

Tubificidae

This family includes most of the species of Oligochaeta known in the Lake (Table 11). As following sections will show, there is considerable ecological differentiation within the family, and markedly different depth preferences and tolerances by different species.

There have been few life-history studies of tubificid species (Jónasson and Thorhauge, 1972). The observations of Kennedy (1966) suggest that the life history of *Limnodrilus hoffmeisteri* depends heavily on local conditions. Knowledge of the life history of tubificids in Lake Michigan is meager, indeed, consisting solely of observations made by Hiltunen (1967) at a station off Grand Haven. Replicate samples taken on ten dates in 1960 provided evidence of a gradual decline in numbers of *Limnodrilus hoffmeisteri* and *Tubifex tubifex* in the fall, suggesting a cessation of sexual activity at this time of year (Fig. 29). Corresponding data on numbers of immature tubificids suggested that recruitment by *T. tubifex* may be gradual from spring to fall and this may be true as well of *L. hoffmeisteri*.

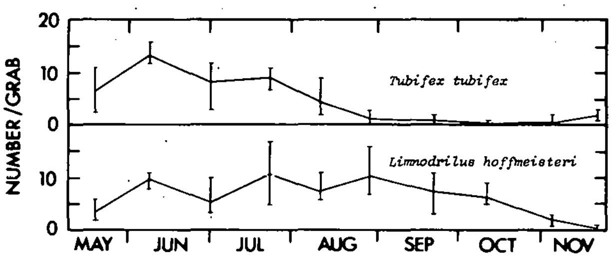


Fig. 29.

Seasonal Changes in Numbers of Mature *Tubifex tubifex* and *Limnodrilus hoffmeisteri*. Based on 3 or 4 samples on each date at a station off Grand Haven, Michigan. Vertical lines are ranges. Slightly modified from Hiltunen (1967) (with permission, see credits).

Composition of the Oligochaete Fauna and Distribution of Species in Lake Michigan

A list assembled from the records of Merna (1960), Hiltunen (1967), and Howmiller (1971a) indicates that the oligochaete fauna of Lake Michigan includes at least forty species of four families (Table 11). Two or three additional species have been reported from Green Bay (Howmiller, 1971a).

Several records in Table 11 require additional comment. Timm (1972) reviewed descriptions and determinations of *Potamothrix bavaricus* from the Great Lakes (Brinkhurst, 1965; Hiltunen, 1967) and concluded that *Potamothrix bedoti*, but not *P. bavaricus*, is present in the lakes. Howmiller and Beeton (1970) discussed several specimens from Green Bay that appeared to be intermediates between *Potamothrix hammoniensis* and *P. bavaricus*. In light of Timm's (1972) comments, these should perhaps be considered *P. bedoti*.

Great Lakes specimens that are unquestionably *Potamothrix hammoniensis* are known only from two stations in Green Bay (Howmiller and Beeton, 1970). Brinkhurst (1967a) reported a tentative record from Saginaw Bay. This oligochaete is probably a recent introduction to North America.

Sparganophilus tamesis (as *S. eiseni*) has been reported in the Lake by Moore (1906) and Merna (1960). These records seemed questionable in view of the absence of *Sparganophilus* in more comprehensive series of samples (Hiltunen, 1967; Howmiller, 1974b). However, a recent communication from Hiltunen (1973--personal communication) indicates that he also has collected *S. tamesis* in Lake Michigan but finds it less common than in Lake Huron. As pointed out by Merna (1960), the absence of *Sparganophilus* in records of other investigations may result from a paucity of shallow-water samples. Other species listed in Table 11 have been found numerous times at many locations.

The Lake obviously has a rich worm fauna. The length of our list is a tribute to the taxonomic work of R. O. Brinkhurst and his keys for identification of worms (Brinkhurst, 1964, 1965; Brinkhurst and Cook, 1966; Brinkhurst and Jamieson, 1971) that have stimulated recent investigations on this group. Just about a decade ago, a reviewer of Great Lakes benthic investigations estimated the worm fauna to consist of only ten species (Henson, 1966).

Composition of the worm fauna in the northern end of the Lake lacks documentation. Brinkhurst *et al.* (1968) reported that a collection made in the "upper part" of the Lake by J. Merna contained "oligotrophic lake species" with the implication that the fauna was much like that found by Hiltunen (1967) at his deepest stations in the southern basin, *viz.* mainly the lumbriculid *Stylodrilus heringianus*. Other scattered collections and studies from ecologically similar areas, such as western Lake Superior (Hiltunen, 1969a) and the central region of Lake Michigan (Howmiller, 1974b), support this contention. The latter investigation revealed that at stations over 70 m deep, *S. heringianus* accounted for almost 90% of the specimens examined. Small numbers of two types of enchytraeids, *Tubifex tubifex* and *Limnodrilus hoffmeisteri*, and unidentified immature tubificids were also collected. Mature *L. hoffmeisteri* were found only at the single station at which *S. heringianus* was not dominant, 11-14 km off Grand Haven and the Grand River. That region is probably influenced by allochthonous inputs from the river.

Hiltunen (1967) presented results of a thorough study of the fauna of the southern basin, based on samples from twenty-five stations (Fig. 30). The fauna at open lake stations was composed almost entirely of the lumbriculid *Stylodrilus heringianus*. At stations closer inshore, *Limnodrilus hoffmeisteri*, *Peloscolex variegatus*, *Potamothrix moldaviensis*, *Potamothrix vejdovskyi*, and *Tubifex tubifex* accounted for a considerable portion of the fauna. *Aulodrilus americanus*, *Aulodrilus pigueti*, *Aulodrilus pluriseta*, *Ilyodrilus templetoni*, *Limnodrilus angustipenis*, *Limnodrilus claparedianus*, *Limnodrilus profundicola*, *Limnodrilus udekemianus*, *Peloscolex freyi*, *Peloscolex multisetosus*, *Peloscolex superiorensis*, *Potamothrix bavaricus*,* *Rhyacodrilus coccineus*, and *Tubifex kessleri americanus* occurred at a few stations in smaller numbers.

Oligochaetes comprise 64% of the macroinvertebrates between depths of 5 and 18 m in Indiana waters of Lake Michigan (Rains, 1971). Worm densities are

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* *See footnote to Table 11.*

5.2× as large as the lakewide average (Powers and Alley, 1967). Rains (1971) concluded that 21% of his samples indicated polluted conditions on the basis of total oligochaete abundance, and supported this judgment with species comparisons. *Stylodrilus heringianus* was rare, whereas the most numerous oligochaetes at all stations combined were *Limnodrilus hoffmeisteri* and *Potamothrix moldaviensis*, plus corresponding immatures. Immature tubificids possessing hair setae were the third most abundant group. *Limnodrilus angustipenis*, *Limnodrilus udekemianus*, and *Peloscolex multisetosus* occurred frequently at Rains' stations. The most saprobiontic worm assemblage, including *Limnodrilus cervix* and *Limnodrilus maumeensis*, occurred near Burns Ditch at a depth of 5 m. Rains' 10-m station near Gary was judged to be least degraded, as evidenced by the regular presence of *Limnodrilus profundicola*. In view of the confusion which has occurred regarding this species and variants of *Limnodrilus hoffmeisteri* [see comments on Hamilton Bay, Lake Ontario, by Cook and Johnson (1974)], these records should be regarded with caution. However, *Limnodrilus profundicola* has been found frequently in adjacent areas (Mozley and Garcia, 1972; Mozley, 1974).

Total oligochaete abundance at Rains' (1971) stations increased from a depth of 5 m down to 15 m, then decreased slightly at 18 m.* Oligochaetes in Indiana waters generally increased from June to October (the entire period of Rains' study). Rains (1971) collected small numbers of Enchytraeidae and the naidids *Stylaria lacustris* and *Vejdovskyella intermedia*.

Mozley and Garcia (1972) examined Oligochaeta from 25 nearshore stations in a region centered 16 km south of Benton Harbor. Oligochaeta comprised 32% of the macroinvertebrates in their samples and included 11 species: *Stylodrilus heringianus*, *Limnodrilus hoffmeisteri*, *Limnodrilus angustipenis*, *Limnodrilus cervix*,** *Limnodrilus profundicola*, *Potamothrix moldaviensis*, *Potamothrix vejdovskyi*, *Peloscolex freyi*, *Peloscolex variegatus*, *Aulodrilus americanus*, and *Tubifex tubifex*. Subsequent work (Mozley, 1973a, 1974) has resulted in adding to the list from this area: *Aulodrilus pluriseta*, *Limnodrilus claparedianus*,** *Peloscolex multisetosus*, and the naidids *Piguetiella michiganensis*, *Chaetogaster* sp., *Uncinais uncinata*, *Stylaria lacustris*, *Nais* sp., and others.

Mozley and Garcia (1972) reported prominent depth stratification of some species. All worms were scarce or absent at depths of less than 8 m. Relatively coarse-grained sediments (pebbles to medium-grained sands) and wave action are understandably inimical to these soft-bodied organisms. *Limnodrilus hoffmeisteri* was numerically dominant in most samples at depths of less than 20 m. *Potamothrix moldaviensis*, *Peloscolex freyi*, and *Stylodrilus heringianus* were also important at depths between 8 and 20 m. At depths between 20 and 41 m (the maximum depth sampled), *S. heringianus* increased and accounted for an average of 77% (range, 61-94%) of total Oligochaeta.

We obtained access to his data too late to incorporate it into this section.

***In Britain, where Limnodrilus cervix was first described (Brinkhurst, 1963) and is apparently a recent introduction (Kennedy, 1965), it appears to be a valid species distinct from Limnodrilus claparedianus. However, in America these two often seem to interbreed and produce hybrid swarms, with forms morphologically intermediate being more common than either species (cf. Hiltunen, 1967; Howmiller and Beeton, 1970).*

Depth distribution of Lake Michigan oligochaete species, over a wide range of depths, can be examined by combining the data of Hiltunen (1967), Howmiller (1974b), and Mozley and Garcia (1972). In so doing, some degree of detail is sacrificed with respect to other variables such as latitude, local differences in sediment composition, and local sources of pollution. Location of stations from which the following data were obtained are shown in Figure 30, whereas Figure 31 indicates the number of stations within each depth range.

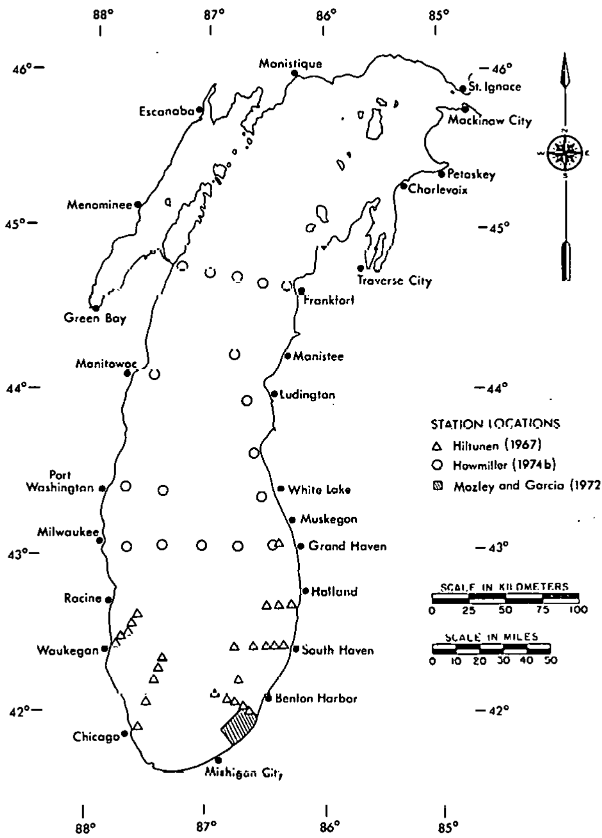


Fig. 30.

Location of Stations in Lake Michigan Sampled by Hiltunen (1967), Howmiller (1974b), and Mozley and Garcia (1972). Data from these stations were used to construct the histograms of the relative frequency and relative abundance of worms as presented in Figures 31-38.

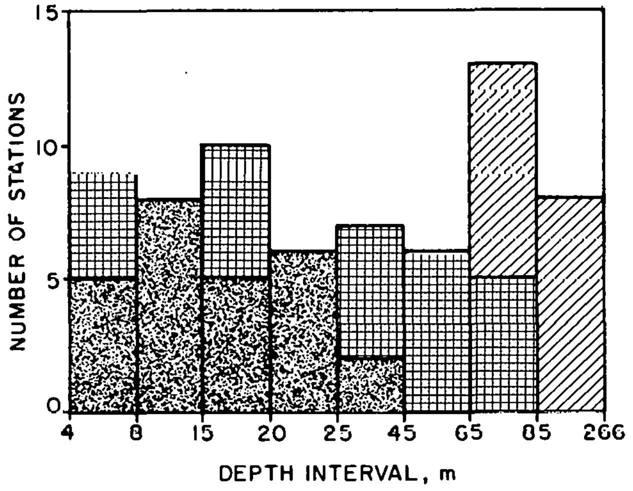


Fig. 31.

Distribution of Number of Sampling Stations with Depth. Stations of Hiltunen (1967) are indicated by the square grid, those of Howmiller (1974b) by diagonal lines, and those of Mozley and Garcia (1972) by the mottled pattern.

Figure 32a shows that *Stylodrilus heringianus* occurs with low frequency (percentage of all samples) at depths less than 8 m, being found at only about 10% of the stations in this range. In the depth range 8-15 m, relative frequency increases to 37.5%, and beyond a depth of 15 m, *S. heringianus* is found in 89-100% of all samples.

Figure 32b depicts relative abundance (percentage of all Oligochaeta) of *Stylodrilus heringianus* by depth intervals. This species is of negligible importance (<1% of the worm fauna) at depths less than 8 m, and even between 8-15 m is quite unimportant, comprising <5% of the fauna. At greater depths, it is a more important component, accounting for 83 and 95% of all worms in the ranges 65-85 and 85-266 m.

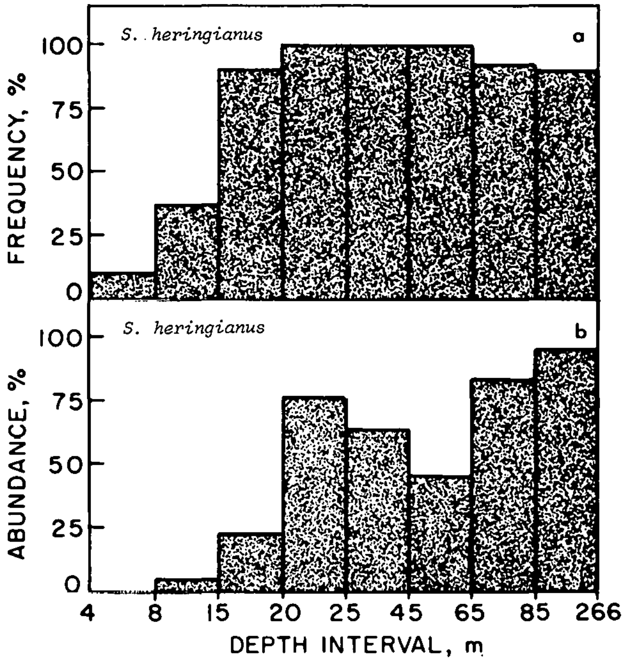


Fig. 32.

(a) Relative Frequency and (b) Relative Abundance of *Stylodrilus heringianus* with Depth in Lake Michigan. Relative frequency is the number of samples in which the worm occurred as a percentage of all samples taken. Relative abundance is the number of individuals as a percentage of all worms. Relative frequency and relative abundance are based on data from the stations shown in Figures 30 and 31.

One is tempted to conclude from these observations that there is a strong temperature limitation on the distribution of *Stylodrilus heringianus* and that this organism does not do well in shallow water because of seasonally higher temperatures or periodic increases associated with internal seiches. *Stylodrilus* becomes abundant below 20 m (Fig. 32b), a depth just below the thermocline for much of the summer. Designation of *S. heringianus* as a cold stenotherm is difficult to reconcile with studies done elsewhere, however. Cook (1967) reported that *Stylodrilus* is found in fast-flowing rivers and streams all over the British Isles. Many, perhaps most, of these streams must exceed temperatures normally occurring at 15-20 m in Lake Michigan. Pickavance (1971) reported *S. heringianus* from a wide range of situations in Newfoundland, from "*wave-washed lake shores and rocky rivers to still, muddy, peat pools*." He studied the life history of the species in two such peat pools. Water in one reached a temperature of nearly 16°C, and the other exceeded 20°C before the pools dried up in midsummer. *Stylodrilus* apparently survives the annual drying of the pools as juvenile and adult worms, and does not rely on resistant cocoons or eggs. We must find some explanation other than low temperature or depth *per se* to explain the preference for depth of *Stylodrilus* in Lake Michigan. This would no doubt be a rewarding problem for physiological ecologists.

With the data (Fig. 32) of relative frequency and relative abundance of *Stylodrilus heringianus* at hand, we are compelled to comment on references to unidentified Oligochaeta in Lake Michigan investigations. Many papers list tubificids or Tubificidae without any indication that the worms were actually identified to the family level (Eggleton, 1936, 1937; Henson, 1962). The ubiquity and high relative abundance of *S. heringianus* at most depths in Lake Michigan suggests that many, if not all, the tubificids were the lumbriculid *S. heringianus*. Often, a description of the habitat leaves little doubt that they were. Investigators who do not completely identify their organisms should refer to them at the lowest possible phylogenetic level of which they are certain, *viz.* Annelida and Oligochaeta.

Peloscolex variegatus shows an even more pronounced restriction to certain depths than *Stylodrilus heringianus*. In the three papers (Hiltunen, 1967; Howmiller, 1974b; Mozley and Garcia, 1972) on which this analysis was based, *P. variegatus* was not reported at less than 20-m depth. Between 25 and 45 m and 45 and 65 m, it had relative frequencies of 57 and 50%, respectively (Fig. 33a). *Peloscolex variegatus* was not found at any of the 21 stations in water deeper than 65 m. This absence from the deepest waters may be only apparent, for few samples have been analyzed from these deep stations. Clearly, *P. variegatus* makes up a very small proportion of the fauna (Fig. 33b) even where the relative frequency is high. Thus, it may be easily overlooked when sample sizes are small.

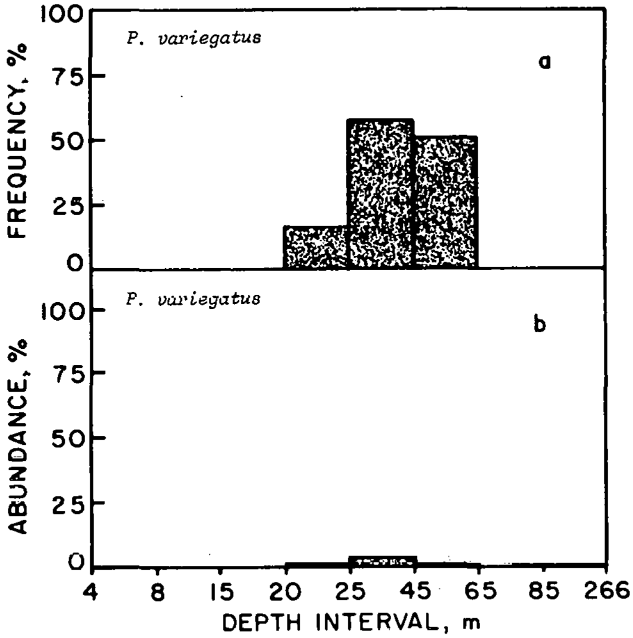


Fig. 33.

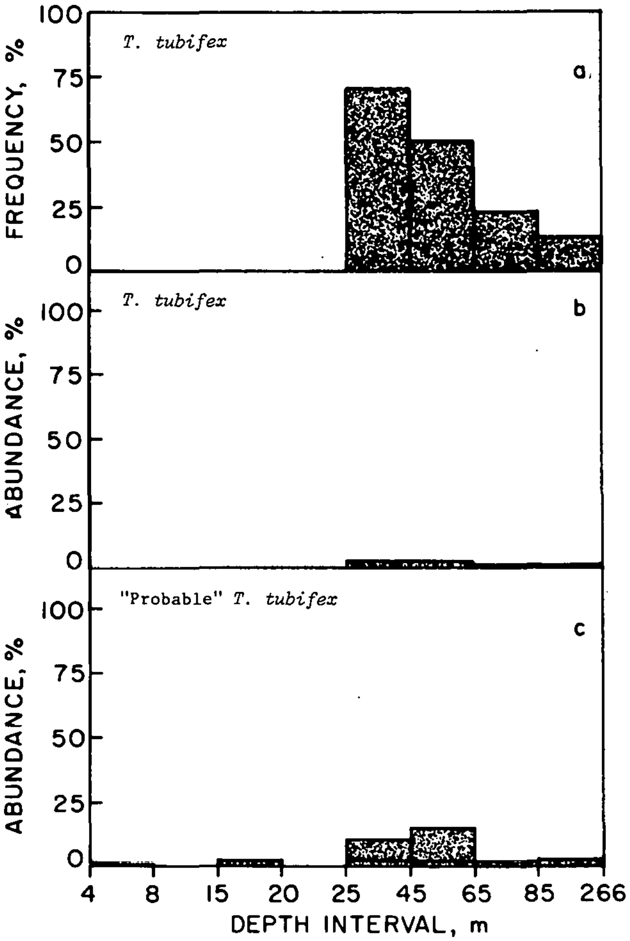
(a) Relative Frequency and (b) Relative Abundance of *Peloscolex variegatus* with Depth in Lake Michigan. Definitions of relative frequency and relative abundance are given in Figure 32.

Tubifex tubifex has a pattern of occurrence much like that of *Peloscolex variegatus*, being absent at depths less than 25 m and occurring with greatest frequency at mid-depths (Fig. 34a). Also, like *P. variegatus*, it is abundant nowhere; its relative abundance is 2% or less in collections analyzed in this report (Fig. 34b).

Since *Tubifex tubifex* can be positively identified in whole mounts only when sexually mature and bearing penis sheathes, the question might be raised whether Figure 34b represents a gross underestimate of numbers by excluding

Fig. 34.

(a) Relative Frequency and (b) Relative Abundance of *Tubifex tubifex* with Depth in Lake Michigan, and (c) Relative Abundance of "Probable" *Tubifex tubifex* with Depth in Lake Michigan. "Probable" *T. tubifex* includes known mature specimens (lower portion of histogram at depth intervals of 24-45 and 45-65 m) plus unidentifiable immature worms lacking hair setae. Definitions of relative frequency and relative abundance are given in Figure 32.



immature individuals. Figure 34c shows the relative abundance with depth of mature *T. tubifex* plus all immature worms having hair (capilliform) setae, *i.e.* all worms that could possibly be *T. tubifex*. The figure refers to abundance of "probable" *Tubifex tubifex* since we feel that in most cases the unidentifiable immature worms with hair setae are indeed *T. tubifex*. However, the figure surely represents an overestimate since these immature worms must also include *Ilyodrilus templetoni*, smaller numbers of *Potamothrix bavaricus* (? = *Potamothrix bedoti*), and perhaps other taxa. Even with the assumption that they are all *T. tubifex*, we are left with the conclusion that this species is not abundant; maximum relative abundance is 15% in the 45-65 m stratum (Fig. 34c).

Figure 35a illustrates that unidentifiable immature worms with hair setae occur commonly at depths to 65 m. No significance should be attached to their absence from the 8- to 15- and 20- to 25-m strata since these worms are never very abundant (Fig. 35b) and are easily missed unless sample sizes are large.

Immature worms without hair setae are more common at depths to 85 m (Fig. 36a). However, they are abundant only to 20 m (Fig. 36b). This group includes all *Limnodrilus* species (though *L. udekemianus* is likely to be recognized when immature), *Potamothrix moldaviensis*, *Peloscolex freyi*, and perhaps very small numbers of other taxa.

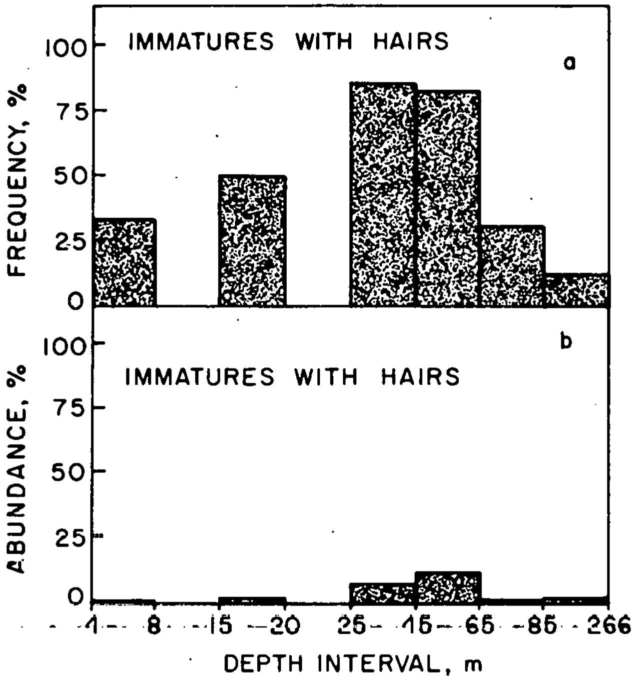
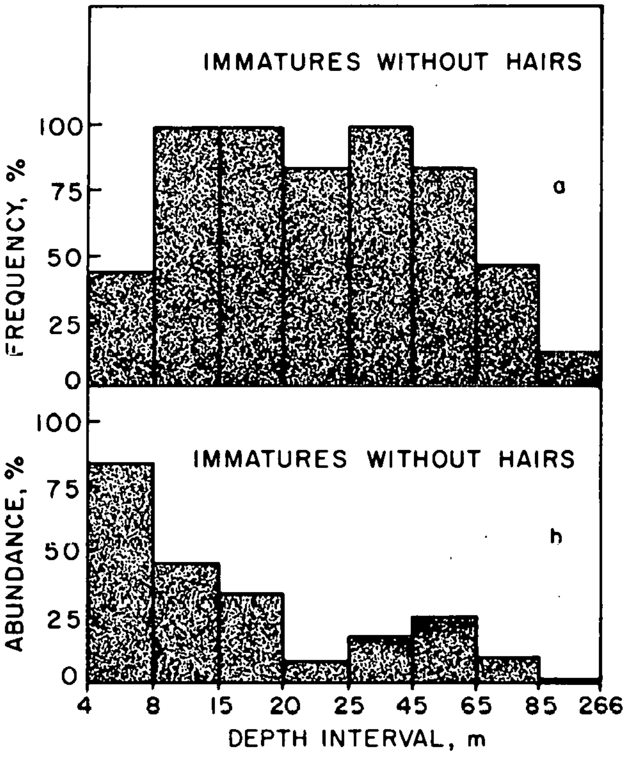


Fig. 35.

(a) Relative Frequency and (b) Relative Abundance of Unidentifiable Immature Worms with Hairs (Setae) with Depth in Lake Michigan. Definitions of relative frequency and relative abundance are given in Figure 32.

Fig. 36.

(a) Relative Frequency and (b) Relative Abundance of Unidentifiable Immature Worms without Hairs (Setae) with Depth in Lake Michigan. Definitions of relative frequency and relative abundance are given in Figure 32.



Limnodrilus hoffmeisteri, like *Tubifex tubifex*, can be positively identified only when mature and bearing penis sheathes. Figures showing relative frequency (Fig. 37a) and relative abundance (Fig. 37b) thus refer only to mature specimens. *Limnodrilus hoffmeisteri* is seen to occur very commonly between 8- to 65-m depths (Fig. 37a), though it seems to become a less important part of the fauna with depth (Fig. 37b). Since a large proportion of the population is frequently immature, these figures are again underestimates. A

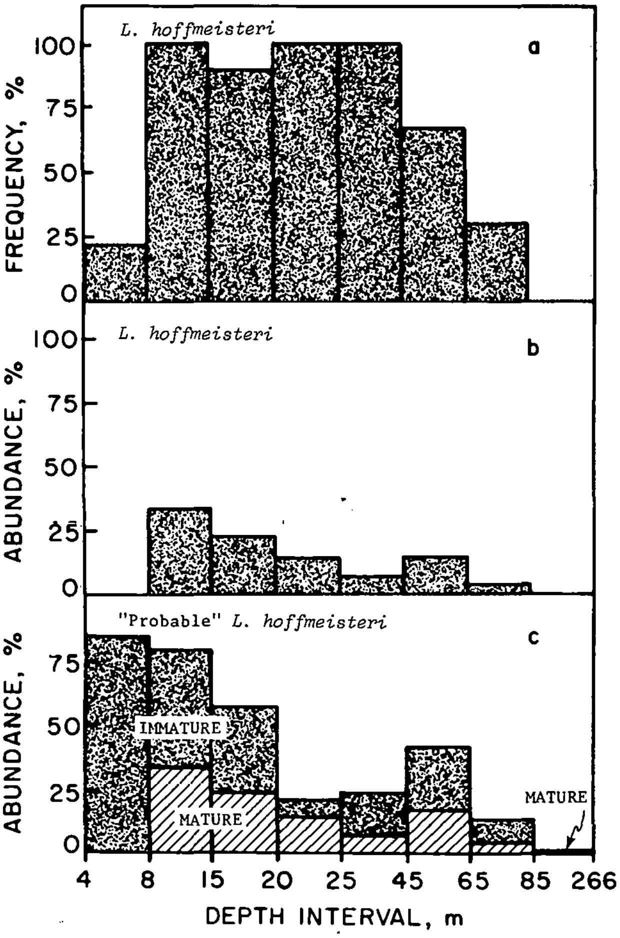


Fig. 37.

(a) Relative Frequency and (b) Relative Abundance of *Limnodrilus hoffmeisteri* with Depth in Lake Michigan, and (c) Relative Abundance of "Probable" *L. hoffmeisteri* with Depth in Lake Michigan. "Probable" *L. hossmeisteri* includes known mature specimens plus unidentifiable immature worms lacking hair setae. Definitions of relative frequency and relative abundance are given in Figure 32.

corresponding overestimate is made by adding all unidentifiable immature worms lacking hair setae to the numbers of *Limnodrilus hoffmeisteri*. The resulting picture (Fig. 37c) is one of much higher relative abundance in shallower waters but still a strong decrease in relative abundance with depth.

Potamothrix moldaviensis is another species recognizable only when mature. Patterns of relative frequency and relative abundance of mature worms are much like those for *Limnodrilus hoffmeisteri*. *Potamothrix moldaviensis* seems somewhat less frequent, except in very shallow water (Fig. 38a), and generally less abundant (Fig. 38b). There appears to be no way, at present, of reliably attributing a certain proportion of the immature worms to *L. hoffmeisteri* and others to *P. moldaviensis*, *Peloscolex freyi*, or both. Under the unlikely assumption that all immature worms were *P. moldaviensis*, the pattern would be essentially that of "probable" *L. hoffmeisteri*. Again, this would be a gross overestimate, but provides an upper limit when trying to decide how seriously we underestimate total numbers by plotting only numbers of mature animals.

The preceding figures and discussion referred to the most common worms found in the three studies (Hiltunen, 1967; Howmiller, 1974b; Mozley and Garcia, 1972). Present data are insufficient to obtain reasonable impressions of frequency and abundance of most other taxa. From the data presented, the reader will recognize that there is considerable difference between oligochaete species in terms of frequency of occurrence and abundance with depth. This ecological differentiation presents an open field for research since we have

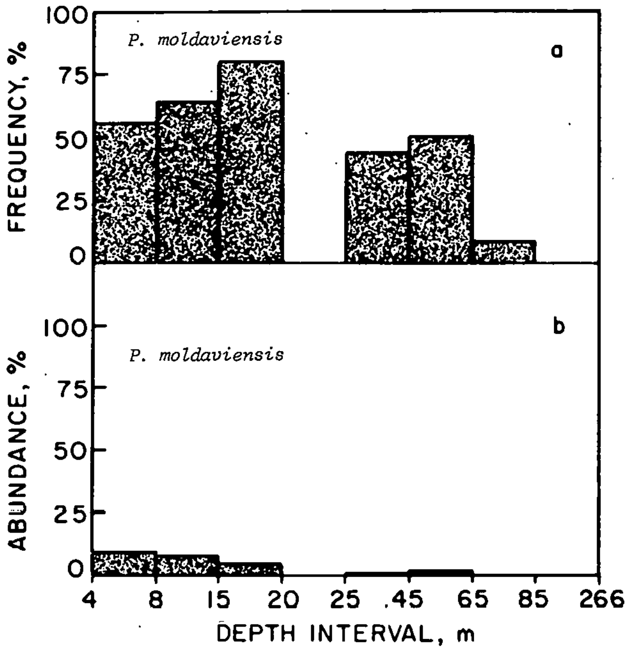


Fig. 38.

(a) Relative Frequency and (b) Relative Abundance of *Potamothrix moldaviensis* with Depth in Lake Michigan. Definitions of relative frequency and relative abundance are given in Figure 32.

little knowledge concerning the relative importance of environmental factors in determining the limits of species distribution in Lake Michigan. This knowledge would have considerable practical value, allowing us to understand the nature of environmental perturbations that influence worm species distributions.

Abundance of Total Oligochaeta

There are far more data, from more stations, on total Oligochaeta than for individual species. Results of numerous studies (Eggleton, 1936, 1937; Merna, 1960; Powers and Robertson, 1965; Robertson and Alley, 1966; Powers and Alley, 1967; and others) indicate that oligochaete worms are among the numerically dominant benthic organisms in Lake Michigan (Fig. 10). Over most of the Lake they are second in abundance to the amphipod *Pontoporeia affinis*, but at the southern end of the Lake, worms frequently exceed amphipods in abundance (Powers and Robertson, 1965; Mozley and Alley, 1973) (Fig. 39).

Estimates of absolute abundance of worms range from a few hundred per square meter in deeper waters of the central and northern basin to over 9000/m^2 at the southern end of the Lake (Powers and Robertson, 1965) (Fig. 39). Hiltunen (1967) found over 13,000/m^2 off Waukegan, and other areas of exceptionally high density occurred off some river mouths. For example, Cook and Powers (1964) found as many as 11,380/m^2 near the mouth of the St. Joseph River. Mozley and Alley (1973) listed numerous samples containing more than 10,000 oligochaetes/m^2 from the southern basin. Rains (1971) reported a mean of 4444/m^2 and a maximum of about 42,000/m^2 for Indiana waters of Lake Michigan; at least eight samples (based on three Ponar grab casts) produced estimates of more than 10,000/m^2. High densities (>10,000/m^2) at depths less than 20 m were believed by Mozley and Alley to be patchy and temporary, since suitable organic sediments may be shifted by storm currents. Also, since a large area near Chicago does not accumulate fine sediments required by most oligochaetes, even heavy organic pollution may not produce extensive areas with large numbers of worms (Mozley and Alley, 1973).

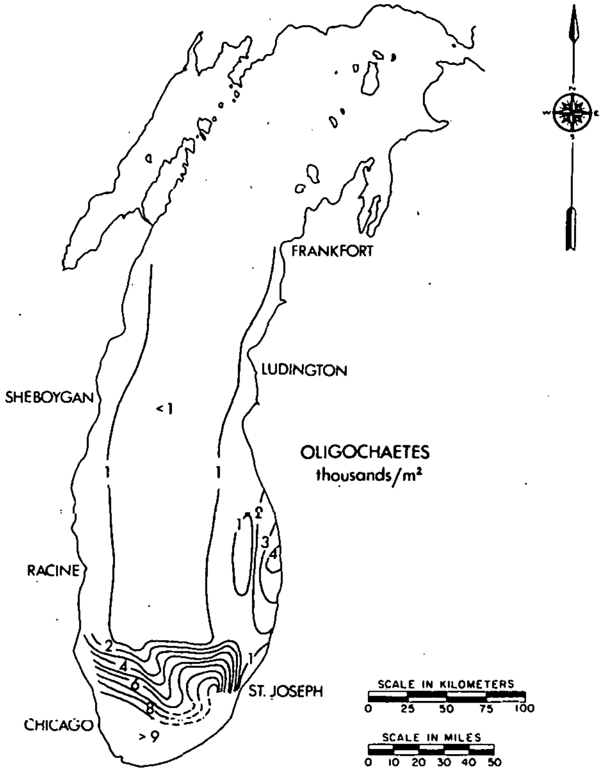


Fig. 39.

Average Numbers of Oligochaetes in Southern Lake Michigan, August-November 1964. Modified from Powers and Robertson (1965) (with permission, see credits).

A 1932 survey included about fifty stations located from the Manitou Islands northward (Eggleton, 1936, 1937). Oligochaetes were second in abundance to *Pontoporeia*, with numbers ranging up to $1525/m^2$, but there were only a few hundred or less at most stations. Numerical data on benthos were also collected more recently in the north during a trace-metal survey in 1969-1970 (Copeland and Ayers, 1972). In only 3 of 16 samples did Oligochaeta contribute more than a quarter of the total fauna. Only one sample was dominated by Oligochaeta (55%); it was taken in the mouth of Little Traverse Bay and yielded an estimate of less than 2000 oligochaetes/m^2.

Henson (1962) found oligochaetes to be a major component of the benthic fauna in the Straits of Mackinac. They were present in 87% of the samples with an average abundance of about $440/m^2$ ($40/ft^2$); only five samples indicated densities exceeding $2200/m^2$ ($200/ft^2$). Since Henson's (1962) samples were taken with an orange-peel grab, these may be serious underestimates.

The role of oligochaetes as food of Great Lakes fishes has not been assessed. Worms are digested so rapidly that they are seldom found in samples of stomach contents from fishes handled in the usual manner. Small numbers of *Limnodrilus hoffmeisteri* in Green Bay and southeastern Lake Michigan have been found to be parasitized by the caryophyllaeid cestode *Archigetes*, which completes its life cycle in carp (*Cyprinus carpio*). This is indirect evidence of consumption of oligochaetes by carp.

Thermal Relations of Oligochaetes

Brinkhurst and Jamieson (1971) have drawn attention to the possible value of one tubificid, *Branchiura sowerbyi*, as an indicator of thermal pollution. This species may have been introduced to America, and perhaps also to Europe, from tropical Asia (Aston, 1968; Brinkhurst and Jamieson, 1971). In Britain, *B. sowerbyi* was initially known only from lily pools of tropical greenhouses, and early records from nature were obtained mostly from waters artificially warmed by electrical generating plants. This prompted an expectation that *B. sowerbyi* would occur in heated waters in North America. To date, that does not appear to be the case. There are records from all corners of the country, but few if any are from heated waters. Observations of Brinkhurst suggest, however, that this species may grow larger in warmer waters; the size of the worms and presence of mature specimens may yet prove to have some indicator value (Brinkhurst and Jamieson, 1971).

Branchiura sowerbyi has not been reported in Lake Michigan. However, it is known in the inland waters of Wisconsin (Howmiller, 1974a) and in western Lake Erie (Brinkhurst *et al.*, 1968; Hiltunen, 1969b), and is the most common species of oligochaete in Sandusky Bay (Wolfert and Hiltunen, 1968). *Branchiura sowerbyi* may thus enter the Lake Michigan fauna eventually, perhaps in the vicinity of thermal outfalls.

The primary sources of information on thermal influences on tubificids are the English power-plant studies. For example, Aston (1968) found that in rivers receiving heat from power plants, cocoon production of *Branchiura sowerbyi* extended over a longer period but that the number of cocoons per sexually mature adult was less than the number in unheated areas. The growth rate was higher in heated areas. In related laboratory experiments, Aston (1968) found that the optimum temperature for growth of immature worms was 25-30°C but that sexually mature worms grew fastest between 10-15°C. Increased temperature had a positive effect upon cocoon production over the range 10-25°C, and over this temperature range there was an inverse relationship between the growth rate of mature worms and the rate of cocoon production. He concluded that at high temperature the growth rate of mature worms is depressed by the high rate of cocoon production.

Further study is needed to fit these observations into a coherent explanation of temperature effects upon *Branchiura*. For example, genetic differences in rate of cocoon production between heated and unheated populations, which were some distance apart, may be confused with thermal effects (Aston, 1968). The results are also not consistent with the observation of Brinkhurst (Brinkhurst and Jamieson, 1971) concerning size of *Branchiura* in relation to water temperature.

At another location, Aston (1969, 1973) found a higher proportion of mature individuals in populations of *Limnodrilus hoffmeisteri* at an artificially heated site than at control stations upstream from the thermal input. There was also a shift in the season of maximum cocoon production. Other tubificid species--*Limnodrilus profundicola, Limnodrilus udekemianus,* and *Tubifex tubifex*--were apparently unaffected by the thermal change.

Aston (1970, 1973) subsequently investigated the effects of temperature upon reproduction of *Limnodrilus hoffmeisteri* and *Tubifex tubifex* in laboratory experiments in which the worms were maintained under constantly well-aerated conditions. He found both species able to reproduce over a wide range of temperatures, extending from 5 to 30°C for *L. hoffmeisteri*, and from 10 to 25°C for *T. tubifex*. The number of eggs per cocoon and the rate of cocoon production by *L. hoffmeisteri* increased with temperature up to 25°C. However, the number of newly hatched worms, expressed as a percentage of the estimated number of eggs produced, increased with temperature to 30°C (Aston, 1970). Thus, increased temperature may have a positive effect upon reproduction over the full range of temperatures studied. In *T. tubifex*, the rate of cocoon production increased with temperature to 25°C, but the number of eggs per cocoon decreased so the net effect was no change in production of embryos. The number of newly hatched worms, as a percentage of estimated number of eggs, increased with temperature in the range 5-20°C but decreased between 20-25°C (Aston, 1970). Thus, increased temperature may promote recruitment by *T. tubifex* up to about 20°C, but beyond that may have a negative effect.

Nonlethal thermal effects on defecation rates (and by inference, feeding rates) of Toronto Harbor Tubificidae were studied by Appleby and Brinkhurst (1970). Maximum amounts of material were egested by *Peloscolex multisetosus* near 14°C, by *Tubifex tubifex* near 18°C, and by *Limnodrilus hoffmeisteri* near or above 20°C. Temperatures at which *L. hoffmeisteri* successfully reproduced also ranged higher than those for *T. tubifex* (Aston, 1970, 1973). The more rapid feeding rates at the warmer temperatures offer a simple explanation for the seasonal pattern of Tubificidae maturation in Lake Michigan (Hiltunen, 1967). When the water is warmed, maturation accelerates, reproduction occurs, and large numbers of young appear some weeks or months later.

Hirudinea

Hirudinea (leeches) are relatives of medicinal bloodsuckers and are seldom longer than 2 cm (exception, *Nephelopsis obscura*, 5-6 cm) in the preserved, contracted condition; however, they can extend themselves to several times that length in life. Leeches are not infrequent in Lake Michigan benthos samples, but no author has made an effort to summarize available data. Mozley (1973a) reported more than four species of Hirudinea from the shore area near the Cook nuclear plant, one of which occurred in more than half of all samples in November 1970. *Helobdella stagnalis* (Fig. 40), the most common

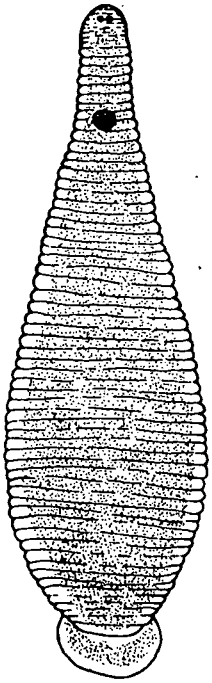


Fig. 40.
Helobdella stagnalis.
From Klemm (1972b).

leech, was mainly responsible for total abundances as high as 620/m^2. The recorded depth range of Hirudinea was 4-32 m; some species possibly extend deeper on occasion. Other species found near the Cook nuclear plant were *Nephelopsis obscura, Glossiphonia complanata,* and *Helobdella elongata. Nephelopsis obscura* was also reported from Little Traverse Bay by Evans (1973). Willson (1969) observed *Helobdella* (as *Glossiphonia*) *stagnalis* in shallow water near Manistique, and Shelford (1913) included this species as a component of the "lower shore belt" (9-27 m) community. Merna (1960) found a few leeches in samples taken shallower than 75 m. Beak Consultants (1973) reported *Dina* sp. in shallow water near Saugatuck. Any of these species may be found either in soft sediments or on hard substrates and, apparently, all become less abundant at greater depths.

Surber and Cooley (1952) reported *Glossiphonia nephreloidea* and *Helobdella* (as *Glossiphonia*) *stagnalis* in Green Bay. The former occurred predominantly in the lower Bay, while the latter was found farther northward. In 1969, Howmiller (1971a) found *Erpobdella punctata, Helobdella stagnalis,* and *Illinobdella* sp. [a fish leech (Piscicolidae)] in Green Bay. Of these, *E. punctata* was the most common, and it was apparently an important predator upon oligochaetes (Howmiller, 1971a). There was a great reduction in distribution and abundance of leeches in the time between these two studies in Green Bay, apparently a result of continued pollution in intervening years (see section on Green Bay Indicators, p. 88).

Klemm's (1972a) recent taxonomic revision and compendium on Hirudinea known from the State of Michigan presents ecological data: zoogeography, reproductive cycle, environmental preferences, and feeding habits. His most interesting observations concern feeding habits. *Helobdella* spp., *Glossiphonia,* and *Nephelopsis* are predators on small aquatic invertebrates--including oligochaetes, chironomids, amphipods, gastropods, and clams; *Helobdella stagnalis* occasionally feeds on carrion. Thus, leeches may prove to be important predators of other zoobenthos. With the advent of several keys to freshwater leeches (Klemm, 1972b; Davies, 1971), we can expect more thorough study of this and other ecological roles of Hirudinea in Lake Michigan.

MINOR OR POORLY KNOWN TAXA

Several types of animals observed in benthos samples are treated cursorily by most investigators or ignored for lack of time to study them properly. For this reason, there is little or no information on their abundance, life history, feeding habits, or distribution in the Lake, even though they may be very important members of some benthic communities.

Aquatic Acari, or water mites, occur occasionally in benthos and plankton samples. They are usually identified only as Hydracarina (an invalid term; see Modlin and Gannon, 1973), because of the difficulty of their taxonomy and lack of numerical importance. Recently, however, the water mites of Lake Michigan have been listed with notes on distribution and ecology (Modlin and Gannon, 1973). Twenty-four species occurred in benthic, planktonic, and even neustonic (interface between air and water) habitats.

Most water mites pass at least part of their lives in association with sediments or hard substrates. Many are parasitic or commensal as larvae or adults on other benthic macroinvertebrates, including Unionidae (freshwater mussels, host of the commensal mite *Unionicola crassipes*), Chironomidae (parasitized by *Hygrobates longipalpis*), and Trichoptera (parasitized by *Lebertia porosa*). Some larvae and many adults are predators on invertebrates. Some attack chironomid larvae (Paterson, 1970) or *Gammarus* eggs, while others become planktonic and feed on Entomostraca. Most benthic mites live in or near aquatic macrophytes or beds of *Cladophora*, and few occur deeper than 20 m. Some appear to be restricted to Green Bay and others have been collected only in the open Lake.

Another poorly known taxon is the Ectoprocta ("bryozoans" of most authors); these organisms occur on hard substrata where they are not collected by bottom grabs. Early studies with trawls and dredges (especially Ward, 1896) turned up at least two species, *Paludicella ehrenbergii* and *Fredericella sultana*. Studies in other Great Lakes suggest that species of *Plumatella* and other genera may also occur in Lake Michigan.

Hydra, or related hydroids, may be very abundant on rocks and other solid substrates at least as deep as 20 m (Mozley, 1975b--unpublished data). Individuals also occur in grab samples from unconsolidated sediments, but these may have become accidentally detached from hard substrates; hydras are frequently caught in the nearshore plankton.

Several unidentified Turbellaria (flatworms) are abundant in beach sands, and a few other species are found occasionally in grab samples from depths of 20 m and more. Limnetics (1973) listed the species *Cura foremanii* as among animals they have collected, without information on its location or abundance. Beak Consultants (1973) listed Neorhabdocoela sp., Planariidae sp., and *Phagocata* sp. in samples taken near shore south of Saugatuck.

Several species of benthic Entomostraca have been reported incidentally in plankton studies. Benthic studies generally omit them because of their small size (which allows most to escape through standard sieves) and difficulty in distinguishing truly benthic specimens from those caught by the open grab as it descends. Cladocera include *Eurycercus lamellatus, Alona* spp., *Ilyocryptus sordidus, Alonella* sp., *Leydigia quadrangularis, Macrothrix laticornis,* and *Pleuroxus denticulatus* (Roth, 1973). Harpacticoid copepods include *Canthocamptus* sp. (probably *C. robertcokeri*) (Ward, 1896; Beak Consultants, 1973; Roth, 1973). A harpacticoid in beach psammon has been tentatively identified as *Parastenocaris* sp. Other Copepoda considered benthic, or littoral, and occurring in Lake Michigan are *Eucyclops agilis* and *Paracyclops fimbriatus poppei* (Roth, 1973). In addition, hand-placed core samples from depths of 6 and 9 m showed that several planktonic species (for example, *Cyclops bicuspidatus*) were much more abundant adjacent to the bottom than higher in the water column (Mozley, 1975b--unpublished data).

INTERSTITIAL MEIOFAUNA OF THE BEACH SANDS (PSAMMON)

The psammon is treated as a unit rather than in taxonomic sections because more is known about the whole than any of its members. Only two investigations of this fauna have been conducted (Pennak, 1940; Seibel *et al.*, 1973). The earlier study of Wisconsin psammon included a single Lake Michigan beach inside the Milwaukee harbor breakwall.

Available data indicate that rotifers, represented by a variety of genera, are the most numerous animals of the psammon. It is likely that they are actually outnumbered by Protozoa, but the protozoans have not been studied in this habitat in Lake Michigan. *Wierzejskiella, Dicranophorus, Lapadella,* and *Proales* are most abundant of the rotifers, and *Colurella, Encentrum, Lecane, Monostyla, Cephalodella,* and *Trichocerca* occur sporadically. Several genera of planktonic rotifers are also found in psammon samples, as are other zooplankton (*e.g.* stranded Cladocera and Copepoda).

Larger animals among the psammon (lengths range up to 6 mm) include an abundant, unidentified turbellarian and at least two chironomid larvae, *Paracladopelma tylus* and *Parachironomus* cf. *demeijerei*, that typify macrobenthos of sandy bottoms at depths less than 8 m. Oligochaeta are also represented by small species, especially the naidid *Chaetogaster*, the aeleosomatid *Aeleosoma*, and a form with reduced numbers of setae (chaetae) that may belong to the genus *Rheomorpha.* Occasional members of the taxa Harpacticoidea (Copepoda), Nematoda (roundworms), Ostracoda, Acari, and Tardigrada are present in samples. Gastrotricha are represented by the genera *Ichthydium* and *Chaetonotus*.

Small size, flexible bodies, armaments of spines, claws or cilia, and elongated, tubular shapes are common among interstitial animals, permitting them to crawl about between the sand grains. The smallest animals crawl on individual grains. Physiological or behavioral adaptations must also exist to enable them to survive in an environment with broad seasonal and daily temperature fluctuations and constant threat of dessication (Seibel *et al.*, 1973).

Numbers of animals appear to vary with time of year. Samples in summer and autumn suggested that a maximum of nearly 10 animals (excluding Protozoa) per milliliter of sand occurred in August. Lowest numbers were found in November. The seasonal cycle of temperature is presumably an important factor, but the severity of wave action on the beach may also affect numbers, more or less independently of season. In comparison with smaller lakes, Pennak (1940) found psammon less abundant but more evenly distributed through the upper 15 cm in the Milwaukee beach.

Interstitial fauna is not restricted entirely to the beach sands. Toward land, the species association grades into that of the soil pore waters, whereas toward the Lake, some species continue out to depths of many meters. A few qualitative observations on these tiny organisms retained by chance in benthos samples (which are screened on sieves with mesh openings much larger than the interstitial animals) suggest that Nematoda, Harpacticoidea, and Ostracoda become more important in the microfauna of deeper, finer-grained benthic habitats. The extreme stresses of temperature, dessication, and substrate instability in the beach can be expected to produce a microfaunal community distinct from that of deeper, more stable habitats.

ZOOBENTHOS AS INDICATORS OF POLLUTION*

Biological assessment of environmental quality is an extension of the sort of knowledge possessed by amateur naturalists and experienced hunters or fishermen. For example, an experienced fisherman shown a bag of carp, buffalo, and catfish, and another catch of whitefish, trout, and sculpins, is immediately aware of the contrasting environments from which the fish were taken. While this sort of intuitive knowledge must have been possessed by earliest man, Aristotle appears to have been the first to record the affinity certain organisms have for polluted aquatic habitats. He wrote of the white color of foul mud and the red threads that grew from it, obviously referring to sewage fungus (*Sphaerotilus*) and sludge worms (Tubificidae) (Thienemann, 1912).

While many organisms are useful in characterizing environmental change, the macroscopic benthic invertebrate fauna has several characteristics that recommend it. Most benthos have very limited mobility: they cannot swim in and out of an area as fishes do, and they are not brought in and out by fluctuating winds or currents as plankton are. Furthermore, most macrobenthic organisms have life cycles of a year or more in contrast to microorganisms which usually have life cycles of a few days or weeks. Thus, the composition of the benthic fauna is relatively stable in space and time and can reflect local conditions over a considerable period.

Also, macrobenthos are relatively easy to collect for environmental surveillance work by state and federal agencies. In many situations, field workers without extensive taxonomic skills can readily separate the community into groups that have significance for water-quality surveillance. Work at the species level, however, generally does require specialized training.

SPECIES DIVERSITY INDEX

A common pattern of change in community structure emerges in work with several groups of organisms: introduction of oxygen-demanding wastes has a fairly predictable impact on benthic species. Species intolerant of low oxygen concentrations disappear from the community. The remaining tolerant ones typically increase in numbers, because predators and competitors are absent and because the wastes generally offer a rich supply of nutrients. With removal of the source, gradual oxidation, or dilution of the wastes, diversity of the community again increases (Fig. 41). In recognition of this, some biologists have used species diversity indices to obtain a single, numerical value for assessing the degree of pollution (Wilhm and Dorris, 1968).

There are several indices or ways of measuring species diversity. The simplest is the number of species in a sample; more elaborate expressions

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**"Pollution" refers to as yet unspecified environmental changes that occur near all major urban effluents and many smaller ones, and that cause characteristic shifts in zoobenthic species composition. Increases in nutrient concentrations, particulate organic matter, and sediment oxygen demand are among the environmental changes presumed to cause the shifts.*

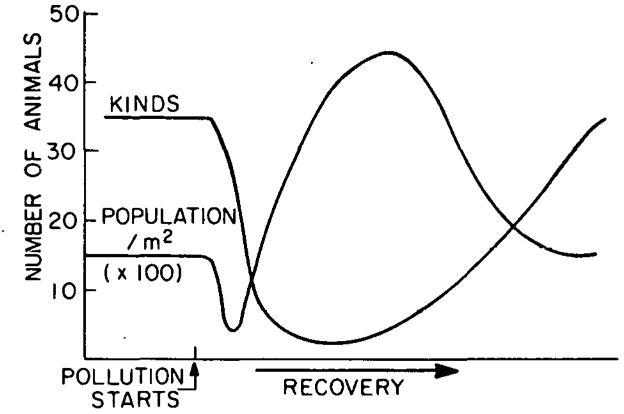


Fig. 41.

The Effects of a Polluting Organic Effluent on the Abundance and Diversity of the Fauna. Redrawn from Mackenthun (1969).

include the proportional contribution of numerically dominant species, or some combination of these characteristics (Hill, 1973). A combination index,

$$\bar{d} = -\Sigma(n_i/n \log_2 n_i/n) ,$$

where n_i is the number of individuals of a given species and n is the total number of individuals in all species, has become widely used in pollution ecology since it was espoused by Wilhm and Dorris (1968). However, benthic samples from southeastern Lake Michigan have shown that taxonomic barriers in several groups (Oligochaeta, Sphaeriidae, Chironomidae) greatly impair its usefulness (Mozley, 1973c). Inevitably, approximations or multispecific categories must be used in calculating the index, with potential loss of details important for assessing water quality.

Use of $\bar{d}$ or similar indices for Great Lakes benthos to assess water quality is further hindered by naturally low diversity, which appears to be a result of severe natural environmental stresses. Both shallow, unstable areas and cold, profundal depths have low diversities because they can be tolerated by few species. At depths of 10-30 m, many more species occur and diversities are higher, but in an occasional sample, *Pontoporeia* may still dominate the benthos so much that diversity drops to values that elsewhere indicate severe pollution.

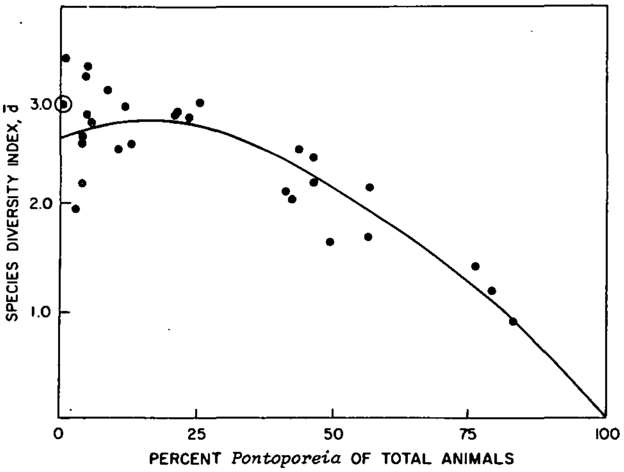
Figure 42 illustrates the effects of the relative abundance of *Pontoporeia affinis* on one species diversity index. A pollution-related increase in the relative abundance of tolerant species of Tubificidae will likely be accompanied by reduced dominance of *Pontoporeia* and cause, at least initially, an increase in the diversity index. There is no simple relationship between diversity and pollution among Great Lakes macrobenthos.

INDICATOR SPECIES

Changes in species composition, on the other hand, have provided useful indices of eutrophication and pollution (Hynes, 1960; Hooper, 1969). In quantitative investigations, the relative abundance of particular species may be considerably more informative than an abstract diversity index. Coupled with a knowledge of ecological requirements of species involved, this approach provides a sensitive index of the state of the environment and may be very effective in revealing changes due to enrichment.

Fig. 42.

Effects of the Relative Abundance of *Pontoporeia affinis* on Zoobenthic Species Diversity. Data from November 1970 survey of southeastern Lake Michigan at depths between 4 and 44 m. The circled dot represents a station with >50,000 Tubificidae/m^2, dominated by pollution-tolerant species. Modified from Mozley (1973c).



The general response of a benthic community to organic pollution is shown diagrammatically in Figure 43 (Hynes, 1960). In a region of intense organic pollution, the diverse assemblage of insects, mollusks, crustaceans, and other invertebrates typical of clean water disappears. These organisms are replaced by tubificid worms, which have adaptations allowing them to obtain oxygen at very low oxygen tensions. These deposit-feeding worms find a rich energy supply in organic wastes and, in the absence of competitors and predators, become very abundant.

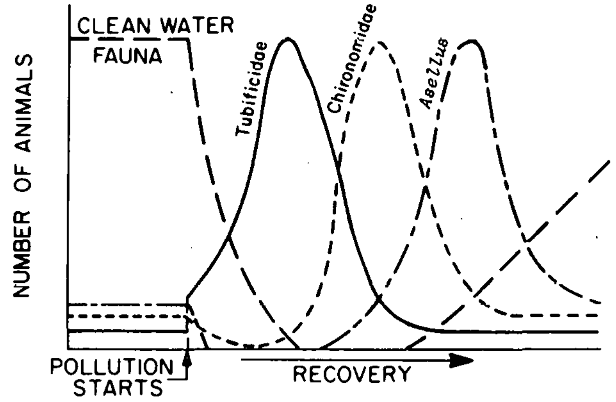


Fig. 43.

Typical Changes in Composition of the Benthic Fauna Resulting from Organic Pollution. Modified from Hynes (1960) (with permission, see credits).

During recovery, or where pollution is not so severe, worms are joined by midge larvae (Chironomidae) similarly adapted to low oxygen concentrations. Midges often become dominant in the fauna as conditions improve. In many situations, midges will be joined by and subsequently yield dominance to aquatic sowbugs (Isopoda: *Asellus*). With thorough oxidation or dilution of the pollutants, clean-water fauna may return gradually.

Each particular type of aquatic environment or area of pollution has more or less characteristic patterns of benthic community response. These patterns are currently being described and correlated with specific types of pollution in the Great Lakes, and several trends have become obvious in polluted benthic areas of Lake Michigan. The best example is that of lower Green Bay.

GREEN BAY INDICATORS

Studies to determine the causes of visible changes in the water quality of lower Green Bay began as early as 1926 (Turner, 1927), and assessment of environmental quality has been one of the goals of most of the more recent investigations (Wis. State Comm. Water Pollut., 1939; Surber and Cooley, 1952; Balch *et al.*, 1956; Scott *et al.*, 1957; U. S. Dep. Inter., 1966a;* Hiltunen, 1967; Schraufnagel *et al.*, 1968; Howmiller, 1971a; Howmiller and Beeton, 1970, 1971). While most of these investigations included analysis of the benthic fauna, some produced data of little comparative value because benthic animals were identified only as "pollution tolerant" or "intolerant." However, the disappearance of the so-called "Green Bay Fly" (*Hexagenia*) can be fixed between 1938 and 1955 on the basis of two of these studies, and subsequent surveys have confirmed its absence. Moreover, Oligochaeta decreased in abundance near the mouth of the Fox River since the early 1930's, but increased farther out in the Bay (Howmiller, 1971a) (Fig. 44). This change was confirmed and corresponding changes in other taxa were described by Howmiller and Beeton (1971), who carefully matched time of year, stations, and methodology with Surber and Cooley (1952). Reductions in numbers of Hirudinea, Gastropoda, and Sphaeriidae occurred over a wide area between 1952 and 1969, but the Chironomidae responded to continuing pollution much as did the Oligochaeta (Figs. 45-47). Species distributions of Oligochaeta showed the general extent of pollution in the Bay, and reflected prevailing patterns of water circulation.

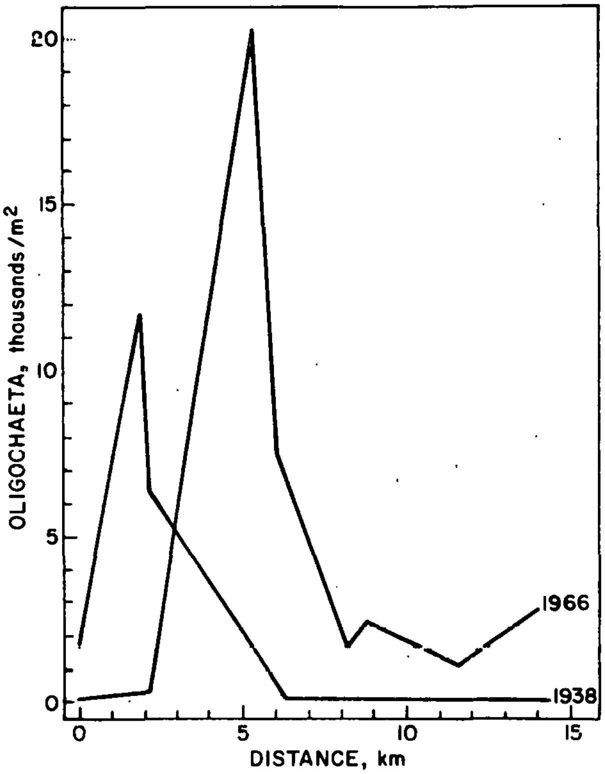
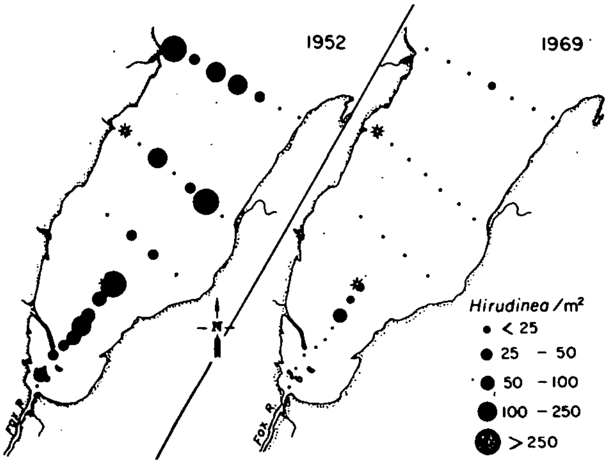
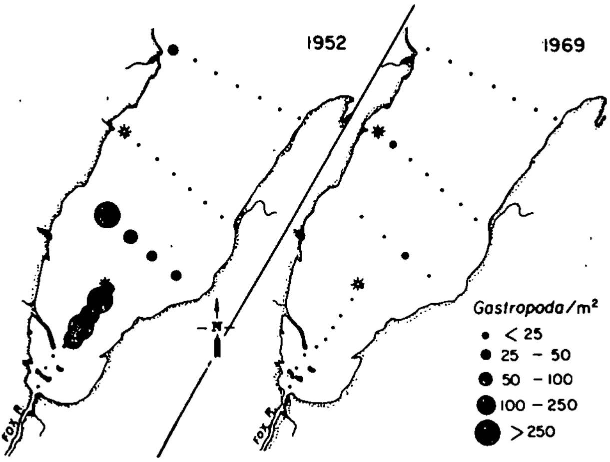


Fig. 44.

Change in Abundance and Distribution of Oligochaeta in Southern Green Bay between 1938 and 1966 in Relation to Distance from the Mouth of the Fox River. Redrawn from Howmiller (1971a).

**The reports of the U. S. Department of the Interior (1966a, 1966b, 1968) are commonly referred to as the FWPCA reports.*





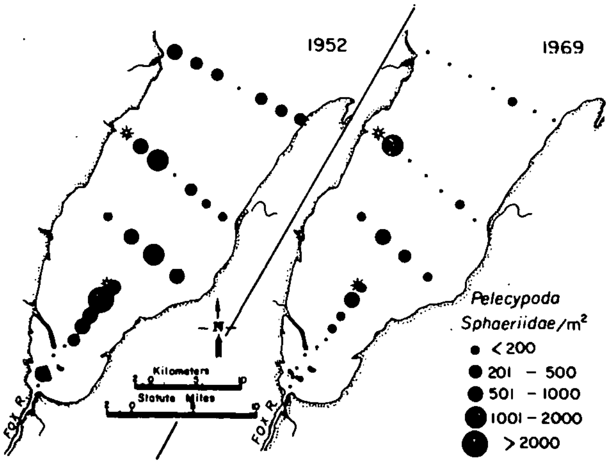


Fig. 45.

Distribution and Abundance of Hirudinea, Gastropoda, and Sphaeriidae in Southern Green Bay in May 1952 and 1969. From Howmiller (1971a).

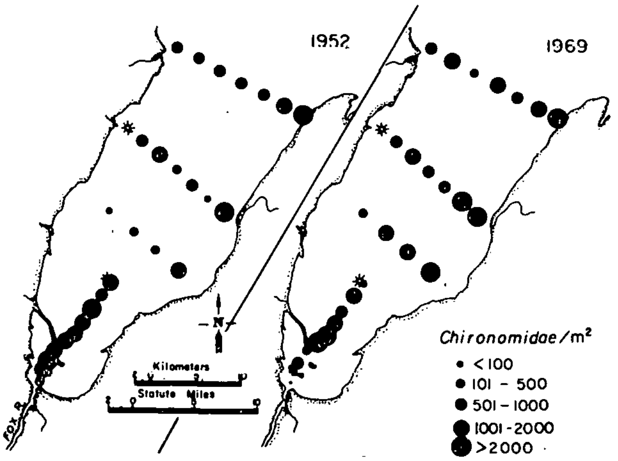


Fig. 46.

Distribution and Abundance of Chironomidae Larvae in May 1952 and 1969. From Howmiller and Beeton (1971) (with permission, see credits).

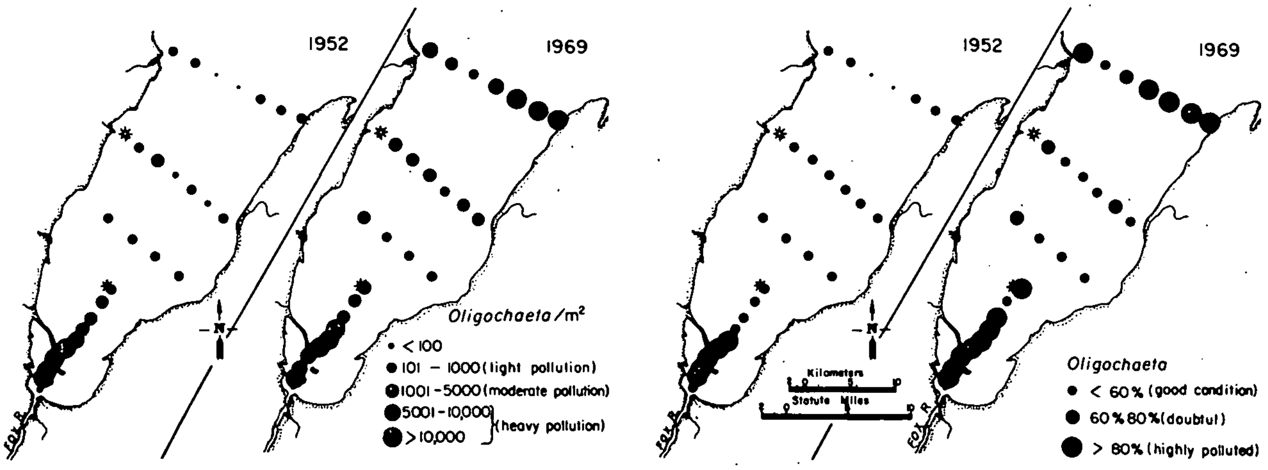


Fig. 47. Distribution and Abundance of Oligochaeta in Southern Green Bay in May 1952 and 1969. From Howmiller (1971a).

Howmiller and Maass (1973--unpublished) attempted to determine whether corresponding changes also occurred in chironomid distribution and abundance between 1952 and 1969. They showed that since 1952 larvae of the genus *Chironomus* have decreased in abundance near the mouth of the Fox River and have increased farther out in the Bay, especially on the eastern side (Fig. 48). Much the same pattern was apparent in the distribution and abundance of *Cryptochironomus* cf. *digitatus* in 1952 and 1969 (Fig. 49).

The most abundant chironomid in the Bay in 1969 was *Procladius* cf. *culiciformis*, which seems to be the most pollution-tolerant species of those present. It retreated least from the vicinity of the river mouth and increased most in an area quite far south, on the eastern side of the Bay (Fig. 50).

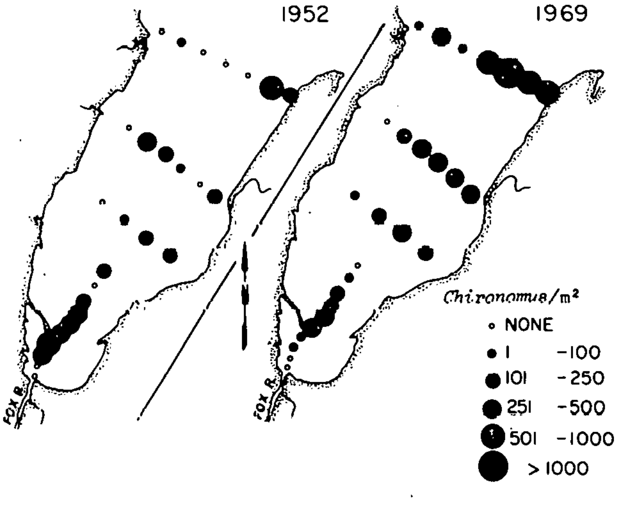


Fig. 48. Distribution and Abundance of *Chironomus* spp. In May 1952 and 1969. From Howmiller and Maass (1973--unpublished).

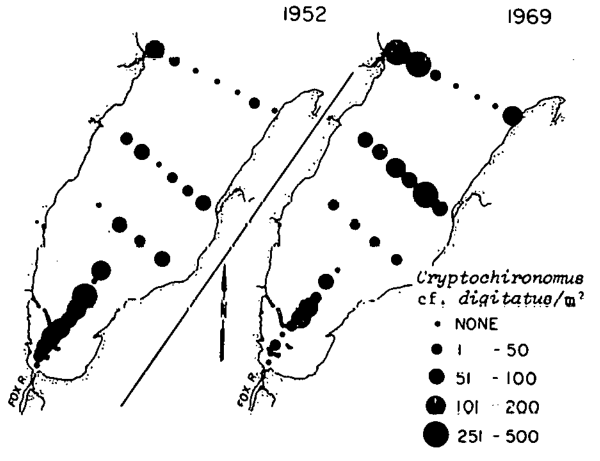


Fig. 49. Distribution and Abundance of *Cryptochironomus* cf. *digitatus* in May 1952 and 1969. From Howmiller and Maass (1973--unpublished).

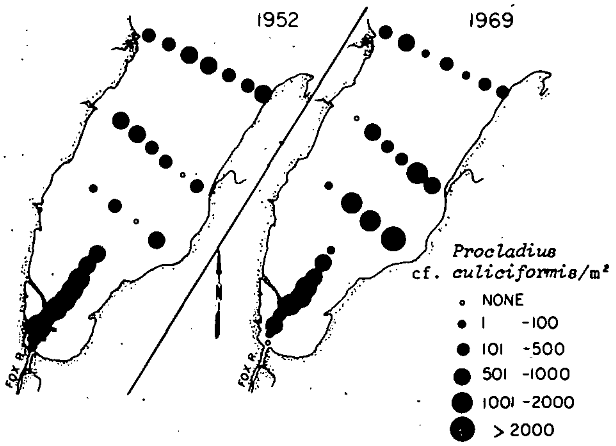


Fig. 50.

Distribution and Abundance of *Procladius* cf. *culiciformis* in May 1952 and 1969. From Howmiller and Maass (1973--unpublished).

Distribution of another important chironomid, *Tanytarsus* spp., is shown in Figure 51. Although no conclusions could be drawn concerning changes in numbers over most of the Bay, the 1952 distribution extended only as far south as the Green Bay entrance light, whereas in 1969 *Tanytarsus* extended approximately 8 km farther (Fig. 51). It seems likely that a change has occurred in the species of *Tanytarsus* occupying the Bay, and that the species present in 1969 was more pollution-tolerant than the species present earlier.

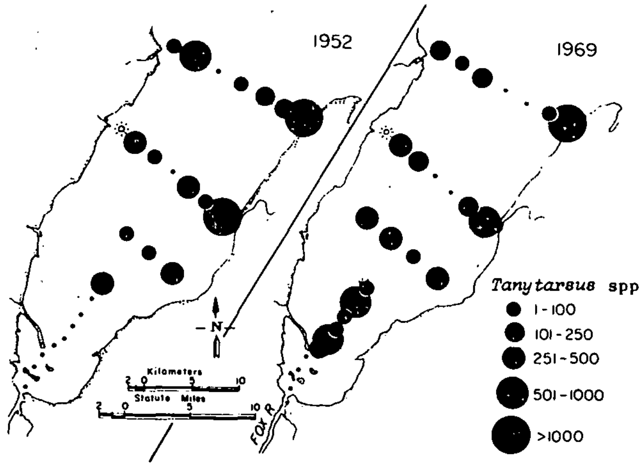


Fig. 51.

Distribution and Abundance of *Tanytarsus* spp. in May 1952 and 1969. From Howmiller and Maass (1973--unpublished).

Harnischia cf. *amachaerus* was reported at 14 of the 27 stations sampled in 1969 but was not recorded in the 1952 study. There is a possibility that the organism was not recognized in 1952 samples. However, Balch *et al.* (1956) reported *H. amachaerus* only at a station north and east of the area under consideration. Since they sampled the southern part of the Bay and did not find *H. amachaerus*, this animal is likely a new addition to the fauna of the lower part of the Bay.

Oligochaeta of Green Bay

In 1969, Oligochaeta comprised 85% of the fauna in the lower Bay (south of the Green Bay entrance light) and 64% of the middle-bay fauna (Howmiller and Beeton, 1971) (see Fig. 47). This represented a substantial increase over 1952, when oligochaetes contributed 66% of the lower-bay and 23% of the middle-bay fauna (Surber and Cooley, 1952) (see Fig. 47). Absolute abundance exceeded 10,000/m^2 at many stations. Since similar percentages occur in other polluted areas (*e.g.* Brinkhurst, 1967a), an understanding of oligochaete species distribution is fundamental to any study of the impact of pollution on Great Lakes benthic communities.

Composition of the Oligochaete Fauna of Green Bay

Oligochaeta from six stations sampled in 1965 were examined by Hiltunen (1967); these included 25 species belonging to three families. His data indicated considerable spatial variation, but *Limnodrilus hoffmeisteri* was found at all stations and all collections were dominated by immatures resembling *Limnodrilus*. The fauna of the lower and middle sections of the Bay, as reflected by these collections, was characteristic of organically enriched areas and quite unlike that of the open Lake.

A more extensive study of Green Bay Oligochaeta was done by Howmiller (1971a) and Howmiller and Beeton (1970). These investigations, conducted in the period 1966-1969, added only a few species to the list compiled by Hiltunen (1967) (Table 11). However, they included collections from over 100 stations and clearly delineated species distributions in the Bay (Figs. 52 and 53).

Limnodrilus hoffmeisteri (Fig. 52) was again ubiquitous and the most abundant oligochaete. *Limnodrilus cervix* and *Limnodrilus claparedianus* were most abundant among other *Limnodrilus* species in the Bay. In these collections, intergrades of the two species were more common than individuals fitting type descriptions; they are thus believed to form a hybrid swarm in the Bay and will be discussed together in this report, under the designation *Limnodrilus cervix-claparedianus* (Fig. 52). *Limnodrilus cervix-claparedianus* seemed to be the best indicator of strong organic pollution since, except for the ubiquitous *L. hoffmeisteri*, this intergrade was the only abundant worm in the lowermost portion of the Bay. It reached its maximum relative abundance there, in highly organic sediments near the mouth of the polluted Fox River (Fig. 52).

At the other extreme, *Stylodrilus heringianus* was found only at the northernmost, *clean-water* stations (Fig. 52). This lumbriculid is apparently intolerant of highly organic sediments and periodic oxygen deficiency associated with polluted benthic habitats in Green Bay.

Peloscolex ferox (Fig. 52) and *Potamothrix moldaviensis* (Fig. 53) seem nearly as intolerant. They occur in abundance only at far northern stations and in the middle Bay on the eastern side where sediments are relatively low in organic content (Howmiller and Beeton, 1970) and where water quality is generally higher (Schraufnagel, 1966; Modlin and Beeton, 1970).

Peloscolex multisetosus, although morphologically similar to *Peloscolex ferox*, has a very different distribution pattern (Fig. 53). *Peloscolex multisetosus* is apparently intolerant of gross pollution, since it is absent from the lowermost portion of the Bay, but seems favored by the organic sediments and corollary conditions near the Fox River (Fig. 53).

Figure 53 also shows patterns of distribution and abundance for several other species, all apparently less tolerant than *Peloscolex multisetosus* but

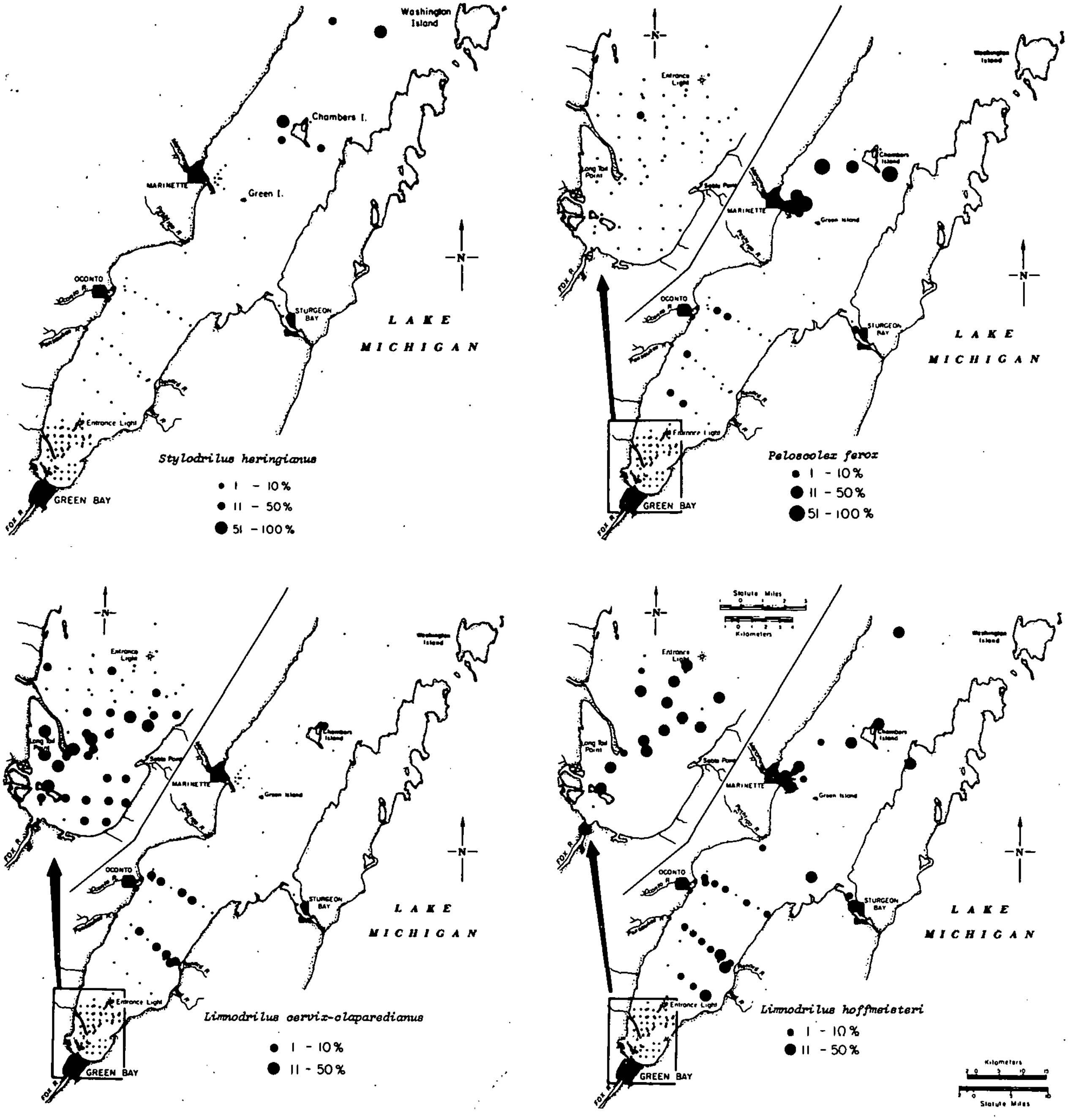


Fig. 52. Relative Abundance of the More Numerous Oligochaeta Species in Southern Green Bay, 1966-1969. Smallest-size dots indicate stations where the species in question was not found. Larger circles indicate relative abundance in accordance with the legends. Slightly modified from Howmiller and Beeton (1970) (with permission, see credits).

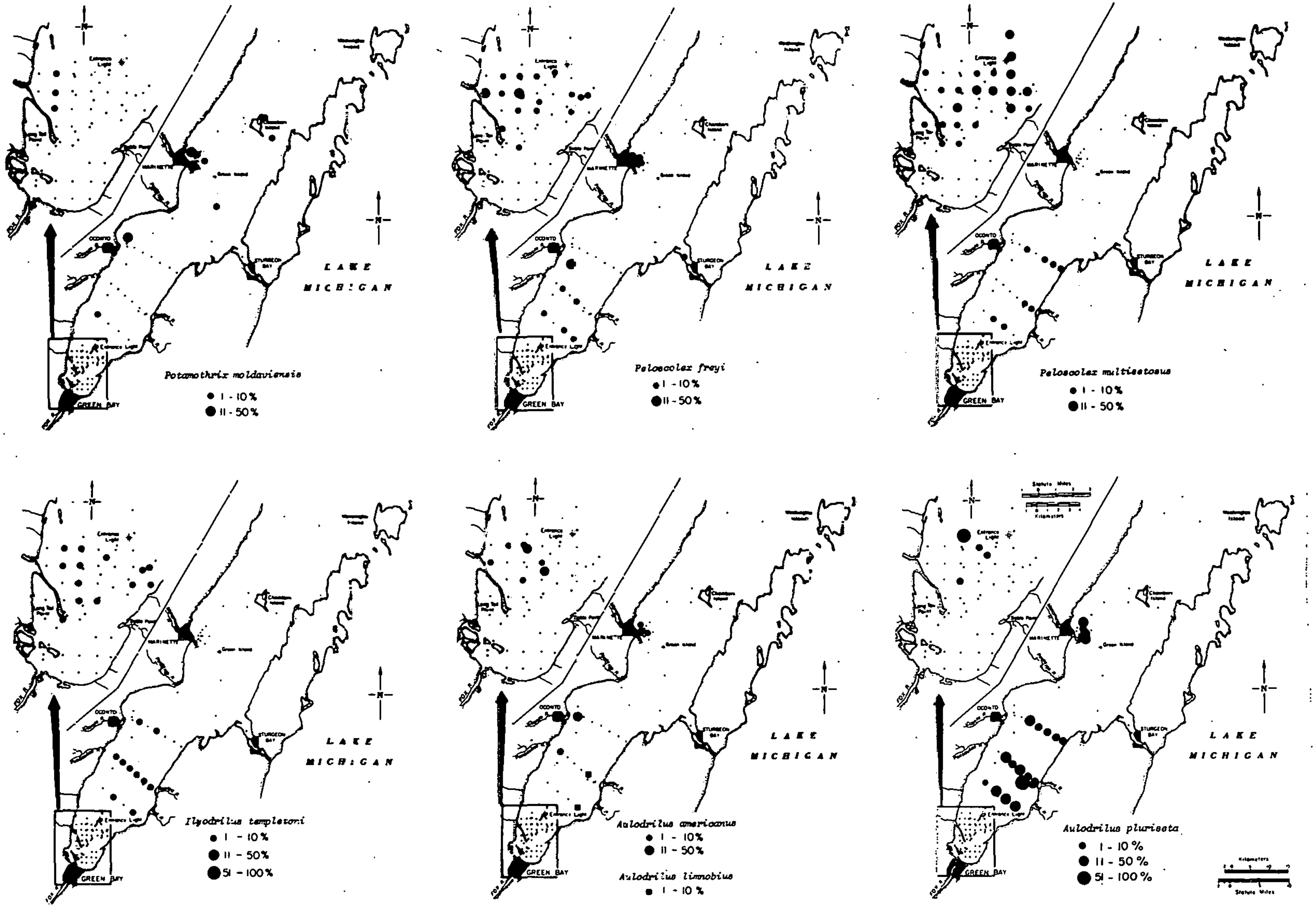


Fig. 53. Relative Abundance of Selected Worm Taxa in Southern Green Bay. Relative abundance is the number of individuals as a percentage of all Oligochaeta. Smallest-size dots indicate stations where the species in question was not found. Larger circles indicate relative abundance in accordance with the legends. Slightly modified from Howmiller and Beeton (1970) (with permission, see credits).

more tolerant than *Peloscolex ferox* and *Potamothrix moldaviensis*. Generalizations made concerning the pollution tolerance and indicator value of these taxa are supported by observations made elsewhere in the Great Lakes (Brinkhurst, 1969; Brinkhurst *et al.*, 1968; Hiltunen, 1967; Veal and Osmond, 1968). Obviously, not all Oligochaeta fit the designation "sludge worm," and any future changes in species distributional patterns may provide valuable documentation of environmental change.

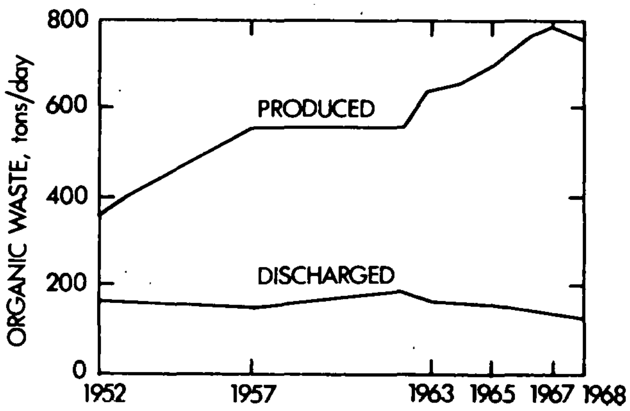
Howmiller and Beeton (1970) postulated changes to be expected if pollution and eutrophication of Green Bay continue unabated. They predicted that, under these circumstances, worms will decrease in a larger area near the Fox River mouth. They expect increased importance of *Limnodrilus* spp. in the lower Bay and the retreat of other species further northward and westward. Increased eutrophication of the Bay as a whole will no doubt result in loss of *Stylodrilus heringianus* and *Tubifex kessleri* from the fauna, with their present localities being taken over by the mesotrophic *Aulodrilus americanus*, *Peloscolex ferox*, and *Potamothrix moldaviensis*. Midge larvae will decrease at more northerly stations, and the demise of other groups will continue. Oligochaeta will assume even greater importance in the benthic community, and with the disappearance of other major groups, it is clear that further changes in the Bay must be assessed by changes in numbers and species composition of Oligochaeta and Chironomidae.

The impact of large effluents of paper-mill wastes and sewage on benthic communities of the Bay has resulted from suspended and sedimented organic material which increased oxygen depletion in water near the bottom. When the Bay is covered with ice or thermally stratified in summer, large areas become anoxic. In order to survive these oxygen-free periods, animals must possess special behavioral and physiological adaptions such as those of Tubificidae and *Chironomus*. However, even the best adapted of these is eliminated by prolonged, complete oxygen depletion.

The predicted changes may take place not only if pollution increases but also if it simply continues at current levels. Pulp and paper-mill waste discharges, the major source of bay pollution (U. S. Dep. Inter., 1966a), did not increase in the period 1952-1968 (Fig. 54), during which profound changes in the bay fauna occurred. The impact of these effluents is apparently cumulative over time.

Fig. 54.

Organic Waste Discharged to the Lower Fox River by Pulp and Paper Mills during the Period 1952-1968. From Wozniak (1971) (with permission, see credits).



Changes observed in Green Bay are similar to those described in Britt (1955), Carr and Hiltunen (1965), and Hiltunen (1969b) in western Lake Erie. Abundance and species composition of Oligochaeta are presently very similar in the two areas, and in Lake Erie, Chironomidae also increased in abundance while *Hexagenia* decreased to less than 1% of its former abundance. Apparently, *Hexagenia* has since completely disappeared from western Lake Erie (Veal and Osmond, 1968). It thus appears that lower Green Bay is ecologically similar to highly polluted areas of western Lake Erie, and more degraded than central portions of the western basin were in 1961.

Indicator Value of Oligochaete Assemblages

Although we know little about the specific factors affecting distribution of oligochaete species, certain species regularly occur in environments with the same general characteristics (Hiltunen, 1967; Brinkhurst, 1969; Howmiller and Beeton, 1970). None of the species in Table 12 are indicators in the sense that their mere presence or absence is evidence of the condition of the environment. Brinkhurst (1967a) has suggested that if enough samples were taken, one could find most worms known in the Great Lakes at a single station. Detection of the presence of a species thus depends largely on sampling effort expended by the investigator. A relatively small number of samples is sufficient to establish the relative abundance of the more common taxa (Brinkhurst, 1967a), and it is this aspect of the composition of the worm assemblage that should be considered in attempting to apply the knowledge summarized in Table 12. For example, high relative abundance of *Limnodrilus hoffmeisteri* seems to be a useful indication of organic enrichment (Brinkhurst, 1967a, 1969), and a high relative abundance of *Stylodrilus heringianus* is generally accepted as evidence that an area receives negligible organic enrichment.

Chironomidae as Indicators of Pollution

The *system* of chironomid indicators is much older than that for Oligochaeta, for it was developed as a part of classical lake typology. Even in its most carefully stated form (Brundin, 1949), however, this system has significant limitations beyond those of the oligochaete system. For instance, only benthic habitats which lie below the thermocline all summer, and in which the hypolimnion is not too different in volume from the epilimnion, sustain the necessary correlation between primary production and the depth-profile of dissolved oxygen concentrations so that effects of eutrophication are transmitted to the bottom fauna. Moreover, it is necessary to identify the midges to species, for different species within a single genus may differ widely in tolerances (Brundin, 1949). Unfortunately, taxonomy of Great Lakes Chironomidae has not yet advanced enough to make species identification straightforward. Brundin's (1958) later assertion that the system has world-wide validity at the generic level does not offer much encouragement to Great Lakes benthologists, who must often deal with essentially littoral-sublittoral chironomid assemblages in shallow areas near shoreline discharges. Areas in which Brundin's (1949) preconditions are met include Green Bay, but not the main basin of Lake Michigan.

These considerations have sometimes been ignored in attempts to utilize chironomids to detect pollution in the Great Lakes. Because of large hypolimnetic water volumes, unusually deep epilimnion, and broad seiches--which cause broad thermal fluctuations to depths of 20 m or more--the expected

Table 12. Classification of Common Oligochaetes According to the Degree of Enrichment of the Environment

Species	Type of Environment* I	II	III	IV
Stylodrilus heringianus	x			
Peloscolex variegatus	x			
Peloscolex superiorensis	x			
Limnodrilus profundicola	x			
Tubifex kessleri	x			
Rhyacodrilus coccineus	x			
Rhyacodrilus montana	x			
Peloscolex ferox		x		
Peloscolex freyi		x		
Ilyodrilus templetoni		x		
Potamothrix moldaviensis		x		
Potamothrix vejdovskyi		x		
Aulodrilus spp.		x		
Limnodrilus hoffmeisteri			x	
Limnodrilus udekemianus			x	
Limnodrilus angustipenis			x	
Tubifex tubifex			x	
Limnodrilus cervix				x
Limnodrilus claparedianus				x
Limnodrilus maumeensis				x
Peloscolex multisetosus				x

**Key: I, Species largely restricted to unpolluted oligotrophic situations (saprophobes); II, Species characteristic of areas that are mesotrophic or only slightly enriched; III, Species tolerating extreme enrichment or organic pollution (saprophiles and saproxenes, see also IV); IV, Species restricted to areas of gross organic pollution (saprobionts).*

relationship between epilimnetic productivity and dissolved oxygen concentrations occurring in small, productive lakes cannot be established in much of Lake Michigan. Detailed taxonomic studies of Chironomidae have shown that larvae that appear very similar to European indicator forms belong to other species (Saether, 1973; Johnson and Brinkhurst, 1971a).

A first effort to devise a North American system of chironomid indicators was made by Brinkhurst *et al.* (1968). They determined the composition of larvae in Lakes Erie, Ontario, and Huron (Georgian Bay) and ranked the forms present by their observed distribution in relation to major urban and industrial effluents. From this, they compiled three groups of larval types which presumably reflected in their distributions a greater or lesser amount of pollution (Table 13). Since different kinds of indicators often occurred together, they proposed a mathematical descriptor--the trophic index value--which would vary from 0 in very oligotrophic lakes to 2.0 in very eutrophic lakes. In this trophic index,

$$\text{Trophic condition} = \frac{\Sigma n_1 + 2\ \Sigma n_2}{\Sigma n_0 + \Sigma n_1 + \Sigma n_2}\ ,$$

n_0 was the number of larvae in intolerant species, n_1 the number in moderately tolerant species, and n_2 the number in tolerant species.

Table 13. Tolerance to Eutrophic Conditions of Profundal Chironomids in the St. Lawrence Great Lakes*

Intolerant (n_0) taxa Index value = 0	*Moderately tolerant (n_1) taxa Index value = 1*	*Tolerant (n_2) taxa Index value = 2*
Monodiamesa cf. *bathyphila*	*Demicryptochironomus* cf. *vulneratus*	*Chironomus* (s.s.) spp.
Protanypus cf. *forcipatus*	*Paralauterborniella* cf. *nigrohalteralis*	*Cryptochironomus* sp.
Potthastia cf. *longimanus*	*Stictochironomus* sp.	*Microtendipes* cf. *pedellus*
Heterotrissocladius cf. *subpilosus*	*Xenochironomus* sp.	*Procladius* cf. *denticulatus*
Paracladopelma cf. *obscura*	*Ablabesmyia* sp.	*Procladius* cf. *bellus*
Tanytarsus sp.	*Thienemannimyia*-group	*Coelotanypus* cf. *concinnus*
Micropsectra sp.		

*From Brinkhurst *et al.*, *1968*.

Rains (1971) provided the only application of the trophic index value to Lake Michigan. He assigned an index value of 1 (moderately tolerant) to two larvae not ranked by Brinkhurst *et al.* (1968), *Paracladopelma* cf. *nais* and *Parachironomus* sp. These were primarily shallow-living species in his samples, and we know of no supportive studies that might justify assignment of trophic-index values to them. Nevertheless, Rains obtained close agreement between regional and station-wise values for the trophic index and an independent classification based on identities of oligochaete species. The 10-m deep station near Gary had both the largest population of *Limnodrilus profundicola*, a saprophobe, and the lowest trophic index value (0.6, oligotrophic range). The Burns Ditch 5-m deep station, where the saprobiontic tubificids *Limnodrilus cervix* and *Limnodrilus maumeensis* were found, had by far the highest trophic index for that depth in Rains' study (1.6, eutrophic range). Tubificid composition ranked the three transects in the same order of relative degree of pollution as the trophic index, with Burns Ditch most polluted and Gary least polluted.

Some caution in application of the index is warranted, however. Brinkhurst *et al.* (1968) pointed out that the parts of the Great Lakes most influenced by urban and industrial wastes are also often the most southerly and probably the warmest areas of each lake. Warmer temperatures may be an important factor in the observed distributions of some of the larvae--having a negative effect on *Heterotrissocladius*, *Monodiamesa*, and *Potthastia*, but a positive effect on *Coelotanypus*. This exerts a *eutrophic* bias on their index in southern areas and an *oligotrophic* bias in northern areas within the Great Lakes. The same type of thermal bias occurs along the depth gradient (see

Rains, 1971). Shallow areas have more *eutrophic* species; deeper areas, more *oligotrophic* ones. Although Brinkhurst *et al.* (1968) implied that only profundal species are to be used in calculating the index, many of the larval types they listed occur shoreward almost to the beach. They included the western basin in their data from Lake Erie, even though it is not deep enough to develop stable stratification, and thus has no true profundal zone.

Lake Michigan is inhabited by at least two species each of *Monodiamesa* (Saether, 1973) and *Heterotrissocladius* (Mozley, 1973a), and members of each pair differ in latitudinal or depth distribution, or both. Rains (1971) found representatives of both these oligotrophic genera at stations near Michigan City and Burns Ditch, Indiana, in company with saprobiontic and saprophilic tubificids. Since each was as numerous at these stations as it was in less disturbed parts of the Great Lakes, we must conclude that trophic-index values for some species may change as additional data and taxonomic expertise accumulate.

Another problem with chironomids is the effect of time of year on species composition and apparent indications of pollution. In October 1966, chironomids in lower Green Bay consisted essentially of two forms of *Chironomus* and *Procladius* cf. *culiciformis* (Howmiller, 1971a; Howmiller and Maass, 1973--unpublished). In the following May and again in May 1969, *Procladius* had become the most abundant form, and *Tanytarsus* species accounted for 13% of the chironomids. Either prior emergence or heavy mortality decimated *Chironomus* over the winter. With the increase (or growth to catchable size) of Tanytarsini, the chironomid assemblage would suggest mesotrophic--or perhaps even oligotrophic--conditions, in strong contrast to the situation in October.

Nevertheless, Howmiller and Maass (1973--unpublished) did find a pattern of changes in the composition of chironomid larvae related to distance from the Fox River mouth. Far from the river in the upper Bay, larval types representing Brinkhurst's "intolerant" (*Heterotrissocladius, Monodiamesa*) and "moderately tolerant" (*Phaenopsectra**) groups appear in samples, together with other taxa (*Mysis, Pontoporeia, Stylodrilus*) indicative of cooler, better-oxygenated water. Representatives of "tolerant" types occurred in the upper Bay as well, indicating it to be a transitional zone between the eutrophic lower Bay and the oligotrophic Lake.

Although a chironomid indicator system may eventually be devised for the Great Lakes, the trophic index and other less thoughtful systems should not be used indiscriminately for water-quality judgments. Just as for European waters, a chironomid system for Lake Michigan must be grounded on species identifications and used with full cognizance of restricting conditions.

HARBOR POLLUTION AND BENTHOS

Harbors around Lake Michigan are very susceptible to pollution, because they are bounded by human population centers and industrial concentrations, and because they are partially cut off from exchange of water with the open

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**Not listed by Brinkhurst et al. (1968), but it is an indicator of mesotrophic lake types in Europe under the former name of Sergentia.*

Lake. These are often the most severely degraded benthic habitats, and harbor muds are often highly toxic to the animals of the open Lake (Gannon and Beeton, 1969).

Helm (1966) presented the results of chemical and biological surveys of a number of Wisconsin harbors on Lake Michigan between 1962 and 1965. Unfortunately, the report is phrased in terms such as "tolerant organisms," "very tolerant organisms," *etc*. Only in the case of the Milwaukee Harbor are we told that the "very tolerant" group was composed largely of "sludge worms." Because organisms were not further identified, Helm's report does not provide a satisfactory indication of conditions prevailing in these harbors. Perhaps it is worth noting, however, that "intolerant organisms" were rare or, at most stations, lacking altogether. All harbors were dominated by "very tolerant organisms."

Some of these same harbors--Manitowoc, Twin Rivers, Sheboygan, and Milwaukee--were sampled in 1962-1963 by the U. S. Department of the Interior (1968) and were found to be degraded, which is in agreement with the report of Helm (1966). This was again evidenced by large numbers of benthic organisms of the "pollution-tolerant group," while "pollution-sensitive" forms were rare or absent. This report (U. S. Dep. Inter., 1968) indicates that the "pollution-tolerant group" in most cases was almost entirely "sludge worms." Milwaukee Harbor data from 1962-1963 were also the subject of a separate report by the U. S. Department of the Interior (1966b). Again the benthic fauna, which consisted of 94-99% "pollution-tolerant forms--mostly sludge worms," indicated degraded conditions.

Ayers and Huang (1967) provided more detailed zoobenthic data from Milwaukee Harbor, and supported these data with measurements of other water-quality parameters. Benthos were strongly dominated by oligochaete worms, with densities exceeding 10,000/m^2, at all stations. Most stations had 50,000-300,000/m^2, and at one, numbers exceeded 383,000/m^2. Several other reports have commented on extremely high densities of oligochaete worms in parts of the Milwaukee Harbor, with estimates of: 150,000/m^2 (U. S. Dep. Inter., 1968), 165,000/m^2 (U. S. Dep. Inter., 1966b), 170,000/m^2 (U. S. Public Health Serv., 1963) and over 1,400,000/m^2 [(132,397/ft^2) (Helm, 1966)]. Bottom samples from some areas of the harbor contained so many tubificids that they resembled hamburger. It is possible that this presents an unusual opportunity for overwintering ducks in the harbor; Rofritz (1972) reported that they feed largely upon oligochaetes, an observation that seems not to have been made elsewhere.

Other benthic organisms reported from the harbor by Ayers and Huang (1967) included sphaeriids, chironomid larvae, and small numbers of leeches, snails, and amphipods. Ash-free dry weight of organisms at eight harbor stations averaged 31.7 g/m^2 with a maximum at one station of 74.1 g/m^2, an extraordinarily high value. Samples of benthic organisms from five stations in the embayment, but outside the harbor, averaged 5.0 g/m^2.

A few samples have been collected on the eastern shore of the Lake from the lower reaches of the St. Joseph River (Cook and Powers, 1964) and the Grand River (Ayers and Rossmann, 1967). In the Grand River, a station 1200 m (3/4 mi) from the mouth had a few amphipods, chironomids, and leeches, but most of the benthic animals were oligochaetes. The number of oligochaetes was not extremely high (6952/m^2). Several kilometers upstream, the benthos consisted solely of oligochaetes and chironomids. The presence of amphipods near the mouth was attributed to the influence of lake water diluting the river water. In the St. Joseph River, as in the Grand, samples inside the breakwater contained mostly oligochaetes and chironomids, with a few amphipods near the mouth. Just outside the breakwater, the sandy, wave-beaten sediments supported few benthos of any kind, and there was no evidence of river influence.

The lower Manistique River, on the northern shore of the Lake, was investigated by the Michigan Water Resources Commission in 1968-1969 (Willson, 1969). The harbor was judged to have high water quality, except in a channel directly influenced by the effluent of a pulp factory. There, oligochaetes made up most of the benthos, and chironomids the remainder. The effect was attributed to deposits of waste fiber on the bottom. Again, the number of oligochaetes was much lower than in severely polluted harbors. Lakeward of the river mouth, one shallow station had a moderately large number of worms--3000/m^2--for such an exposed location, but other stations around the river mouth showed no evidence of the river's influence.

Comparisons Based on Abundances of Higher Taxa

The ratio of the number of amphipods to the number of oligochaetes ranged from zero over much of Milwaukee Harbor to 1.0 at some distance out into the Lake (Ayers and Huang, 1967) (Fig. 55). An amphipod:oligochaete ratio smaller than 0.001 was taken as indicative of definite pollution, and a value in the range 0.01-0.001 as indicative of marginal pollution (see also Powers and Robertson, 1965).

In the open Lake, the relative abundance of amphipods decreased and that of oligochaetes increased toward the southern end (Powers and Robertson, 1965) (Fig. 56). Cook and Powers (1964) found Oligochaeta much more abundant and amphipods much less abundant near the St. Joseph River than in a shore region far to the north. Powers and Robertson (1965) extended this general relationship, as influenced by depth, to much larger areas of the Lake. The U. S. Department of the Interior (1968) (see also U. S. Public Health Serv., 1963) mapped abundances of these two organisms, and concluded from the patterns that extensive regions of southern Lake Michigan suffer from heavy pollution. Mozley and Alley (1973) compared abundances of the two taxa within restricted depth zones over wide areas of the southern and central regions of the Lake, and again found that the south end had more oligochaetes and fewer amphipods.

Ultimately, the use of the amphipod:oligochaete ratio to compare southern and northern parts of Lake Michigan depends on the unconfirmed assumption that the south end of the Lake was the same as the north end before the influence of European man. It is undeniable that modern man has had a greater impact on the southern end of the Lake, but factors such as bottom slope, sedimentation and erosion rates, and temperature probably differ between the two regions under natural conditions.

Two historical comparisons do suggest, however, that the amphipod:oligochaete ratio is decreasing over wide areas of the Lake. Robertson and Alley (1966) compared results of a survey in 1964 with data of Eggleton (1936, 1937) from 1931-1932. Both oligochaetes *and* amphipods increased in abundance in the intervening years, but the increase was greater for oligochaetes. The U. S.

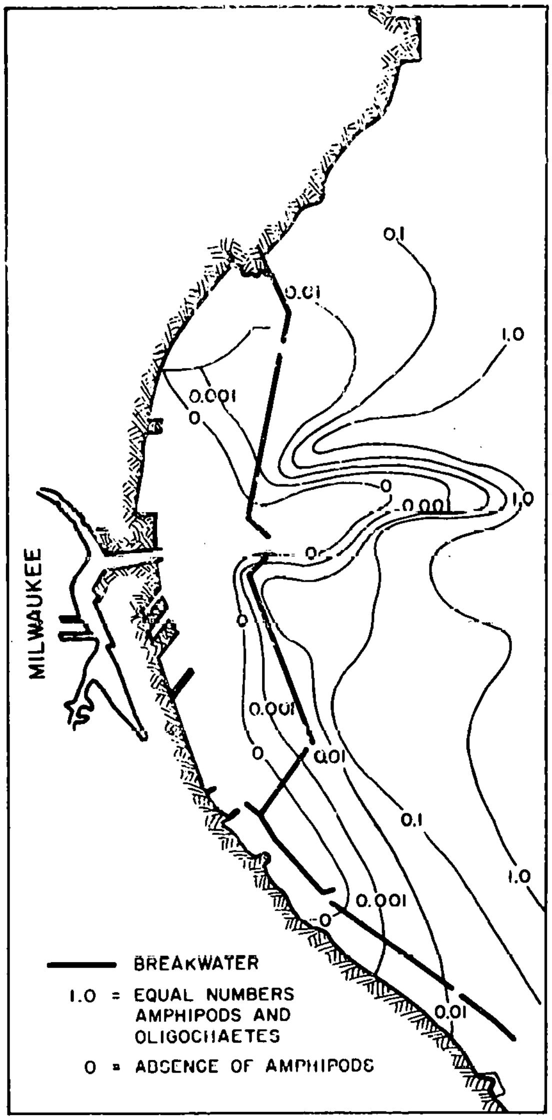


Fig. 55.

Ratio of Numbers of Amphipods to Numbers of Oligochaetes in Sediments of the Milwaukee Harbor and Embayment. Modified from Ayers and Huang (1967) (with permission, see credits).

Public Health Service (1963) also conducted a comparison between the number of benthos in 1962 and the number found by Eggleton (1936, 1937) in the 1930's. The Service pointed out that in 1931-1932, Lake Michigan benthos were comparable in abundance to the bottom fauna of the large, northern Canadian Lakes Churchill and Athabasca, and to Lake Huron; but in 1962, the average number per unit area was about three and one-half times higher in Lake Michigan than it had been in 1931-1932. They also observed higher densities of oligochaetes near Benton Harbor and Michigan City in the southeastern part of the Lake (up to $7000/m^2$) than in the northern basin (up to $1816/m^2$). Overall, they found Chironomidae larvae to be more frequent in samples than sphaeriid clams, the reverse of Eggleton's (1936, 1937) results in 1931-1932. The U. S. Public Health Service concluded that the large increases in numbers of oligochaetes and relative frequency of Chironomidae, and the decrease in amphipod numbers as a proportion of total zoobenthos, were caused by increasing organic sedimentation.

Although the numbers of oligochaetes and amphipods or ratios of them may have some value as a rough measure of environmental quality, they do not offer

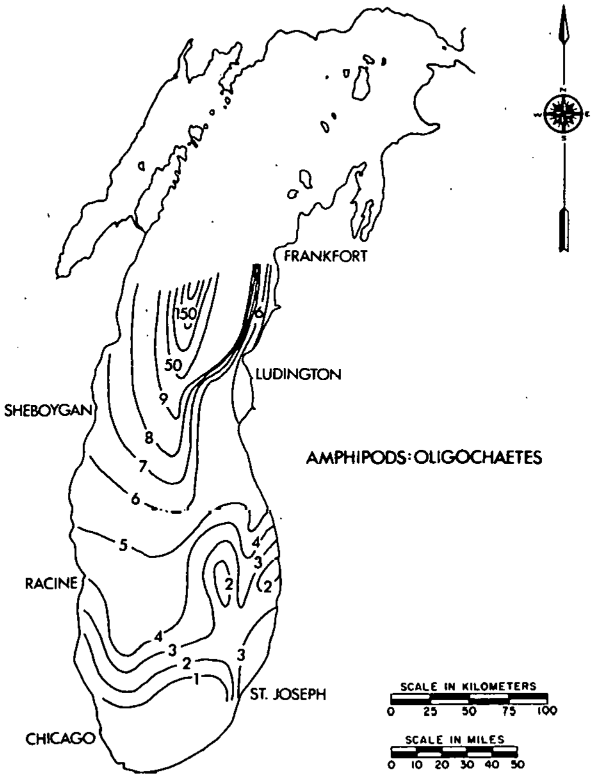


Fig. 56.

Average Distribution Ratios of Numbers of Amphipods to Numbers of Oligochaetes in Southern Lake Michigan, August to November 1965. Modified from Powers and Robertson (1965) (with permission, see credits).

the sensitivity of investigations at the species level, and there are several practical difficulties that restrict their usefulness. As one moves from open lake waters into shallower, warmer bays and rivers along the shore, the prevailing amphipod--*Pontoporeia affinis*--decreases or drops completely out of the fauna, whether or not the shallows are polluted. In the open Lake, the amphipod:oligochaete ratio is also affected by depth and sediment grain size. Mozley and Alley (1973) showed that coarser sediments and medium to coarse sands, common around the southern tip of the Lake, tended to have fewer total animals but a higher relative abundance of amphipods than finer sediments (fine sand or silt) (Figs. 57 and 58). Finally, since oligochaetes escape readily through standard sieve meshes, the value of the ratio may vary with the care taken in sieving.

Furthermore, species of oligochaetes in harbors and the open Lake are ecologically very different. For example, the worm fauna of Milwaukee Harbor is very similar to that of lower Green Bay--being dominated by *Limnodrilus hoffmeisteri*, with smaller numbers of *Limnodrilus cervix*, *Tubifex tubifex*, and *Peloscolex multisetosus* (Howmiller, 1973--unpublished data)--and is much the same as that in Toronto Harbor on Lake Ontario (Brinkhurst, 1970). When the worms and amphipods represented in the ratio are so ecologically different in harbors and the open Lake, the ratio of these forms is not likely to have the same index value in these two environments.

OTHER APPROACHES

The emphasis on objective demonstration of possible zoobenthic changes around the many power plants in early operational or preoperational stages along Lake Michigan's shores has led to more statistically oriented assessments. The bivariate control charts developed by Beak Consultants (1973) were

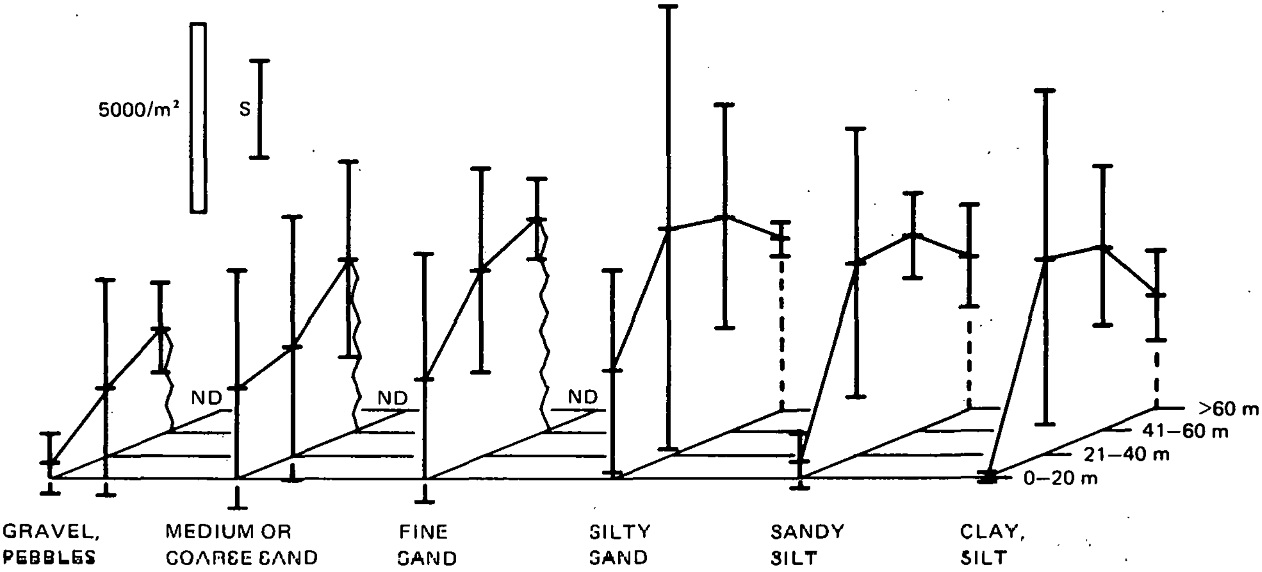


Fig. 57. Relationship between Total Amphipoda Abundance and Depth and Sediment Type in Southern Lake Michigan. Slightly modified from Mozley and Alley (1973) (with permission, see credits).

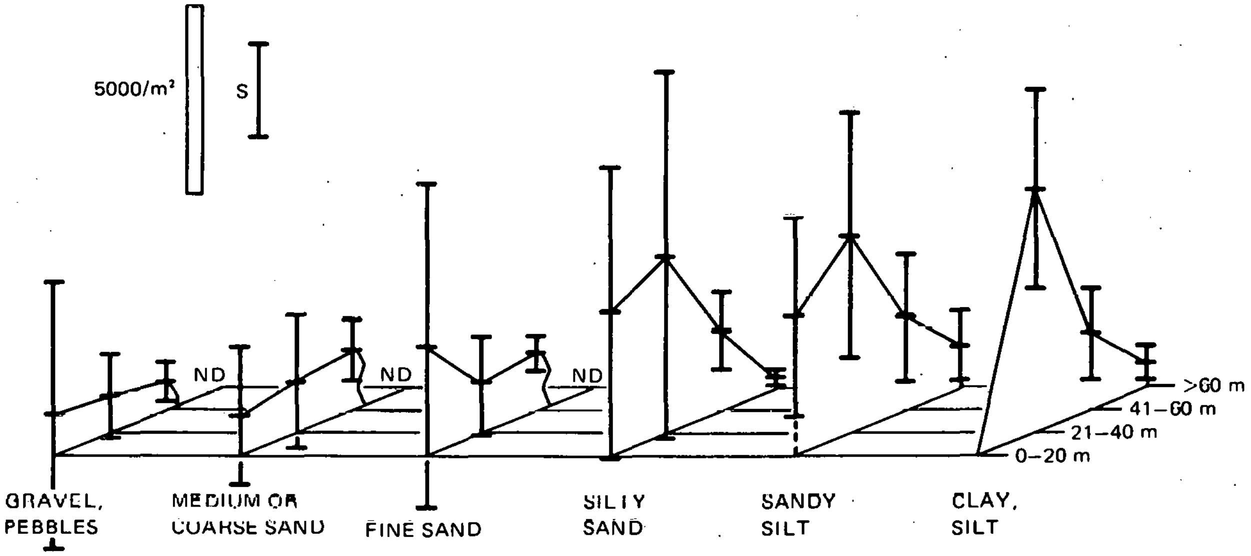


Fig. 58. Relationship between Oligochaeta Abundance and Depth and Sediment Type in Southern Lake Michigan. Slightly modified from Mozley and Alley (1973) (with permission, see credits).

an attempt to compare sites near a power plant with similar sites farther away. To avoid potentially confounding influences--such as depth, time of year, year-to-year variations, and pre-existing differences in zoobenthos at the sites under comparison--they held month and depth interval constant and computed the *ratios* of numbers per unit area for near-plant (inner) sites to more distant (outer) sites. Several confidence levels were computed for the three years' ratios and plotted on two-dimensional (inner *vs.* outer) graphs. New data for that month and depth interval in postoperational years could be located rapidly on the graph and their general tendency to differ from preoperational data could be seen immediately. The test only indicates the appropriateness of more rigorous techniques of analysis. The main weakness of bivariate control charts is that simultaneous changes in inner and outer data in the same direction can indicate highly significant departures from preoperational data unrelated to effects of the power plant, complicating the explanation of results.

Limnetics (1974a) adopted a more rigorous approach based on analysis of variance to compare reference areas with areas near the Point Beach Nuclear Power Plant (no preoperational data available). In addition to variables considered by Beak Consultants (1973), they also determined variance due to sediment types. Results of the initial analysis indicated significant contributions of variance from all sources, but no consistent effects of proximity to the plant over all sampling areas and seasons.

In both cases, the more numerous taxa of zoobenthos were analyzed individually, as were total numbers, biomass, and various diversity indices. Large variances associated with replication at single sites and visits, however, can introduce broad limits to the sensitivity of statistical tests (see Alley and Anderson, 1968). Results must be interpreted carefully to avoid Type II errors, *i.e.* concluding there is no difference when a real, but undetected, difference exists. Considerable attention has been devoted recently to problems of statistical analysis of zoobenthic data in the Great Lakes, and major advances can be expected in the near future.

ZOOBENTHIC ACCUMULATION OF RADIOACTIVE WASTES

For many of the same reasons cited for the efficacy of zoobenthos as indicators of damage to the benthic environment, these animals have also been studied as monitors of the entry of radioactive materials into the aquatic food web near nuclear power plants around the Great Lakes.

Kidd (1970) found natural concentration factors (related to average water concentrations and based on wet weight) for strontium (Sr), manganese (Mn), and zinc (Zn) of 260, 5840, and 3540, respectively, in *Pontoporeia affinis*. In low ambient concentrations of radioisotopes of these elements in the laboratory, the amphipods reached quasi-equilibrium levels in about 10 days for Mn and Zn, and in 23 days for Sr. The main route of uptake was apparently through ingestion, since sterilization of the sediments to remove the bacteria on which this amphipod feeds greatly reduced the accumulation of Zn and Mn. Kidd (1970) concluded that *Pontoporeia* was a suitable monitor for radioactive Zn and Mn.

Fetterolf and Seeburger (1971) collected specimens of many aquatic organisms from the vicinity of the Big Rock Nuclear Power Plant near Charlevoix on Lake Michigan preceding and following startup of the plant. Natural gross-β radioactivity levels were much lower for leeches, crayfish, and snails than for plankton and attached algae, but about the same as for fish. The crayfish were selected as postoperational zoobenthic indicators of radionuclide reconcentration. Concentrations of waste radionuclides increased in the water in the first few years of operation due to world-wide nuclear weapons testing. This was reflected as increased concentrations in crayfish at locations both near and far from the plant. With the decline of weapons testing, gross-β levels in crayfish from reference locations declined to about half those in crayfish near the plant. Year-to-year variation was large at both locations. A comparison of the levels of ^{65}Zn (an emitter of γ-rays) in crayfish in 1969 indicated concentrations almost 25 times higher in those directly exposed to the plant's effluent than in reference areas. Crayfish had the largest concentration ratios for ^{65}Zn (the concentration in reference-area specimens divided by those in specimens collected close to the plant) among all the aquatic organisms measured at Big Rock by Fetterolf and Seeburger (1971).

Nelson *et al.* (1971) also measured γ-emitting radionuclide concentrations in crayfish as a function of distance from the Big Rock Nuclear Power Plant. They found a rapid decline in concentrations within the first 600 m along shore, away from the plant, in specimens of this animal. These authors, too, found crayfish to be among the most effective concentrators of radioactive zinc among the aquatic biota, but also found them to be good concentrators of cesium, cobalt, and, to a lesser extent, zirconium. Neither Nelson *et al.* (1971) nor Fetterolf and Seeburger (1971) found levels of radioactivity hazardous to human health in the aquatic organisms near Big Rock.

Mozley (1973b) conducted laboratory studies on the affinity of several kinds of Lake Michigan zoobenthos for γ-emitting radionuclides in aqueous solution. Mixed-species assemblages were exposed in sand-water systems at summer temperatures. Small chironomid larvae in the tribe Tanytarsini showed the greatest affinity for cesium, cerium, and manganese, whereas *Pisidium* spp. were the best among those tested as concentrators of barium and *Valvata* (a snail) took up more zinc than the others (all comparisons based on counts per unit wet weight in the animals relative to counts in the sand in which they were living). Two *Sphaerium* species, *Lymnaea* (Gastropoda), Oligochaeta (a mixture of *Stylodrilus* and several Tubificidae species), *Procladius* and *Chironomus* (Chironomidae), and *Helobdella* (Hirudinea) were generally poor concentrators of the five radionuclides tested, accumulating little more than the amount associated with the sand around them.

Pontoporeia was intermediate between these groups as a concentrator of these radionuclides, but most of the experimental animals were in the smaller size classes. Kidd (1970) showed small *Pontoporeia* are much less effective concentrators of Zn and Mn than large ones. Mozley (1973b) recommended the use of *Pontoporeia* as the principal monitor organism for γ-emitting, metallic ions in Lake Michigan, because of the relative ease of collecting large quantities of this animal. He also pointed out the value of measuring uptake by a variety of zoobenthic taxa and surrounding sediments for a complete picture of the dispersal of radionuclides through the benthic environment.

DEPTH DISTRIBUTION OF TOTAL MACROINVERTEBRATES

All extensive surveys of Lake Michigan have found the same relationship between depth and benthic abundance or biomass in the profundal zone (Eggleton, 1936, 1937; Merna, 1960; U. S. Dep. Inter., 1968; Powers and Alley, 1967; Robertson and Alley, 1966; Powers and Robertson, 1965). Whereas *Pontoporeia* essentially sets the pattern because of its overwhelming dominance in the macrofauna, the same pattern is found for Oligochaeta, Sphaeriidae and

Chironomidae (Fig. 10). This suggests that some environmental factor affecting these taxa decreases in suitability with increasing depth. One factor that seems likely to satisfy this criterion is the quality of organic matter that reaches the bottom and becomes available as food for the invertebrate benthos. However, total organic matter, as usually measured, is not a useful parameter in this regard. Total organic carbon in profundal muds tends to increase with increasing depth (Powers and Robertson, 1968) (Fig. 8). Large proportions of the organic matter in Great Lakes sediments are composed of barely digestible humic acids and kerogen (Kemp, 1969). Marzolf (1965b) found that numbers of bacteria in the sediments were better predictors of *Pontoporeia* abundance than weight loss on ignition (an estimate of total organic matter obtained by ashing the sediments).

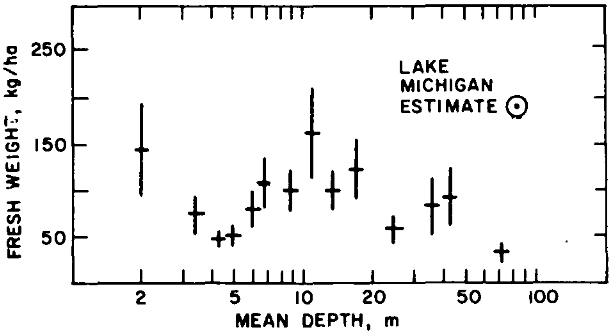
Suspended organic matter can perhaps provide a better estimate of the amount of food available to benthos in a given locality. Phytoplankton production rates and standing crops are almost always higher (per unit volume) within a few kilometers of shore--the initial and principal point of introduction of allochthonous materials--than in the central Lake (Holland and Beeton, 1972; Tarapchak and Stoermer, 1976). Long-term deposition of finer organic particles does not occur in the coastal area, however, as evidenced by sandy bottoms extending to depths of 30 to 50 m (Powers and Robertson, 1968). However, since the largest sources of organic sedimentation are coastal, it is reasonable to presume that the profundal areas nearest shore receive the largest amounts of relatively undecomposed organic matter. If so, disruptions of shore-zone ecology, such as increased shore erosion or phytoplankton blooms, may affect deeper benthic communities several kilometers toward the center of the Lake (see Mozley and Alley, 1973).

BIOMASS AND TROPHIC STATUS

Both fisheries biologists and lake typologists have long pursued the idea that standing stocks of zoobenthos are indicative of the trophic status and the potential fish yield of a lake. The mean depth of a lake, a morphometric parameter, is often thought to have an effect on both benthic biomass and lake productivity. Rawson (1930) plotted benthic biomass against mean depth for some large Canadian lakes and found as a general rule that deep lakes had small standing stocks. Hayes (1957) provided a more thorough consideration of these interactions and concluded that mean depth was unrelated to benthic standing stocks. Nevertheless, his data (Fig. 59) suggest that very deep lakes typically have low standing stocks.

Fig. 59.

Effect of Depth on Fresh Weight of Bottom Fauna (excluding mollusks). The lakes used numbered 158--from the Alps, North Germany, Northern Canada, and the USA. Each point represents an average of 6 to 16 lakes of similar depth, the mean group being 10 lakes. The length of each vertical line is the standard error of the mean. Modified from Hayes (1957) (with permission, see credits).



Alley and Powers (1970) plotted the Great Lakes on Rawson's (1930) diagram and discovered that Lake Michigan had a substantially larger average dry-weight biomass than other lakes approaching it in depth. For comparison with the more extensive data used by Hayes (1957), it is necessary to convert dry-weight data to fresh-weight-minus-mollusks. We have approximated that parameter by multiplying ash-free dry weights (from Alley and Powers, 1970) by five. Sphaeriidae contribute less than 10% of the ash-free dry weight of zoobenthos even near shore in Lake Michigan (Powers *et al.*, 1967), so a correction for Sphaeriidae is not critical to the comparison. This approximation (ca. 150 kg wet weight/ha) places Lake Michigan into Hayes' figure (Fig. 59) at a point several standard errors above lakes with similar mean depths, and as high as the average for lakes with shallow mean depths. The depth interval of maximum biomass in Lake Michigan [25-34 m (Powers and Alley, 1967)] supports a standing stock of over 7 g/m^2 ash-free dry weight. This amount of benthic tissue is seldom recorded, even in the richest zones of eutrophic North American lakes (Cole and Underhill, 1965). Lake Michigan is clearly an unusual deep lake, and despite the strictly oligotrophic character of the profundal species, it appears to be eutrophic in terms of standing stock of macrobenthos.

As we pointed out in the section on methodology, comparisons of this nature are beset with many pitfalls, including differing effectiveness of sampling devices and nonvalidity of biomass measurements based on formalin-preserved samples. The differences between the Lake Michigan estimate and those from other deep lakes are so great, however, that it is difficult to imagine how they could be due solely to methodological factors.

Why is Lake Michigan so rich in benthic biomass? Two answers appear plausible. First, as suggested by Alley and Powers (1970), Lake Michigan is relatively *eutrophic* or enriched in phytoplankton nutrients, especially near shore. This is partly because of human wastes, but also stems from the fertile, calcareous soil in its drainage basin. Lake Superior, parts of Lake Huron, and most of the large Swedish and Canadian lakes lie in less fertile, granitic drainage basins. Second, benthos in Lake Michigan, unlike that in smaller enriched lakes, can continue to exploit increasing food supplies with larger standing stocks, because the hypolimnion is much larger than the epilimnion and contains an enormous supply of dissolved oxygen. In eutrophic shallow lakes, high phytoplankton production leads to seasonal depletion of hypolimnetic oxygen as sinking algae decompose. This excludes most invertebrates and severely curtails the growth of those surviving in anoxic profundal zones. The result is incomplete utilization of the abundant food sinking from the euphotic zone in smaller lakes (cf. Johnson and Brinkhurst, 1971b). This uncoupling of hypolimnetic oxygen depletion from eutrophication has been called "morphometric oligotrophy" by Beeton (1969).

EFFECTS OF BENTHOS ON SEDIMENT AND SEDIMENT-WATER EXCHANGES

It is becoming increasingly clear that burrowing benthic invertebrates may strongly influence the character of the sediments and may affect exchange of substances between sediments and water. Such effects may be caused by mechanical overturn of sediments, irrigation of burrows, or chemical transformation within the gut of the animals. Alsterberg (1922) pointed out that tubificids effect substantial rearrangement of sediments, and both he and Brundin (1949) commented that fecal pellets of the worms and chironomid larvae are a conspicuous component of the sediments in some lakes. Solowiew (1924) observed that the fecal layer brought to the surface by *Tubifex tubifex* differs in its structure, chemistry, and microbiology from the underlying sediments. Ivlev (1939), Ravera (1955), Westlake and Edwards (1957), Poddubnaya (1961) and others have attempted to measure the magnitude of this transport by worms. Results have been variable, doubtless because of differences in density of animals and physicochemical aspects of the environments being studied, but transport may be as great as 612 kg/m^2/yr (Lundbeck, 1926) or 2400 ml/m^2/yr (Davis, 1974a).

This continuous overturn of sediments might be expected to cause some problems for paleolimnologists attempting to study prehistoric conditions and biota of the Lake or its watershed by examining microfossils from sediment cores. This question has been pursued by Davis (1974a), who concluded that *Limnodrilus* may significantly alter pollen stratigraphy. Exotic pollen in experimental columns was cast by *Limnodrilus* onto the sediment surface from strata as deep as 15 cm.

This plowing of sediments by benthos can have marked chemical effects. Under experimental conditions, tubificids (Zvetlova, 1972; Edwards and Rolley, 1965) and chironomid larvae (Rossolimo, 1939; Edwards, 1958) have been observed to increase the rate of oxygen consumption by sediments. Schumacher (1963) observed a correlation between density of tubificids and thickness of the oxidized surface layer of sediments in a freshwater portion of the River Elbe estuary. Edwards (1958) reported that larvae of *Chironomus riparius* increased the depth of a surface layer characterized by high redox potential. Similarly, Davis (1974b) showed that *Limnodrilus* caused a downward shift of 0.3-1.6 cm in redox potential, with significant effects to a depth of 4 cm in the sediment.

Under experimental conditions, *Chironomus* larvae caused an increase in ammonia (Rossolimo, 1939; Edwards, 1958) and iron (Rossolimo, 1939) in the water over sediments. Also, Tessenow (1964) demonstrated that larvae of *Chironomus* increased the rate of regeneration of sedimented diatomaceous silica and the depth in the mud from which regeneration occurred.

Howmiller (1973--unpublished data) conducted an experiment in which tubificids (*Limnodrilus hoffmeisteri*) at densities corresponding to 10,000/m^2 and 50,000/m^2 were placed in Milwaukee Harbor mud covered with filtered Lake Michigan water. Three sets of conditions were established: (*i*) high oxygen concentrations, maintained by aeration; (*ii*) a medium range of oxygen concentrations, with containers open to the atmosphere; and (*iii*) anoxic conditions, established by covering the water with about 0.5 cm of paraffin oil. Under all three conditions, the water increased more in phosphate concentration than it did in comparable control chambers lacking worms. Effects of *Limnodrilus* on phosphorus exchange are being pursued in a more detailed manner by Davis (1973--personal communication) using ^{32}P and intact cores of sediment from a Maine lake.

Benthos may have important effects by facilitating the release of pollutants as well as nutrients. Jernelov (1970) showed that tubificids and clams (*Anodonta*) increase the depth in sediments from which mercury is released to the overlying water.

These experiments indicate that benthic organisms may have an influence on movement of pollutants and regeneration of nutrients. These processes deserve more intensive study in the laboratory as well as under natural conditions, since they have obvious relevance for the control of eutrophication and the rate of release of many pollutants.

IMMEDIATE RESEARCH NEEDS ON LAKE MICHIGAN BENTHOS

The following recommendations for research needs on Lake Michigan benthos are largely adapted from a presentation to the Second Federal Conference on the Great Lakes, March 1975 (Mozley, 1975a).

1. The largely descriptive but well-established knowledge of benthic responses to organic loading should be placed on a more quantitative and experimental basis. Changes in benthic communities and cause-and-effect connections between various types of effluents should be defined, with particular attention to micro-biological responses to enrichment and how they transmit its effects to larger zoobenthos.

2. Coordination of hydrodynamic and sedimentary studies with investigations of benthic communities is needed to develop a capability to predict distance and direction of dispersal of waste materials in various types of basins and exposures.

3. Basic descriptive data are needed for rocky-bottom communities--including their productivity, nutrient-uptake capacity, plankton removal rate, and transfer of fixed energy to adjacent benthic habitats and fish.

4. Rates and pathways of energy flow between fish and benthos (including soft-bodied forms) in all parts of the Lake should be determined, both as an aid in understanding dynamics of pelagic and benthic communities and to ascertain the potential for reconcentration of dangerous substances through the food chain.

5. Continued study and laboratory experimentation are needed near installations using large volumes of lake water to determine whether entrainment of swimming benthos, release of residual chlorine, and emission of a winter, sinking plume have significant impacts on benthic communities.

6. Improvement of the methods for field studies, so that data are truly quantitative, is a fundamental need to all areas of research. This may require extensive redesigning of sampling devices, use of smaller-meshed sieves, experimental development of optimal sample sizes and distribution of sampling effort for representation of benthic communities, and use of improved statistical analysis procedures.

7. Controlled studies of the influence of macroinvertebrates on regenerative processes are needed. Since benthic animals facilitate sediment-water exchange in a variety of ways (incorporation, physical mixing of upper layers, circulation of water in burrows, *etc.*), their influence on the regeneration of undesirable materials may be considerable. As numbers of tubificid worms

increase, pesticides, radionuclides, toxic metals, or nutrients removed from lake waters by sedimentation may once again enter aqueous phases.

Additional discussion of research needs may be found in Cook and Johnson (1974).

ACKNOWLEDGEMENTS

We are grateful for the extensive editorial assistance and patience of Dr. Don McGregor during the entire period of work on this review. We also express appreciation to others in the Division of Environmental Impact Studies, Argonne National Laboratory, who assisted in the preparation of this volume--especially C. D. Meyers, Dee Wyman, Guynn Waggoner, Shari Zussman, and John Martens. Credit is given for editorial assistance during all stages of report preparation. This included drawing or redrawing the majority of the figures.

The literature on which this volume is based was published or in preparation by mid-1974 in most cases, and the present version of the text is little changed from a 1974 draft. Since that time, there have been several additions to knowledge of benthos in Lake Michigan and taxonomy of chironomid groups which are important in Lake Michigan. All the data from the 1964-1967 Coherent Area Study (University of Michigan), with extensive analysis and interpretation, have been published by Alley and Mozley (1975), and an overall summary of the preoperational surveys at the Donald C. Cook Power Plant was offered by Mozley (1975c), including further information on pelagic occurrence of nearshore benthos, identities and abundances of smaller benthic animals near shore, and seasonal fluctuations of many chironomid and oligochaete species. Other power plant survey groups have continued to issue reports in the series cited herein under Limnetics, Inc., and Industrial Bio-Test Laboratories, Inc. (now Nalco Chemical Company Environmental Sciences Group, Northbrook, Illinois). Stimpson *et al.* (1975) give more information on seasonal and spatial distribution of Tubificidae in southwestern Lake Michigan to a depth of 18 m. Ole A. Saether has published a number of major taxonomic revisions of Chironomidae, therein changing or adding many names of Lake Michigan chironomids, as well as providing excellent keys for the identification to species of each group in all life stages (Saether, 1975a, 1975b, 1976, 1977). Jackson (1977) has revised *Paracladopelma* and renamed the most common surf-zone chironomid in the southeastern part of the Lake as *Saetheria tylus* (Townes). It is now possible to identify to species most larvae of the subfamilies Orthocladiinae and Diamesinae and the tribe Chironomini which are common in Lake Michigan. Unfortunately, it has not been feasible to incorporate the extensive name changes into the present volume.

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