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The benthic micrometazoans of Mirror Lake, New Hampshire

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With 68 figures and 39 tables in the text

Abstract

The entire zoobenthic community (including the micro- and meiofauna, but excluding the Protozoa) of this small, oligotrophic lake is described in detail. The fauna is dominated by chironomids, oligochaetes, copepods, chaoborids, and nematodes, and contains at least 322 species from 12 phyla. I discuss the distribution, abundance, and natural history of 81 common species. Community composition varies strongly with water depth and weakly with season. Most (51%) of the animals live in the top centimeter of sediment in Mirror Lake. Mean annual density and biomass are 1,200,000 m^{-2} and 2.5 g dry weight m^{-2}, respectively, and annual production is about 14 g dry weight m^{-2} yr^{-1}. I estimate that micro- and meiobenthic animals contribute 68% of the species, 98% of the individuals, 25% of the biomass, and 35% of the production of the zoobenthos in Mirror Lake.

Introduction

The majority of limnological studies have been concerned with the pelagic zone and the planktonic organisms that live there. The justification for such a focus is simply that it is logistically much easier to work in the pelagic zone than in the sediments or vegetation. However, most species of freshwater organisms, both plant and animal, live on or around surfaces rather than in the open water. Furthermore, much of the metabolic activity in lake ecosystems may be concentrated in the sediments and vegetation, particularly in small lakes (WETZEL 1983). As a result, the same emphasis by limnologists on the pelagic zone that has revealed so much about lakes has also left us with some fundamental gaps in our understanding of lacustrine organisms and ecosystems. This paper is an attempt to fill one small gap by describing, quantitatively and in detail, the zoobenthic community of one lake. My emphasis is on the small benthic animals, the meiofauna and the microfauna, that have been especially neglected by limnologists. A brief, preliminary account of this work has already been published (STRAYER 1985a).

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Quantitative studies of benthic animals have always been hampered by the difficulty of removing all of the benthic animals of interest from their associated substrata. Benthic ecologists have used many methods to separate animals from sediments (see, e. g., EDMONDSON & WINBERG 1971; HOLME & MCINTYRE 1971; HULINGS & GRAY 1971; BRINKHURST 1974), but almost all of them involve washing the sediment sample through a sieve. In the ideal case, the mesh size of the sieve is chosen so that all of the animals are retained on the screen, while all of the sediment passes through the mesh and is discarded. In practice, the best that an ecologist can hope for is that the sieve will retain many animals and not too much sediment. Other methods (e. g., elutriation, flotation in sugar solutions) may be used to aid in removing the animals from the sediment, but the separation is almost inevitably incomplete (cf. WELCH 1976).

While sieving is certainly a reasonable approach, its efficiency obviously depends very strongly on the mesh size of the sieve used. Here lies the difficulty. Because of time constraints, and because of the objectives of their studies, benthic ecologists have usually chosen to use sieves of 0.2-mm (200-μm) to 2-mm mesh. Most freshwater animals are too small to be retained on such coarse sieves (HUMMON 1981; NALEPA & ROBERTSON 1981b; see also my general discussion below). As a result of the almost complete reliance of benthic ecologists on such sieves, we know very little about the smaller benthic animals of lakes. In fact, we have almost no information about what an entire lacustrine zoobenthic community actually looks like, in terms of species composition, density, trophic interactions, size structure, and so forth.

My approach has been to examine unsieved sediment, as well as sediment that has been washed through a fine (105-μm) sieve, to try to put together a quantitative, taxonomically detailed description of the entire metazoan benthos of a single lake, including its variation in space and time. Because of the difficulties in carrying out such an ambitious project, many of my results are flawed and incomplete. In particular, I have had to ignore the benthic Protozoa, which may be abundant on lake sediments, and certainly interact with the metazoan benthos. Nonetheless, I believe that my results do offer some new insights into the lacustrine zoobenthos.

Benthic ecologists have adopted three general size categories to describe the zoobenthos. The macrofauna includes all of the animals that are caught on coarse sieves (i. e., 200-μm to 2000-μm mesh). The meiofauna passes coarse sieves, but is retained on fine sieves (i. e., 40-μm to 200-μm mesh), and the microfauna passes even the fine sieves. These size categories are useful, but are arbitrary and do not correspond to any natural ecological or taxonomic groups.

Limnologists have not always ignored the meio- and microfauna. In fact, some of the earliest scientific surveys of the lacustrine benthos contained information on protozoans and micrometazoans as well as macrobenthic animals (e. g., FEHLMANN 1912; BIGELOW 1928; RAWSON 1930). Perhaps the outstanding example of such an early study is MONARD's (1920) detailed and insightful study of the entire zoobenthic community in the profundal sediments of the oligotrophic Lac de Neuchatel in Switzerland. Unfortunately, for reasons that are not clear to me, MONARD's work has been almost forgotten by limnologists (but see BRINKHURST 1974).

Following these initial studies, the lacustrine meio- and microfauna suffered from a long period of neglect. In North America, only MOORE (1939) and COLE (1955) carried out intensive studies on the meio- and microfauna. Neither study seems to have attracted much attention from the limnological community. In a related study, PENNAK (1940) described in detail the interstitial fauna of lake beaches in Wisconsin. In Europe, many authors published papers on selected parts of the zoobenthos, including some of the smaller forms (see references cited in "Results and Discussion" below). However, MUCKLE's (1942) work on the Bodensee in Germany seems to have been the only reasonably comprehensive study of the lacustrine meiofauna. Of these authors, all but PENNAK adopted an essentially qualitative approach.

More recently, following the lead of the marine biologists, who have conducted numerous studies on the small benthic animals (MCINTYRE 1969; FENCHEL 1978), there has been a renewed interest in the meio- and microfauna of lakes. Several European workers have conducted quantitative studies of the lacustrine meiofauna (STANCZYKOWSKA & PRZYTOCKA-JUSIAK 1968; HOLOPAINEN & PAASIVIRTA 1977; RANTA & SARVALA 1978; SARKKA 1979; SCHIEMER 1979; BABITSKY 1981; WHITESIDE & LINDEGAARD 1982). In North America, FENCHEL (1975), ODEN (1979), ANDERSON & DE HENAU (1980), HUMMON (1981), NALEPA & ROBERTSON (1981a, b), EVANS (1982), and NALEPA & QUIGLEY (1983) all have published on the freshwater meiofauna. However, most of these studies have not been detailed taxonomically, and few of them have included the protozoans or smallest metazoans (e. g., gastrotrichs).

The study area

This work was carried out during 1979–81 at Mirror Lake, a small oligotrophic lake near the Hubbard Brook Experimental Forest in central New Hampshire (Fig. 1). I have listed some of the limnological characteristics of Mirror Lake in Table 1; more information is available in a forthcoming book (LIKENS 1985).

Mirror Lake is dimictic with a long period of ice cover (Fig. 2). In many years, spring turnover is incomplete, as it was in 1981. Even though the lake is unproductive, the lower hypolimnion usually becomes anoxic twice a year (Fig. 2). Hydrogen sulfide appears near the sediment surface late in summer stratification, and sometimes late in winter stratification. This seasonal anoxia is probably of great importance to the zoobenthos of Mirror lake, since most free-living metazoans are obligate aerobes (e. g., von BRAND 1946).

The sediments of Mirror Lake are heterogeneous (Fig. 3). The shallow-water sediments are especially varied, ranging from boulders and cobbles to mud and leafy debris. Beyond approximately the 5-m depth contour, the lake bottom is covered by gyttja, a watery, organic sediment that consists largely of the fecal pellets of benthic animals. The gyttja has been

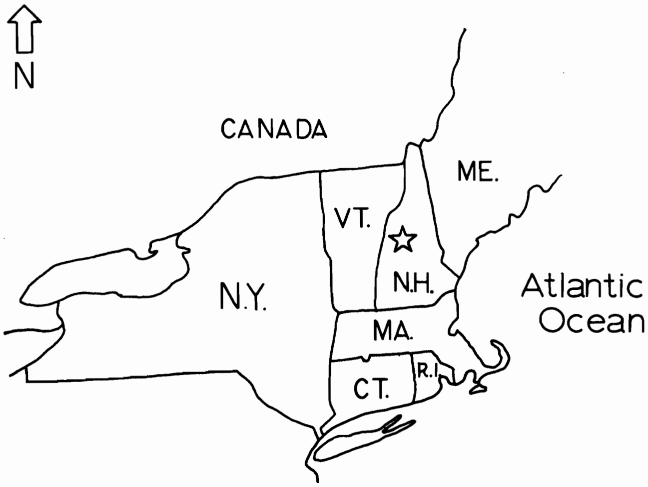


Fig. 1. Location of Mirror Lake and the Hubbard Brook Experimental Forest in central New Hampshire.

Table 1. Some limnological characteristics of Mirror Lake. Data from LIKENS (1985), unless noted otherwise.

Surface area	15 ha
Mean depth	5.75 m
Maximum depth	11 m
Mean duration of ice cover	138 d
pH	6.4[a]
Ca^{+2}	2.4[a] mg l^{-1}
Dissolved organic carbon	2.8[a] mg l^{-1}
Secchi disc	6.3[b] m
Carbon inputs	
phytoplankton	56[c] g m^{-2} yr^{-1}
macrophytes	2.5[c] g m^{-2} yr^{-1}
allochthonous	17 g m^{-2} yr^{-1}

[a] lakewide annual mean
[b] mean of 8 readings taken during the ice-free season, 1979–81
[c] gross primary productivity

deposited as a gently undulating, almost featureless, expanse. Even the gyttja is not uniform, though. As one proceeds from the margin of the gyttja towards the center of Mirror Lake, the gyttja becomes more watery and flocculant, and has a lower ash content (Fig. 4). There are some differences in sediment quality among sites along the same depth contour as well (Fig. 4). Sediments from the southwest quadrant of the gyttja are denser and have a higher ash content than sediments from other sites. Also, at any site, the density of the gyttja increases with increasing depth within the sediment (Fig. 4).

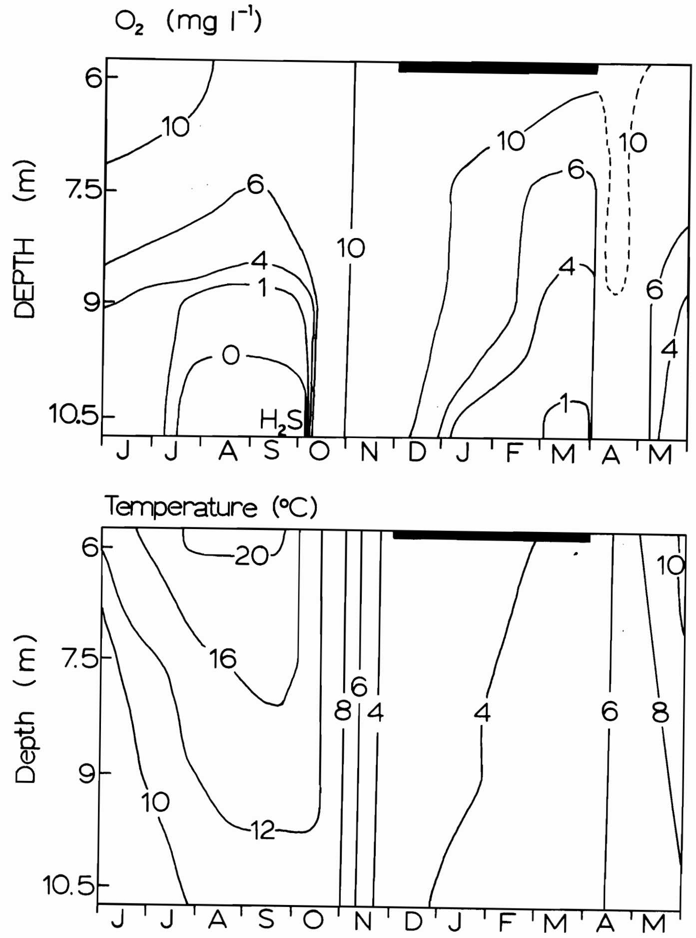


Fig. 2. Upper: Concentrations of dissolved oxygen (mg l^{-1}) at the surface of the gyttja sediments in Mirror Lake. Lower: Temperature (°C) of the surface of the gyttja sediments in Mirror Lake. The black bar shows ice cover.

Benthic macrophytes are scarce in Mirror Lake (Fig. 5; Moeller 1975). The 0- to 6-m depth zone is occupied by about 22 species of macrophytes, but none is abundant. Very few vascular plants live on the gyttja in Mirror Lake, but there is a bed of *Potamogeton berchtoldii* along the 6-m contour at my southern sampling site (Fig. 3). However, the macroalga *Nitella flexilis* is abundant between 6.5-m and 7-m (Moeller 1975), and accounts for the lower peak of macrophyte biomass shown in Fig. 5. *N. flexilis* may have had a slightly different distribution in 1979–81 than when Moeller did his study, since I frequently found the alga along the 7.5-m depth contour.

There have been no detailed studies of the benthic microalgae of Mirror Lake. The following summary is taken from my casual observations. Algae, especially pennate diatoms and desmids, are abundant on the sediments of Mirror Lake from the shoreline to the 7.5-m depth contour. I found many small pennate diatoms along the 9-m depth contour, but other

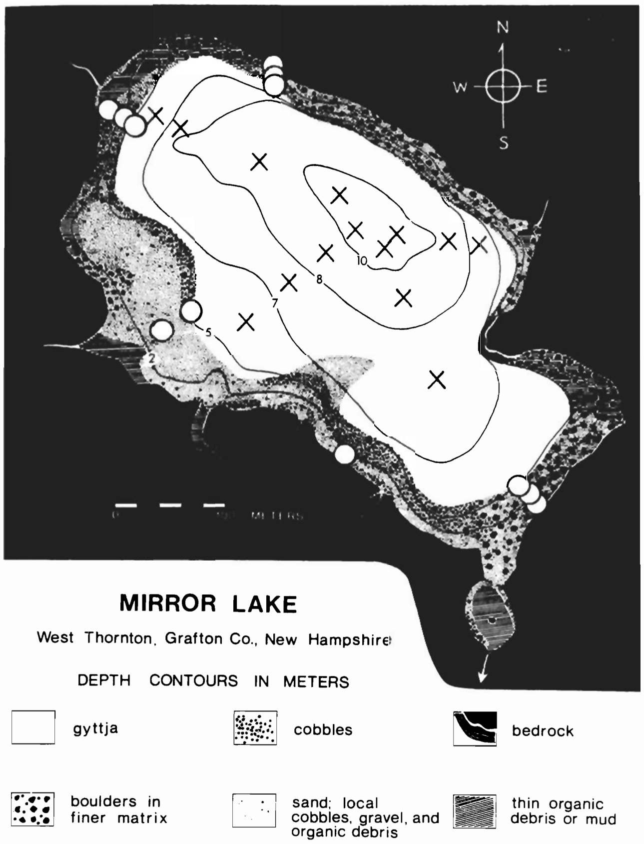


Fig. 3. Sediment and bathymetric map of Mirror Lake, after MOELLER (1978). Sampling locations for the gyttja are marked by "X", and littoral sampling stations for the transect are shown by "O". The 7.5-m and 10.5-m stations for the transect are the same as those shown for the gyttja survey.

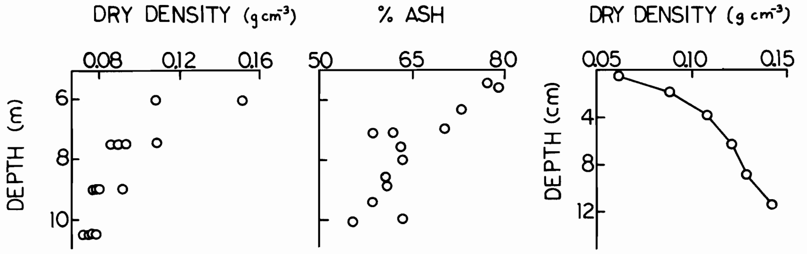


Fig. 4. Left: Dry density of the top 5 cm of gyttja sediments in Mirror Lake. Each point is the mean of three samples from a single site. There are highly significant differences (ANOVA) among sites at 6 m, 7.5 m, and 9 m. Center: Ash content of the upper 5 cm of gyttja sediments in Mirror Lake. Each point represents a single site. Data from R. E. MOELLER (pers. comm.). Right: Dry density of the gyttja sediments of Mirror Lake, as a function of depth from the sediment surface. Data are means of 12 samples each from 6 m, 7.5 m, 9 m, and 10.5 m.

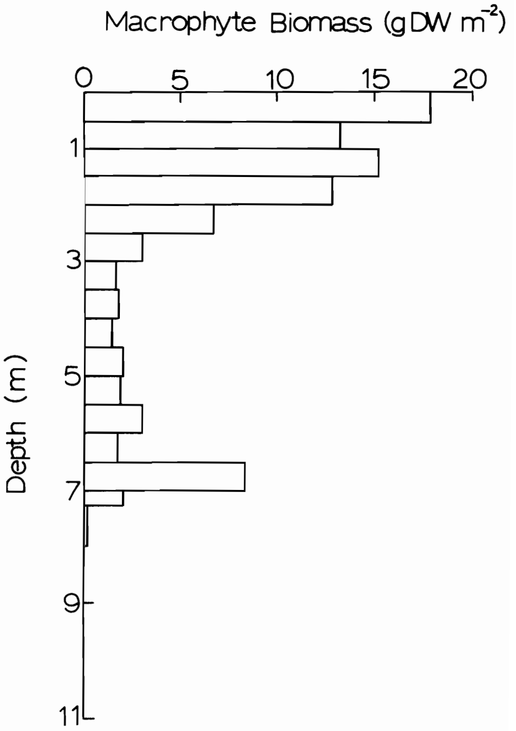


Fig. 5. Depth distribution of macrophyte biomass in Mirror Lake. Redrawn from MOELLER (1975).

algae were rare at this depth. At 10.5-m, eukaryotic algae are rare, except during turnover. However, about the time that the sediment surface becomes anoxic in July, a mat-forming *Oscillatoria* appears on the sediments at 10.5-m. By September, mats of this alga cover the sediments at 10.5-m, and have spread outward along the anoxic sediment surface to the 9-m depth contour. This alga disappears shortly after autumnal turnover in October.

Of the numerous studies that have been conducted on Mirror Lake (LIKENS 1985), only a few have been concerned with the zoobenthos. LIKENS (1972) compiled a partial list of the organisms living in Mirror Lake, including some benthic animals. Detailed studies have been made of two benthic species: the lepidopteran larva *Eoparargyractis plevie* (FIANCE & MOELLER 1977), and the large bivalve *Elliptio complanata* (STRAYER et al. 1981). GOULDEN & VOSTREYS (1985) described the paleoecology of some of the benthic cladocerans of Mirror Lake. In their studies of the vertebrates of Mirror Lake, both MASZA (1973) and BURTON (1977) included data on the benthic invertebrates that are eaten by fish and salamanders.

However, the most important previous study of the Mirror Lake zoobenthos is certainly RHODA WALTER's work on the macrozoobenthos of the lake (WALTER 1976, 1985 a, b). Since I will be referring repeatedly to this work, I will describe WALTER's approach and methods briefly. WALTER took 140 samples during 1973–74 with an Ekman grab, a multiple corer, or hand-held cores. She took samples from throughout the lake, according to a stratified random design. She took most of her samples in July or August, but did collect some material in January and March. Samples were sieved through a 250-µm mesh screen, except during the winter, when a 500-µm mesh screen was used. Because of the objectives of the study, WALTER did not identify many of the animals beyond the level of family; she did, though, present considerable quantitative information about the abundance and biomass of the benthic macrofauna. She also monitored insect emergence, and made some estimates of macrozoobenthic respiration and secondary production.

Materials and methods

I used the multiple corer of HAMILTON et al. (1970), modified as described by WALTER (1976, 1985 a) to sample the gyttja sediment. This corer collects four sediment cores simultaneously, each with an area of 15.5 cm^2 and a length of up to 20 cm, depending upon the texture of the sediment. The modified corer contains clear plexiglass tubes, rather than metal tubes, allowing the investigator to notice and discard samples that have been disturbed in the sampling process. The clear tubes also facilitate the sectioning of cores (see below).

Before I lifted the multiple corer out of the water, I corked the bottom of each tube with neoprene stoppers that fit the inside diameter of the coring tubes. In spite of this precaution, the watery gyttja sediments commonly slipped from one or two of the tubes of a set and were lost. I set aside two of the cores (if possible) as a source for dissolved oxygen samples (see below) and processed one core immediately for the faunal sample. The fourth core, if collected at all, was not used. Normally, the sediment-water interface was sharp, and the water overlying the sediments was clear. If appreciable sediment was mixed into the overlying water, I discarded the core and took a second sample. It was unusual for me to have to take more than two pulls to get an acceptable sample, but occasionally when I was sampling in a macrophyte bed, more than 10 pulls were needed to get a clean sample. It is therefore likely that samples from macrophyte beds are biased toward vegetation-free areas, since the macrophytes in a sample often mixed the sample badly.

I used a small hand pump to siphon off the water above the sediments in the core chosen for the faunal sample. This overlying water was filtered through a cup fitted with 45-µm mesh Nitex netting, and the material retained on the netting was backwashed into 5% formalin. Then, I used a wooden dowel to push the neoprene stopper and the sediments that it held to the top of the coring tube, where the sediments were extruded and sliced into sections (Table 2). The sections listed in Table 2 were chosen after analysis of 28 cores taken in 1979 suggested that most of the animals live in the top few centimeters of sediment, with few penetrating beyond 5 cm (cf. Fig. 65), but that some animals living in the deepwater sediments penetrate relatively deeply (e.g. Fig. 59). I placed each sediment section in a glass jar, covered it with filtered lake water, and put it in a dark cooler for transport to the laboratory. Usually, this entire process took place in the boat or on the ice immediately following sample collection, but on two dates in the winter, when cold air temperatures made the process impractical, I placed the intact sediment cores upright in a specially made, dark, insulated box, and took them into the laboratory, where they were processed less than an hour after they were collected.

Table 2. Sectioning scheme used to sample sediments in Mirror Lake. Tabled values are distances from the sediment surface, in cm.

Sample type	Sections used
Gyttja survey, 6 m	0–1, 1–2, 2–6
Gyttja survey, 7.5 m	0–1, 1–4, 4–8
Gyttja survey, 9 m	0–1, 1–4, 4–10
Gyttja survey, 10.5 m	0–1, 1–6, 6–12
Transect, all depths	0–1, 1–2, 2–4, 4–6, 6–8

The multiple corer functions only on soft sediments such as gyttja. For sampling the littoral sediments in Mirror Lake, I used the coring tubes from the multiple corer, but pushed them into the sediment by hand. The samples were then treated like those from the gyttja.

Once in the laboratory, I put the jars containing sediment samples into the refrigerator to await sorting. My sorting procedure was very simple. I chose a sample section for sorting, brought it up to a known volume with filtered (48-μm) lake water or tap water, mixed the sample thoroughly, and took a 1-ml subsample with a Hensen-Stempel pipette. I put this subsample into a scored Syracuse watch glass, covered it with filtered lake water, and examined it carefully at 25 power under a dissecting microscope. I then removed all of the animals that I found, and identified or preserved them. After sorting as many subsamples as time would allow, I sieved the remainder of the sample through a 105-μm mesh soil sieve, and examined it at 12 power. I examined some of the sieved samples from the deeper sections of the sediment cores under 6 power, since most of the animals that penetrate the sediments deeply are large. I usually sorted the entire sieved fraction, but time constraints sometimes demanded subsampling here as well. The sorting procedure just described is straightforward, but very time-consuming; it took me about 20–40 hours at the microscope to sort a single core. The sorting procedure is also subject to two potential problems: animals could die (or reproduce) in the refrigerator before the samples were sorted and, more seriously, the procedure might not yield all of the animals that are living in the sediments; i. e., it might not be perfectly efficient.

Because many meio- and microbenthic animals are inconspicuous, even under a dissecting microscope, they are easily overlooked. However, to get a quantitative estimate of the population densities of the micrometazoans, it is necessary to recover all of the animals from the sediments, or at least to know the proportion of the population that is being overlooked. It would be extremely tedious and time consuming to try to find all of the micrometazoans living in sediment samples, so complete extraction by visual examination is not practical. On the other hand, it is possible to estimate sorting efficiency directly; for example, by releasing a known number of animals into a sediment sample, sorting the sample routinely, and calculating the recovery rate (cf. VIGLIERCHIO & SCHMITT 1983). Unfortunately, sorting efficiency undoubtedly varies widely among taxa, and probably varies considerably among investigators or even among days for a single investigator. It would therefore take a whole battery of efficiency tests to develop useful estimates of sorting efficiencies for a speciose community like the benthic micrometazoans.

Instead, I borrowed a statistical technique from fisheries science to provide individual estimates of sorting efficiencies for various micrometazoan taxa. To see how this technique works, consider the following ideal description of sorting. Suppose I sort a sediment sample and find and remove n_1 individuals of a taxon. Since my sorting procedure is imperfect, n_1 is actually only some proportion of p of the true population N present in the sediment sample. If I then sort the same sample again, I might expect to find and remove the same proportion p of the $(N-n_1) = (N-Np)$ individuals that remain. Each time that I repeat this procedure, I will find and remove the same proportion p of the animals remaining in the counting dish, so my count of the animals found on the i^{th} trial will be:

$$n_i = N(l-p)^{i-l}p$$

These counts can then be used to solve for the sorting efficiency p and the actual number of animals in the sample N.

In practice, of course, an element of chance is involved, so the actual counts do not follow the ideal series described above, and a statistical procedure must be used to solve for p and N. I used ZIPPIN's (1958) method, but WHITE et al. (1982) have recently described a better, maximum likelihood estimator of p and N.

There are several important assumptions associated with this procedure, which is known as the "removal method" of population estimation in fisheries biology (see WHITE et al. 1982: chapter 4). For my application of the method, the two important assumptions are: (i) each of the animals within a taxon is assumed to have an equal probability of being found, and (ii) the effort expended in sorting is the same in each trial. Both of these assumptions are violated to some extent in my work, probably resulting in a slight underestimation of N.

I collected my data on sorting efficiencies as follows. Every sample section that I collected was sorted 2–4 times. I recorded the number of animals found and removed each trial by the lowest taxonomic level possible. For example, I could distinguish the families of Cladocera at 25 power, so I recorded data separately for each family, but all nematodes were lumped together.

Ideally, these data could be used to provide separate estimates of sorting efficiencies for each taxon in each sample, but the estimates of N and p are most reliable when Σn_i is at least 50 or so (BOHLIN 1983). Since I collected far fewer than 50 animals of each taxon in most samples, I pooled the data from many samples (cf. BOHLIN 1983) to calculate a common estimate of sorting efficiency for periods ranging in length from a few months to the entire duration of the study. I then applied these estimates of p to my data to calculate the actual population densities of micrometazoans in my samples. The sorting efficiencies that I used are listed in my thesis (STRAYER 1984). It is important to note that p is relatively low (<0.5) for many of the smaller benthic animals. If I had not corrected for sorting efficiencies, my population estimates would have been far too low for these animals (cf. WELCH 1976).

Because it is flexible and relatively easy to apply, the removal method should be useful in many benthic studies, including those of the macrobenthos. The excellent guide of WHITE et al. (1982) should be consulted for details.

As a check on mortality (or reproduction) of micrometazoans during the period of sample storage in the refrigerator, I subsampled selected sediment samples both before and after storage. The results of this check, which involved 48 sections of sediment, showed no evidence of statistically significant changes in the populations of any micrometazoan taxon (STRAYER 1984b), suggesting that storage of samples for periods of up to a few days had no effect on my results.

Environmental measurements

I collected data on the temperature of the surface sediments, the concentration of dissolved oxygen in the water immediately overlying the sediments, and the composition of the surface sediments at all of my stations on the gyttja. I measured the temperature of the surface sediments every time that I collected faunal samples by lowering a Whitney underwater thermometer to the sediment surface. I used the Winkler method (WETZEL & LIKENS 1979) to measure dissolved oxygen. I collected samples for the analysis of dissolved oxygen by using a small hand pump to flush water from just above the sediments in my coring tubes into a 30-ml glass-stoppered bottle. The oxygen samples were usually fixed within 10 to 30 minutes of sample collection, returned to the laboratory, and titrated within 24 hours of collection. In October, 1981, I used the multiple corer to collect triplicate sediment samples from each of my stations on the gyttja (see below). I sectioned these samples at 1.27-cm intervals, and dried the sections to constant weight at 60°C to determine the dry weight density of the Mirror Lake sediments.

In 1979–80, I took 28 samples from water depths of 5.5 m, 7.5 m, and 10.5 m. These sites were chosen to include the full range of animal communities that live on the gyttja, since 5.5 m is near the shoreward edge of this sediment (Fig. 3) and 10.5 m is near the deepest point in the lake. These preliminary samples showed that there were great changes in community composition between 7.5 m and 10.5 m. Also, the sediments at 5.5 m are sometimes too compact for effective penetration of the multiple corer. To correct these problems, I established sampling stations water depths of 6 m, 7.5 m, 9 m, and 10.5 m for the main part of my study. I will refer to my year-long study of these stations as the "gyttja" study.

To document within-depth variation in faunal composition, I established four stations at 7.5 m and 9 m, and two stations at 6 m (I was limited by the amount of soft sediment available at the latter depth). I sampled haphazardly on the 10.5-m contour. During each sampling period, which lasted about two months, I took four samples from each depth contour, visiting each of the stations shown in Fig. 3. I was able to complete five such sampling periods between 5 June 1980 and 4 June 1981, comprising a total of 80 samples.

Because of sampling difficulties associated with the early freezing of Mirror Lake in November, 1980, I was unable to complete the "autumn" sampling period until early January, 1981 (Fig. 6). I have included these late samples, actually taken in December and January, with the autumn period to preserve the symmetry of the statistical design. Because seasonal change in the fauna is relatively slight (see general discussion), I doubt that any great error is introduced into the isopleth diagrams by this procedure.

Most of the results from this survey of the gyttja are shown in the form of isopleth diagrams. To construct these diagrams, I calculated the arithmetic mean of a parameter in the four samples taken from one depth during a sampling period. I then used the 20 mean values as a basis for constructing the isopleths, which were drawn by hand. The purpose of this procedure, which is illustrated more fully in Fig. 6, was to reduce the "noise" due to among-sample variation within each depth.

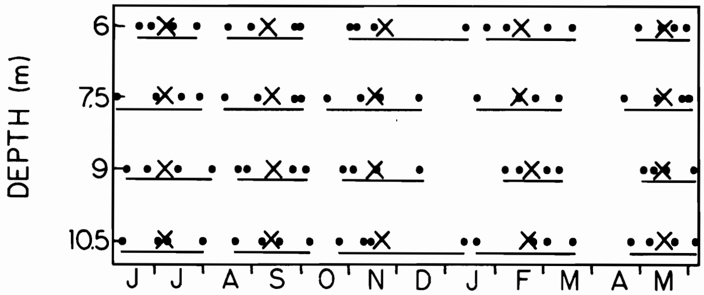


Fig. 6. Treatment of data for construction of the isopleths. The small circles show the actual dates and depths when samples were collected. Four such samples were averaged within each sampling period (indicated by underlining) to produce a single mean upon which the isopleths were based. The locations of the means in time and space are shown by "X".

In the summer of 1981, I established four stations on each of five depth contours: 1-m, 3-m, 5-m, 7.5 m, and 10.5-m (Fig. 3). I sampled from each water depth three times between 23 June and 27 October. During each of these sampling visits, I collected four cores, one from each of the stations shown in Fig. 3. The four cores were combined and sorted. I will refer to these samples as the transect study. The results from the transect study are usually expressed as the mean value of a parameter at a given water depth. Species richness is calculated as the total number of species collected during the three sampling dates.

To calculate lakewide mean values of various parameters, I weighted my data by the proportion of the lake bottom represented by each sampling station, using the bathymetric data of LIKENS (1985). Since my samples were not spaced evenly throughout the year (Fig. 6), I included analogous seasonal weighting factors when I calculated annual means.

Taxonomy

One of the goals of this study was to identify all of the animals collected to species, or at least to genus. This task proved to be very difficult, especially since many of the benthic micrometazoans are poorly known taxonomically in North America. My main taxonomic sources, listed by taxonomic group, were: Coelenterata: PENNAK (1978); Turbellaria: NUTTYCOMBE & WATERS (1938), FERGUSON (1939–40), JONES (1959), LUTHER (1960, 1962, 1963), KARLING (1963), and PENNAK (1978); Nematoda: GOODEY (1963), and FERRIS et al. (1973); Gastrotricha: REMANE (1936), BRUNSON (1950, 1959), VOIGT (1960), and PENNAK (1978); Rotatoria: BARTOS (1951), EDMONDSON (1959), PENNAK (1978), and KOSTE (1978); Oligochaeta: SPERBER (1948, 1950), BRINKHURST & JAMIESON (1971), HILTUNEN & KLEMM (1980), and STIMPSON et al. (1982); Tardigrada: SCHUSTER et al. (1980); Cladocera: BROOKS (1959), FREY (1959, 1962, 1965), MEGARD (1967), SMIRNOV (1974, 1976), PENNAK (1978), and WILLIAMS (1978); Copepoda: CHAPPUIS (1957), WILSON & YEATMAN (1959), YEATMAN (1959), DUSSART (1967, 1969), PENNAK (1978), and SMITH & FERNANDO (1978); Ostracoda: TRESSLER (1959), DELORME (1970–71), and PENNAK (1978); Chironomidae: COFFMAN (1978), ROBACK (1978, 1980, 1981), SIMPSON & BODE (1980), HILSENHOFF (1981), and WIEDERHOLM (1983); Chaoboridae: SAETHER (1972); Acari: NEWELL (1959), PRASAD & COOK (1972), and PENNAK (1978).

I would be much less confident in the accuracy of my identifications if I had not had the help of the following experts, who verified or corrected the identifications of selected speciments from Mirror Lake: Dr. ILSE BARTSCH, who provided species names for the halacarid mites, Dr. RALPH BRINKHURST, who examined some of the tubificid oligochaetes; Dr. L. D. DELORME, who examined the ostracods; Dr. DAVID FREY, who verified or identified all of the chydorid cladocerans; Dr. WALTER HARMAN, who verified all of the naidid oligochaetes; Dr. JERZY KOLASA, who examined some of the turbellarians and the nemertine; Dr. DIANE NELSON, who identified all of the tardigrades; Dr. MARCEL REEVES, who identified the oribatid mites; Dr. KARL SIMPSON, who verified or corrected my determinations of chironomid larvae; Dr. BRUCE SMITH, who verified all of the Parasitengona; and Drs. D. OLIVER, B. BILYJ, and S. S. ROBACK, who examined some chironomid larvae. I am very grateful to all of these people for their generosity. Nonetheless, I made all of the routine identifications of all taxa, and must be held responsible for any errors.

Because of time constraints, I was able to identify only the specimens collected on the transect study for the Nematoda, Ostracoda, Copepoda, and Chironomidae.

Biomass

I used a mixture of methods to estimate dry weights of the benthic micrometazoans of Mirror Lake. If possible, I used published data on dry weights obtained by direct measurement, or better yet, published regressions of dry weight on body length, for species that are found in Mirror Lake. These estimates were then scaled to the measured dimensions of specimens collected from Mirror Lake. If such data were not available, I estimated the average biovolume of each species in Mirror Lake by using measured dimensions of animals from the lake and approximating the shape of each animal by a series of geometric forms. Unless noted otherwise, I assumed a specific gravity of 1.05 g cm^{-3} and a dry weight content of 15% (cf. Kajak et al. 1980). In the few cases for which I had neither published dry weights nor measurements of Mirror Lake specimens, I simply made an educated guess of the dry weight of the animal, based on the dry weights of animals of roughly comparable size. The estimated dry weight of each of the major species of benthic micrometazoans in Mirror Lake is listed in Table 5 of Strayer (1984).

Metabolic parameters

Neither abundance nor biomass is an entirely satisfactory way to express the ecological "importance" of a population, since both are static quantities and do not include any measure of the turnover rate of the population. However, almost nothing is known about the metabolic rates of micrometazoans in nature, and the direct in situ measurement of these quantities in a benthic community would be an ambitious project in itself. Although accurate estimates of the metabolism of the meio- and microfauna cannot be made without considerable further research, it is possible to make use of some recently published regressions of metabolic rate on body size to make some very tentative estimates of the importance of the benthic micrometazoans in the energetics of the Mirror Lake ecosystem. I made the following calculations to suggest the general range in which meio- and microbenthic metabolism in natural communities might fall. Although illuminating, they must be interpreted cautiously, as they are very approximate.

Respiration

Banse (1982) analyzed the respiration rates of various small invertebrates as a function of body size. I used his regression for nematodes (from his table 1) to estimate the respiration rates of all animals in Mirror Lake that have a body size of less than 50 µg DW. I chose this regression because it falls in the middle of the range of observations for small metazoans such as copepods and rotifers, as well as nematodes, and thus seemed of fairly general application. Since Banse's (1982) regression is based on data at 20 °C, I adjusted the results by using a Q_{10} of 1.7 (Robinson et al. 1983) and temperature data from Mirror Lake. I used density data from my transect, and assumed a respiratory quotient of 0.83. I used Walter's (1985 b) estimates of respiration for the benthic macrofauna.

Secondary production

Banse & Mosher (1980) compiled annual P/B (production/mean biomass) ratios for animal populations in nature and regressed them against adult body size of each species. I used equation 3 in their table 2 to estimate P/B ratios and production for all of the benthic animals in Mirror Lake except the ostracods, amphipods, insects, and mollusks. I used values of standing stock biomass from the transect study, and assumed an energy content of 5000 cal/gDW (cf. Cummins & Wuycheck 1971). Since Banse & Mosher (1980) found no evidence of temperature dependence in P/B ratios, it was not necessary to adjust for the water temperatures in Mirror Lake. However, on the basis of the few available data, Banse & Mosher (1980) suggested that the P/B ratios for the meiofauna were considerably lower than those predicted by their regressions. Accordingly, I have followed their suggestion and divided the predicted P/B ratios by four. For the amphipods, insects, and sphaeriid clams, I used the P/B ratios in Water's (1977) table 4. I used Strayer et al.'s (1981) estimate of production of the bivalve *Elliptio complanata.* Methods for estimating production of the ostracods are described in the "Results and discussion" section.

Comparisons with other studies

I have compared my results with those of other workers. In most cases, I simply used the figures that were published by these workers, but in two cases, I adjusted their results to make them more directly comparable with my results. To estimate lakewide mean densities of the benthic meiofauna of the Finnish lake Paavarvi, I derived approximate bathymetric weighting factors from the map published by PAASIVIRTA (1975) and applied these factors to the data in tables 2 and 4 of HOLOPAINEN & PAASIVIRTA (1977).

NALEPA & QUIGLEY (1980, 1983) took samples during April–November in the nearshore zone ($z = 11-23$ m) of Lake Michigan. For comparison, I took the simple arithmetic mean of the values reported in tables 4 and 5 of their 1983 paper.

Results and discussion

The following long section contains most of the results of my study. I have adopted a phylogenetic organization for this section, each major taxonomic unit (e.g., Cladocera) constituting a more or less independent subsection. Within each of these subsections, the species are discussed in alphabetical order. Each subsection concludes with a brief discussion of the ecology of the lacustrine members of the taxonomic group under consideration.

Porifera (sponges)

I collected a colony of the common species *Spongilla lacustris* at 6 m. This species is abundant in the littoral zone of Mirror Lake, where it grows both on objects such as macrophytes and wood debris and on gently sloping bare sand bottoms. Three other species of sponges have been taken in the lake, although they were not found in my core samples. *Eunapius fragilis* is abundant in very shallow water (<1 m), where it grows on rocks, macrophytes, and wood debris, and I found a single colony of *Anheteromeyenia argyrosperma* growing on a twig. WALTER (1985a) reported *Ephydatia mülleri* as well.

Coelenterata

One of the most surprising finds of my survey was the occurrence of large numbers of hydrids in samples taken from the gyttja in the fall and spring (Fig. 7). More than one-third of the samples taken around the time of overturn contained hydrids, sometimes in unexpectedly high concentrations (>50 dm^{-2}). During the same time, lines and floats in the pelagic zone were colonized by large numbers of hydrids. The sudden appearance of large numbers of these typically littoral animals in deep-water samples can be explained only by postulating a large-scale migration from the littoral zone.

REISA (1973) has described how hydrids may leave their substrata and become planktonic when faced with unfavorable environmental conditions, such as starvation. REISA (1973) also reviewed reports of the sudden appearance of hydrids

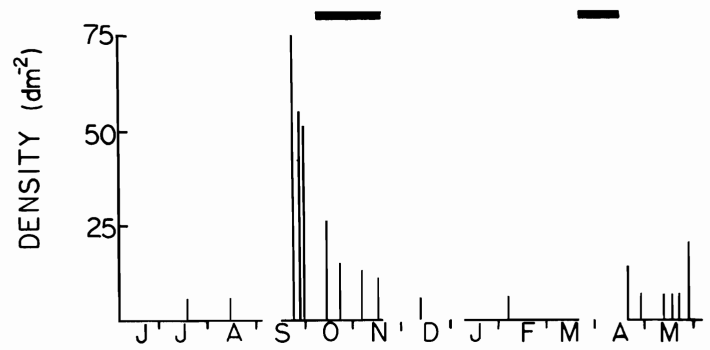


Fig. 7. Density of Hydridae from all stations on the gyttja in 1980–81. Samples lacking hydrids are not shown, but samples were taken twice a week, on average, except where the abcissa shows gaps. Black bars indicate turnover.

in lakes and rivers, and concluded that such planktonic behavior is a common and important means of dispersal in natural populations. One case was described in detail by WELCH & LOOMIS (1924), who found that *Hydra oligactis* disappeared from littoral vegetation in Douglas Lake, Michigan, after water temperatures rose to 21 °C in July. Presumably, changing water temperatures or food supplies triggers the migration of hydrids in Mirror Lake.

During thermal stratification, hydrids were found only occasionally on the gyttja. They are fairly abundant on the littoral sediment (Fig. 8), and are especially abundant on littoral vegetation. A single individual of *Chlorohydra viridissima* was collected in benthic samples; all other specimens were *Hydra americana*, according to PENNAK's (1978) key.

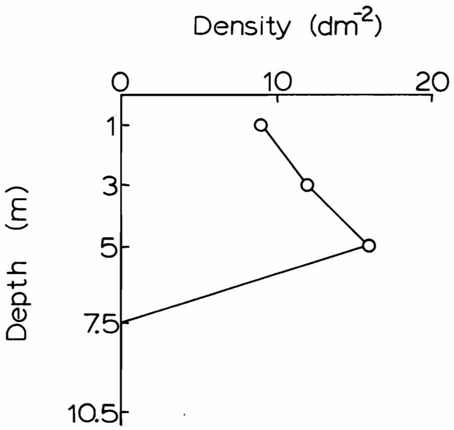


Fig. 8. Density of Hydridae in Mirror Lake, from transect data.

Turbellaria (flatworms)

Turbellarians are well represented in the freshwater fauna. These animals swim or creep along sediments or vegetation, where they feed on small animals, or less commonly, algae and bacteria. Among the predatory species, many mechanisms of prey capture have evolved (see KEPNER et al. 1938; HYMAN 1949; and CASE & WASHINO 1979 for some fascinating examples). Many species reproduce asexually by budding, but most turbellarians are sexually reproducing hermaphrodites.

The large triclad turbellarians ("planarians") are well known to most freshwater biologists, and have received much taxonomic and ecological study (see the works of KENK 1972, 1974, and REYNOLDSON 1983, for an introduction). However, the triclads constitute only a small fraction of the freshwater turbellarians, and are quantitatively outnumbered in most lakes by a diverse assemblage of small flatworms. These "microturbellaria" (a term without taxonomic standing) have received much attention from biologists in Europe (e. g., LUTHER 1955, 1960, 1962, 1963; RIXEN 1961, 1968; KARLING 1963, 1980; BAUCHNESS 1969, 1971; YOUNG 1970, 1973; KOLASA 1977, 1979; SCHWANK 1981–82; HEITKAMP 1982). However, except for the extensive work on taxonomy and morphology by KEPNER and his colleagues in the eastern United States (e. g., NUTTYCOMBE & WATERS 1938; FERGUSON 1939–40, 1954; RUEBUSH 1941), the microturbellarians have been largely neglected in North America.

Macrostomum sp.

This species was found regularly, but in small numbers (ca. 10 dm^{-2}) at the 1-m to 6-m stations (Fig. 9). I found sexually mature specimens in January, March through May, and August. Diatoms, desmids, shelled amoebae, and oligochaetes were seen in *Macrostomum* guts.

The penis stylet of this species (Fig. 12) does not match any of the species discussed by FERGUSON (1939–40) or LUTHER (1960). Animals from Mirror Lake are 0.8- to 1.4-mm long when mature, and have black eyes. Species of *Macrostomum* are often found in the lake benthos (e.g., MOORE 1939; RIXEN 1961; YOUNG 1973; KOLASA 1977, 1979).

Microstomum lineare

M. lineare is widespread on the oxic sediments of Mirror Lake, but is abundant only during the cooler months of the year (Fig. 9). It reaches its maximum density in April–May, and is entirely absent during August through October. Most of my specimens contained nematocysts, which are appropriated from the hydrids that *M. lineare* eats, and then used by *M. lineare* to sting and capture prey (KEPNER et al. 1938; HYMAN 1949). Both individuals with and without pigment spots were collected.

This species, which preys on various small animals from rotifers to insect larvae (HEITKAMP 1982), is widely distributed throughout the world in diverse habitats (LUTHER 1960; YOUNG 1970; BAUCHNESS 1971). It often is abundant in lakes (RIXEN 1961, 1968; KOLASA 1977, 1979), and often is found throughout the year (e.g. BAUCHNESS 1971; YOUNG 1973; see also HEITKAMP 1982).

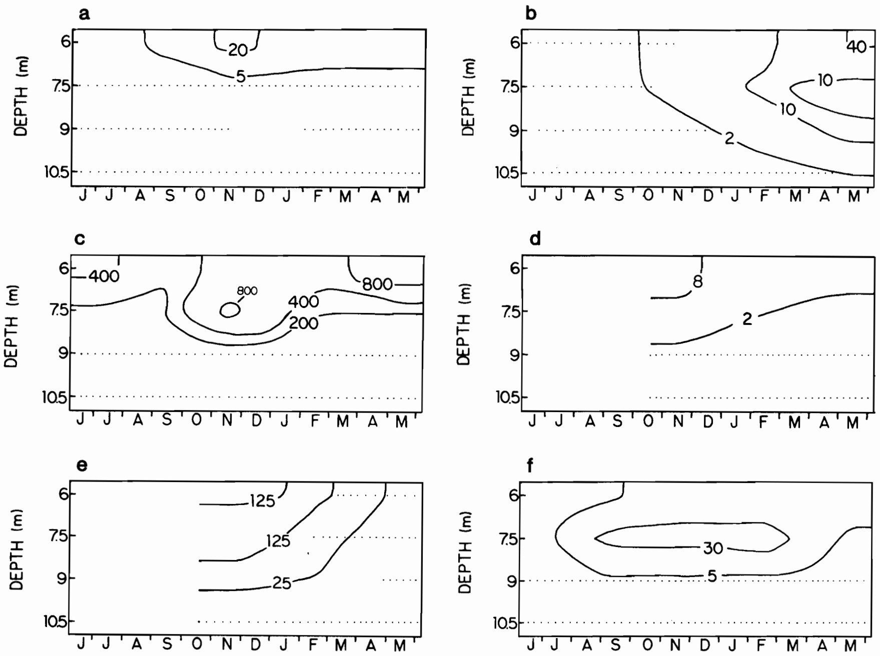


Fig. 9. Abundance (dm^{-2}) of flatworms in Mirror Lake. (a) *Macrostomum* sp., (b) *Microstomum lineare,* (c) *Rhynchoscolex simplex,* (d) *Stenostomum leucops,* (e) *Stenostomum unicolor,* (f) Dalyelloidea gen. sp. Dotted lines show extended periods when the species were absent from the indicated stations.

Rhynchoscolex simplex

This unusual worm is easily the most abundant flatworm in Mirror Lake, constituting 84% and 52% of flatworm numbers and biomass, respectively. In fact, it is one of the most abundant benthic animals in the lake. I never found this species at 9 m or 10.5 m, but it is abundant throughout the year elsewhere (Figs. 9, 11), and it occurred in 46 of the 52 samples taken from 1 m to 7.5 m. Unlike the other flatworms, *R. simplex* frequently is found below the top centimeter of sediment (Fig. 10). It is of interest to note that other workers have reported this species living in interstitial waters (Rixen 1961; Schwank 1981), and that its reported prey, oligochaetes (Luther 1960), also burrow into the sediments of Mirror Lake (cf. Fig. 38). I never found any recognizable items in the gut contents of these animals, nor did I see any sexually mature animals.

I was surprised to find this worm to be so abundant in Mirror Lake. *R. simplex* has been reported from many parts of the world: Europe, North America, South America, and Japan (Schwank 1981), but is almost always rare. It also has a reputation for frequenting odd habitats: springs, interstitial waters, and brown-water streams, for example, although it has been reported from ordinary lake sediments (Ferguson et al. 1939; Hazen 1953; Luther 1960; Rixen 1961, 1968; Kolasa 1977). Only further studies will show whether *R. simplex* is a common member of the lacustrine benthos or whether its abundance in Mirror Lake is truly exceptional. It is worth noting, though, that the techniques commonly used for collecting freshwater flatworms are selective for active and conspicuous species, so the secretive *R. simplex* may simply have been overlooked (cf. Luther 1960).

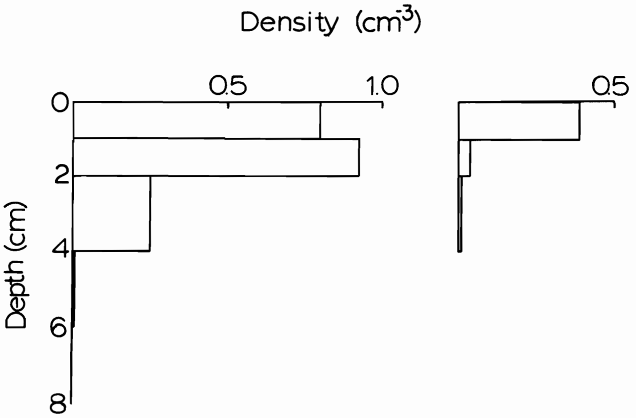


Fig. 10. Vertical distribution within the sediments of Mirror Lake of *Rhynchoscolex simplex* (left) and all other flatworms (right), as a function of depth from the sediment surface. Data are lakewide means from the transect.

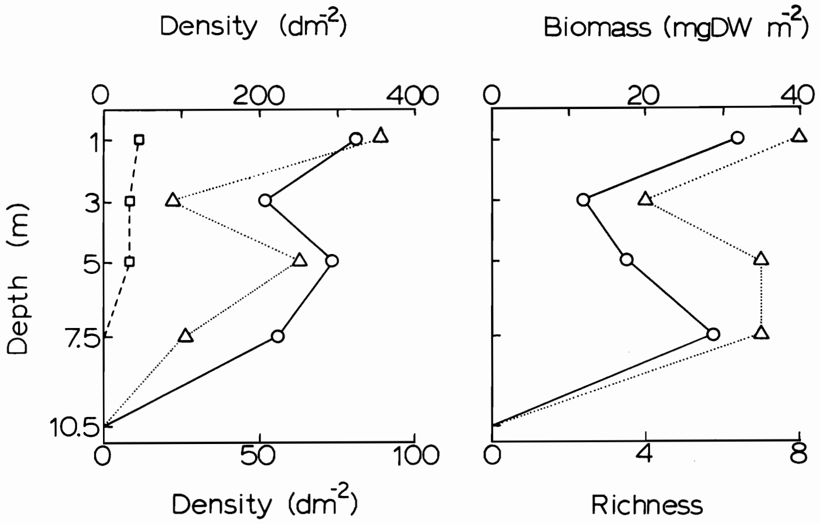


Fig. 11. Left: Density of flatworms in Mirror Lake: *R. simplex* (○, upper scale), *Macrostomum* sp. (□, lower scale), and all other species (△, lower scale). Right: Biomass (○) and species richness (△) of flatworms in Mirror Lake. All data from transect.

Stenostomum leucops s. l.

This species is present throughout the year at the 1-m to 7.5-m stations, but is never abundant (Fig. 9). *S. leucops*, which has been called *S. tenuicauda* by most American workers (Luther 1960), is one of the most abundant and widely distributed flatworms in the world. Heitkamp (1982) summarized the ecological distribution of this species: it is very eurytopic. Its diet includes various algae, protozoans, and micrometazoans (Heitkamp 1982). *S. leucops* as presently defined is probably a complex of closely related species (see Heitkamp 1982, for a discussion).

Stenostomum unicolor s.l.

The second most abundant flatworm in Mirror Lake, this species was commonly found at the 6-m and 7.5-m stations (Fig. 9). When the surface sediments at 9-m and 10.5-m were well oxygenated, a few specimens of *S. unicolor* were found there. The species has a marked seasonal minimum in March through June, and is entirely absent in April and May. Except for a few diatom frustules, the gut contents of this species were unrecognizable.

S. unicolor is widespread in the Old World, and has been found under many different environmental conditions (Heitkamp 1982). Although *S. unicolor* has not been reported previously from North America, *S. virginianum*, which Marcus (1945) and Schwank (1981) regarded as a synonym of *S. unicolor*, has been found at many sites in eastern North America (Nuttycombe & Waters 1938; Ferguson et al. 1939). *S. unicolor* apparently feeds on bacteria, algae, and protozoans (Luther 1960; Schwank 1981); *S. virginianum* has been reported to eat protozoans and small metazoans (Nuttycombe & Waters 1938). As Heitkamp (1982) emphasized, it is likely that "*S. unicolor*" is actually a complex of species.

Dalyelloidea gen. sp.

Scattered individuals of this tiny neorhabdocoel were found throughout the year at the 5-m, 6-m, and 7.5-m stations (Fig. 9). Sexually mature animals were taken in January through May, but I found too few animals at other seasons to determine whether sexual activity is truly seasonal.

As far as I am able to tell, this species does not match any of the species described by Luther (1955, 1962) or Jones (1959) and, in fact, does not seem to belong to any known genus. It may belong to the Provorticidae. Individuals of this species are unfortunately very difficult to narcotize and fix, so I can offer only the following preliminary description of its morphology, taken from living specimens.

The mature animal is 0.6- to 0.7-mm long, grey-green and opaque, and sometimes contains zoochlorellae. The body is rounded at both ends. Two black eyes are present

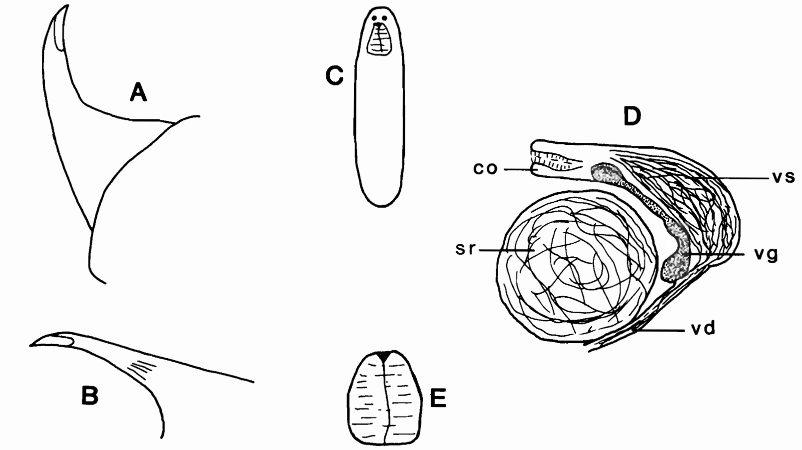


Fig. 12. Morphology of some flatworms from Mirror Lake. A, B: Penis stylets of *Macrostomum* sp. Camera lucida. C: Dalyelloidea gen. sp., Habitus. D: Dalyelloidea gen. sp., pharynx. E: Dalyelloidea gen. sp., male reproductive tract. co = copulatory organ, sr = seminal recepticle, vd = vas deferens, vg = vesicula granulorum, vs = vesicula seminalis. Freehand, from living animals.

(Fig. 12). The pharynx is anterior, doliiform, and 100-μm long (Fig. 12). The testes lie in the posterior half of the body. The seminal receptable is subcircular in dorsal view, and 100-μm in diameter. The vas deferens, vesicular granulorum, and vesicula seminalis are shown in Fig. 12. The muscular copulatory organ is 35- to 40-μm long and without a cuticular penis sheath (Fig. 12).

Other species

Seventeen additional species of flatworms were found in Mirror Lake (Table 3), but all are too scarce for me to describe their ecology in the lake. Brief descriptions and illustrations of some of the species are given by STRAYER (1984).

Table 3. List of rare flatworms from Mirror Lake.

Castrada sp.	*Prorhynchus stagnalis*
Gyratrix hermaphroditus	*Rhynchomesostoma* sp.
Mesostoma sp.	*Stenostomum* sp. 3
Microdalyellia sp.	*Stenostomum* sp. 4
Myostenostomum cf. *tauricum*	*Strongylostoma* sp.
Opisthocystis goetti	Acoela indet.
Otomesostoma auditivum	Kalyptorhyncha indet.
Phagocata sp.	Typhloplanida indet.
Prorhynchella minuta	

Prorhynchella minuta was described from ponds in Connecticut (RUEBUSH 1939), and has not been reported since. The four animals that I found compare well with RUEBUSH's description in size and general appearance, and show the characteristic "rüssel" organ and lateral ciliated pits that distinguish this species. *Stongylostoma* sp. (called "*Mesostoma* sp." by STRAYER 1985a), although represented by only a few collections from the sediments, was found in fair numbers in plankton tows taken from July to October, 1981. The undetermined species of kalyptorhynch was taken in a preliminary sample from a sand beach and, unfortunately, was not observed in detail or rediscovered. It belongs to the Eukalyptorhyncha and has its pharynx well behind the midbody. It is either new to North America or an entirely new species.

Perhaps the most interesting find was the discovery of an acoel in Mirror Lake. Only a single example was found. I do not have detailed drawings or a good preserved specimen, but according to Dr. JERZY KOLASA, who identified the animal, it is not either of the freshwater species known from Europe. Until the 1960's, all acoels were thought to be marine. Since that time, only two species have been found in freshwater, both from Europe (AX & DORJES 1966; FAUBEL & KOLASA 1978). The discovery of a presumed third species, the first freshwater acoel found outside of Europe, is of great zoogeographic interest.

Discussion

I found 23 species of flatworms in Mirror Lake, but more species are undoubtedly present. The fauna probably contains 30 to 50 species, a value comparable with other lakes (Table 4). Most of the species living in Mirror Lake

Table 4. Abundance (m^{-2}), biomass ($mg\ m^{-2}$), and species richness of turbellarians in some well studied lakes, in comparison with Mirror Lake.

Lake	MESH (µm)	Abundance	Biomass	Richness	Notes	Source
Mirror	–	27,000	24[b]	23	lakewide mean, July–Oct.	this study
Ponds, Germany	80	9,500	–	11	mean of 17 ponds	Heitkamp 1982
Paajarvi, Finland	100	3,100	10[c]	–	annual lakewide mean; oligotrophic	Holopainen & Paasivirta 1977
Michigan, USA	45	800	3[b]	–	mean, Apr.–Nov., 11–23 m	Nalepa & Quigley 1983
Zbechy, Poland	a	–	–	57	year-round study, eutrophic lake	Kolasa 1979
Ohrid, Yugoslavia	a	–	–	49		An der Lan 1961
Harsz, Poland	a	–	–	40	year-round study, mesotrophic lake	Chodorowski 1959
Neuchatel, Switzerland	a	–	–	36	large oligotrophic lake	Monard 1920
Konin lakes, Poland	a	–	–	29	mean for 5 productive lakes	Kolasa 1977
Bodensee, Germany	a	–	–	27	year-round study	Rixen 1968
Mountain, USA	a	–	–	19		Ferguson et al. 1939
Six softwater lakes, Britain	a	–	–	10[d]	mean value, littoral zone only	Young 1973
Six hardwater lakes, Britain	a	–	–	10[d]	mean value, littoral zone only	Young 1973

[a] not relevant
[b] dry weight
[c] ash-free dry weight
[d] excluding triclads

are eurytopic, widely distributed species (cf. Kolasa 1979), but at least two or three are new to science. The fauna is strongly dominated by a single species, *Rhynchoscolex simplex,* which constitutes more than half of flatworm numbers and biomass. Most flatworm species are rare in Mirror Lake; in fact, 12 of the 23 species that I found were represented by only one or two individuals.

Flatworms are abundant everywhere except on the deepwater sediments in Mirror Lake (Figs. 9, 11, 13). Most flatworms are obligate aerobes, although Schwank (1981) found *Rhynchoscolex simplex* in anaerobic sites, and Pennak (1978) stated that *Pseudophaenocora* lives "in the presence of only a trace of oxygen". Hence the absence of flatworms from the deep water in Mirror Lake is very likely due to their requirement for ample oxygen; I never found flatworms in any sample that had less then 3 mg l^{-1} of dissolved oxygen. In oligotrophic lakes, where hypolimnetic dissolved oxygen is plentiful, flatworms live at much greater depths; to 65 m in Lake Paajarvi, Finland (Holopainen & Paasivirta 1977), and to 144 m in the Lac de Neuchatel, Switzerland (Monard 1920).

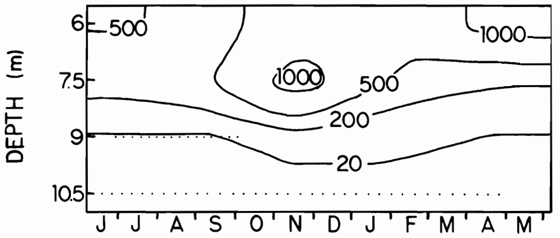


Fig. 13. Density (dm^{-2}) of all flatworms in Mirror Lake. Dotted lines show extended periods when flatworms were absent from the indicated stations.

Most of the common flatworms are present throughout the year in Mirror Lake, but *Microstomum lineare* and *Stenostomum unicolor* are of distinctly seasonal occurrence (Fig. 9). Previous authors have found many species of flatworms to be seasonal; information on the phenology of various species is available in the papers of Rixen (1961), Young (1970, 1973), Bauchness (1971), Kolasa (1979), and Heitkamp (1982). Several authors have noted that the species richness of turbellarian communities is lowest during the winter (see fig. 44 and table 9 of Heitkamp 1982, for a summary). Kolasa (1979) found an analogous winter minimum in flatworm density in Lake Zbechy, Poland. However, there is no evidence of winter minima in species richness and density in Mirror Lake (Strayer 1984); both parameters are more or less constant throughout the year.

Flatworms have a mean density and biomass of 41,000 m^{-2} and 21 mg dry weight m^{-2} on the gyttja and 27,000 m^{-2} and 24 mg dry weight m^{-2} lakewide. The few available comparable data are shown in Table 4. In all, flatworms constitute 2% and 1% of benthic metazoan numbers and biomass respectively, in Mirror

Lake. My preliminary estimates suggest that flatworms are responsible for about 2–3% of zoobenthic metabolism (Table 35). They are, therefore, not one of the major groups of benthic animals in the lake, and are probably not of great importance in lake metabolism and biogeochemistry.

Rhynchoscolex simplex is abundant enough that it may be an important predator of the oligochaetes and chironomids in Mirror Lake. However, since nothing is known of the feeding rates and prey selectivity of this animal, it is impossible to assign it a definite role in community dynamics. Most of the other flatworm species are probably too rare to exert any major influence on community composition.

Nemertea

I collected a single individual of *Prostoma* sp. from a water depth of 6 m during May 1981. According to PENNAK (1978), *P. rubrum* is the only freshwater nemertean known from North America. Nemerteans are found regularly in the shallow waters of lakes and ponds (KOLASA 1977; PENNAK 1978).

Nematoda (roundworms)

The benthic nematodes form a large and diversified group that has received little attention from limnologists. Because the group is so diverse, it is difficult to generalize about nematode biology. Many feeding types are represented in the freshwater nematodes: various species feed on bacteria and detritus, algae, macrophytes, protozoans, small metazoans, and perhaps dissolved organic matter (LOPEZ et al. 1979). Many species reproduce sexually, but parthenogenetic species are known. Terrestrial ecologists have found nematodes to be a dominant element in the soil fauna, and have suggested that nematodes might be important in nutrient cycling and decomposition of organic matter (e.g., YEATES 1979; FRECKMAN 1982). Freshwater nematodes may play similar roles. Since no guides to species-level taxonomy are available for the North American freshwater nematodes, I carried my identification only to the generic level.

Achromadora

This genus is common at the 1-m and 3-m stations in Mirror Lake (Fig. 14). Members of this genus (*terricola* and less commonly *ruricola* and *dubia*) are regularly reported from the littoral sediments of lakes, but they are rarely abundant (e.g., STEFÁNSKI 1938; MUCKLE 1942; BIRO 1973; PREJS 1977a, b). Species are aligivorous or omnivorous (GOODEY 1963; MOTT & HARRISON 1983).

Anonchus

Anonchus was found occasionally at depths between 3 m and 7.5 m in the 1981 transect (Fig. 14), and at all depths in the 1980–81 survey of the gyttja. PREJS (1977a) found *A. mirabilis* in small numbers throughout Mikolajskie Lake in Poland, but the genus has not been found in most other lakes that have received study.

Aphanolaimus

Members of this genus were found in small numbers at the 1-m and 5-m stations in the 1981 transect (Fig. 14), and at the 6-m stations in the 1980–81 study of the gyttja. Two species of the genus, *A. attentus* and *A. aquaticus,* have been found commonly in lakes, usually at low density in the littoral zone (e.g., STEFÁNSKI 1938; BIRO 1973; PREJS 1977a, b; COOMANS & DEWAELE 1983).

Chromadorita

This genus is restricted to the upper littoral zone in Mirror Lake, where it is abundant (Fig. 14). *C. leuckarti,* the only member of this genus found commonly in lakes, is abundant in the littoral zone of many lakes. Some members of the genus eat diatoms (GOODEY 1963; JENSEN 1982).

Dorylaimoidea

I could not identify any members of this superfamily to genus or species. Dorylaimoids are widely distributed in Mirror Lake, but are not very abundant (Fig. 14). They are most abundant in the littoral zone, but were found also in the 1980–81 survey of the gyttja. Dorylaimoids have been found in most lakes where nematodes have been studied; several species have been reported.

Ethmolaimus

This is the second most abundant nematode in Mirror Lake. It is found at all depths, often at densities of more than 100,000 m^{-2}, but has a peculiar depth distribution (Fig. 14). The strong minimum at 7.5 m appears to be real; preliminary results from the 1980–81 survey also show low densities (ca. 10,000 m^{-2}) at this station.

Ethmolaimus has been reported from many lakes, although under various species names, which according to GOODEY (1963) can all be referred to a single species, *E. pratensis. Ethmolaimus* has been found everywhere from the upper littoral zone to the anaerobic profundal zone in lakes. It is often abundant, especially in oligotrophic lakes (STEFÁNSKI 1938; PREJS 1977b). According to MOTT & HARRISON (1983), this nematode is omnivorous.

Ironus

This worm is abundant at the 1-m to 5-m stations (and at 6 m), but missing entirely from the deepwater sediments (Fig. 14). Because of its large size, *Ironus* constitutes a large fraction (18%) of nematode biomass in Mirror Lake. Several species of the genus have been found in lakes; *I. longicaudatus* and *I. ignavus* are especially abundant and widely distributed. *Ironus* has been found in large numbers both in the littoral zone (e. g., MUCKLE 1942; BRETSCHKO 1973) and the profundal zone (e.g., MONARD 1920; HOLOPAINEN & PAASIVIRTA 1977) in lakes. It is presumably predaceous (GOODEY 1963).

Monhystera

Monhystera is the most abundant nematode in Mirror Lake, and was taken at every water depth (Fig. 14). It is especially abundant at the 10.5-m station, where it constitutes more than 40% of all benthic animals. At least two species of *Monhystera* are found in Mirror Lake; different species are dominant in the littoral and the profundal. Members of this genus have been reported, often in large numbers, from nearly every lake where nematodes have received study (e. g., PREJS 1977b). Many species have been reported. MOTT & HARRISON (1983) classified *Monhystera* as an omnivore.

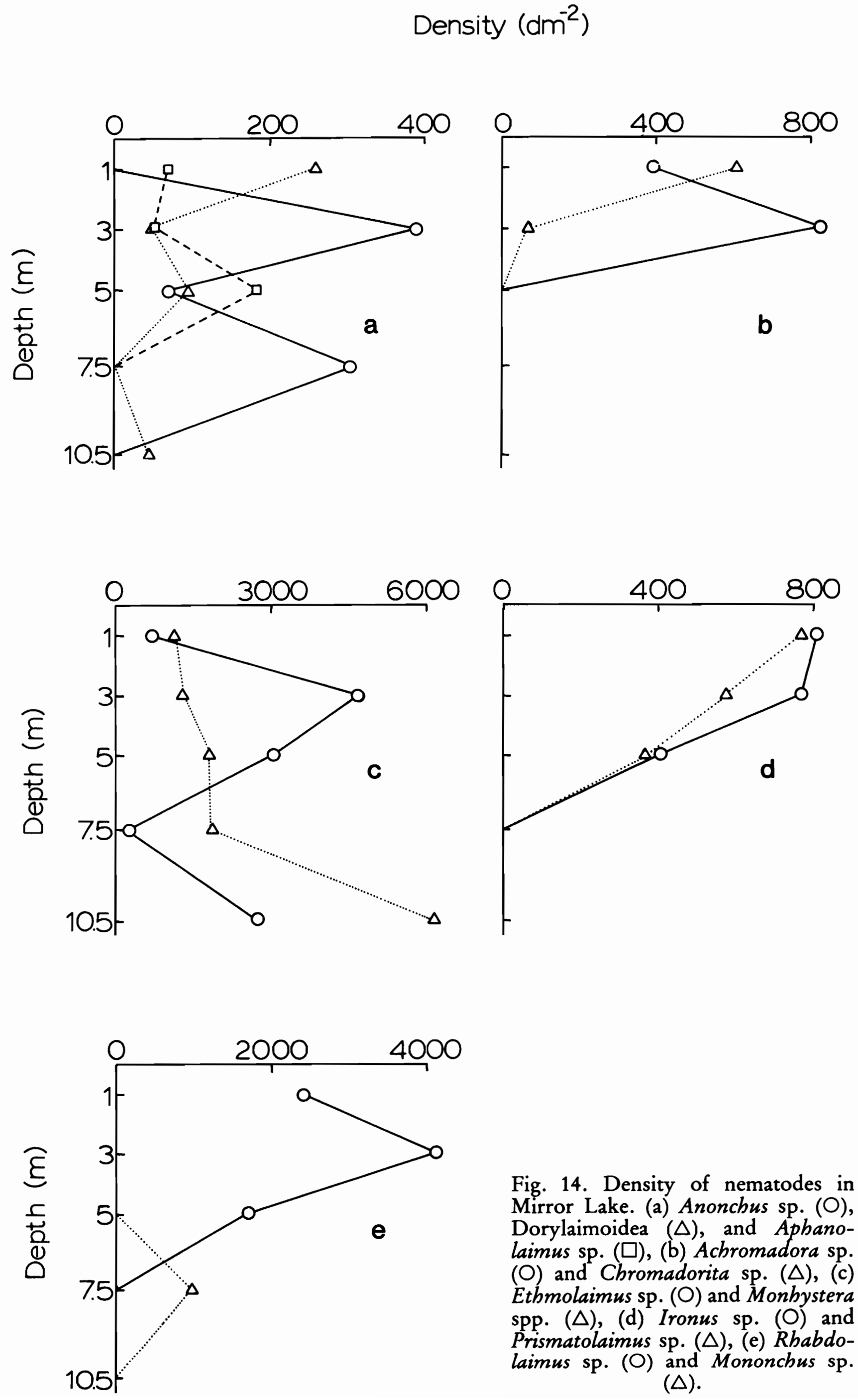


Fig. 14. Density of nematodes in Mirror Lake. (a) *Anonchus* sp. (○), Dorylaimoidea (△), and *Aphanolaimus* sp. (□), (b) *Achromadora* sp. (○) and *Chromadorita* sp. (△), (c) *Ethmolaimus* sp. (○) and *Monhystera* spp. (△), (d) *Ironus* sp. (○) and *Prismatolaimus* sp. (△), (e) *Rhabdolaimus* sp. (○) and *Mononchus* sp. (△).

Mononchus

This large predatory nematode was abundant at the 7.5-m station and absent elsewhere in the 1981 transect (Fig. 14). In the 1980–81 survey, I found a few animals at 6-m, but again the greatest densities were found at 7.5-m. Because of its large size, *Mononchus* accounts for most (60%) of the biomass of nematodes in Mirror Lake. Several species have been found in lakes, but this genus is not usually abundant. However, in ultraoligotrophic Char Lake, Canada, PREJS (1977a) found *M. niddensis* to be widespread and fairly abundant, and in the oligotrophic lake Paajarvi in Finland, *Mononchus* was widely distributed (HOLOPAINEN & PAASIVIRTA 1977). *Mononchus* feeds on small metazoans, including other nematodes (GOODEY 1963).

Prismatolaimus

This genus is abundant on the littoral sediments of Mirror Lake (Fig. 14), and was found occasionally at the 6-m station in 1980–81. Two species of the genus (*P. dolichurus* and *P. intermedius*) are reported occasionally from lakes, usually from the littoral zone and in small numbers (STEFÁNSKI 1938; BIRO 1973; PREJS 1977a, b). They may be omnivorous (MOTT & HARRISON 1983).

Rhabdolaimus

Rhabdolaimus is the most abundant nematode in the littoral zone of Mirror Lake, and the third most abundant lakewide (Fig. 14). I found a few specimens at the 6-m station in 1980–81. There have been very few reports of this genus from lakes. MUCKLE (1942) found a few individuals of *R. terrestris* in the Bodensee in Germany and ANDERSON & DE HENAU (1980) recorded *Rhabdolaimus* sp. from three high elevation lakes in Canada. STEFÁNSKI (1938) found *R. aquaticus* to be very common in dystrophic lakes in the Polish Tatras, especially on muddy substrata. MOTT & HARRISON (1983) called *Rhabdolaimus* a microbiovore.

Other Nematoda

Several other nematodes were found only rarely in Mirror Lake (Table 5). I have not found any previous reports of *Criconemoides* from lakes; its occurrence in Mirror Lake is probably accidental.

Table 5. List of rare nematodes in Mirror Lake.

Alaimus sp.	*Tobrilus* sp.
Criconemoides sp.	Tylenchidae
Monhystrella sp.	Nematoda indet. 1
Prodesmodora sp.	Nematoda indet. 2

Discussion

Nematodes are the most abundant and widespread members of the zoobenthos in Mirror Lake. I found nematodes in every sample that I took. Although nematode species richness is highest in the littoral zone (Fig. 15), two species (*Ethmolaimus*

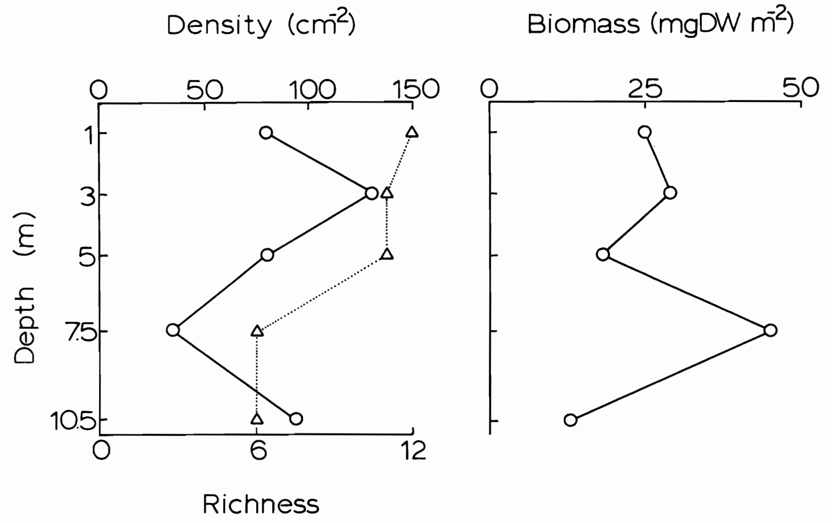


Fig. 15. Density (O), generic richness (△), and biomass of nematodes in Mirror Lake, from transect data.

and *Monhystera*) are very abundant in the anaerobic sediments at 10.5-m. Several other workers have found benthic nematodes to be abundant under anaerobic conditions (e.g., MOORE 1939; COLE 1955; POR & MASRY 1968). Species richness is typically highest on the oxygenated sediments of the littoral zone (e.g., PREJS 1977a).

Nematodes are far and away the most numerous benthic metazoans in Mirror Lake, constituting 60% of all of the benthic metazoans in the lake (Table 35). Because some nematodes pass sieves as fine as 37-µm (HUMMON 1981), most of the published data on the abundance of benthic nematodes in lakes are probably underestimates. Nevertheless, it is apparent that nematodes are very abundant in most lakes (Table 6), and are almost certainly the most abundant benthic animals in freshwater. Incidentally, the density, biomass (Table 6), and species richness (Table 7) of nematodes in lakes are similar to those reported from terrestrial soils (e.g., YEATES 1979).

In Mirror Lake, nematode abundance has a distinct depth distribution, with a strong minimum at 7.5 m (Figs. 15, 16). More than 90% of the nematode biomass at 7.5 m is associated with *Mononchus*, a large predatory nematode whose diet includes other nematodes (GOODEY 1963). It is thus possible that strong predation pressure from *Mononchus* keeps down the population densities of all other nematodes at 7.5 m, and so effects a major change in the composition of the zoobenthic community at 7.5 m. This idea, along with the question of why *Mononchus* itself has such a limited distribution in Mirror Lake (Fig. 14), could be interesting topics for future research.

Table 6. Abundance (m^{-2}) and biomass (mg m^{-2}) of nematodes in some lakes. Many of the data are probably underestimates (see text).

Lake	MESH (µm)	Abundance	Biomass	Notes	Source
Mirror	–	680,000	30[a]	lakewide mean, June–Oct.	this study
Mirror	–	920,000	90[a]	annual mean for gyttja	this study
Par, USA	63	1,500,000	760[a]	annual mean at reference site (z = 1 m)	Oden 1979
Char, Canada	45	720,000	160[a]	summer samples from profundal	Prejs 1977a, b
Michigan, USA	45	260,000	240[a]	z = 11–23 m, Apr.–Nov.	Nalepa & Quigley 1983
Neusiedlersee, Austria	50?	230,000	9–36[a,c]	data from one station	Schiemer 1979
Vorderer Finstertalersee, Austria	100	230,000	70[a,d]	annual lakewide mean	Bretschko 1973
Paajarvi, Finland	100	100,000	150[b]	annual lakewide mean	Holopainen & Paasivirta 1977
Balaton, Hungary	64?	31,000	2[a,d]	approximate annual lakewide mean	data of Biro 1973
Mikolajskie, Poland	45	20,000	21[a]	year-round samples from the profundal	Prejs 1977a, b
Tiberias, Israel	?	8,100	77[a,d]	annual lakewide mean	Por & Eitan 1970
Zarnowieckie, Poland	45	7,500	8[a]	year-round samples from the profundal	Prejs 1977a, b

[a] dry weight

[b] ash-free dry weight

[c] annual range

[d] converted from wet weight by assuming a dry weight content of 20% (cf. Prejs 1977a, b)

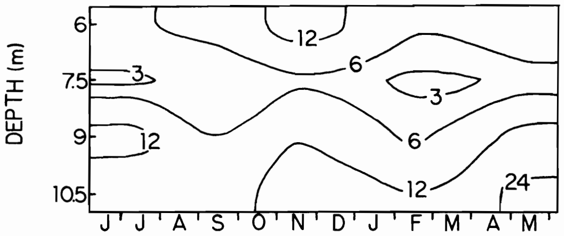


Fig. 16. Density (thousands per dm^{-2}) of benthic nematodes in Mirror Lake.

Because I did not identify the nematodes that I collected during my survey of the gyttja, I have no phenological data on individual nematode species. There are no clear seasonal trends in total nematode density on the gyttja, however (Fig. 16). Other authors have reported seasonal changes both in the density of individual species and in the abundance of all nematodes combined (e.g., **Biro** 1968, 1973; **Prejs** 1970; **Bretschko** 1973). However, the pattern of seasonality varies among lakes. For example, in Lake Balaton, Hungary, peak nematode densities occur in May (**Biro** 1968, 1973), while in the alpine Vorderer Finstertalersee, nematodes are most abundant during mid-winter (**Bretschko** 1973).

Nematodes burrow more deeply into lake sediments than do most metazoans. In Mirror Lake, 63% of the nematodes live in the top 2 cm of sediment; but many (18%) individuals penetrate to more than 4 cm below the sediment surface (Fig. 17). Other authors likewise have found peak densities of nematodes at the sediment surface, but substantial numbers (2–11% of the population) below 5 cm (e.g., **Moore** 1939; **Cole** 1955; **Bryant** & **Laybourn** 1972; **Sarkka** & **Paasivirta** 1972, **Nalepa** & **Robertson** 1981a). **Moore** (1939) found a few nematodes as deep as 17–20 cm in the muck sediments of Douglas Lake, Michigan.

I found 20 species of nematodes in Mirror Lake, but more are certainly present. In particular, I ignored the epiphytic fauna, which contains its own

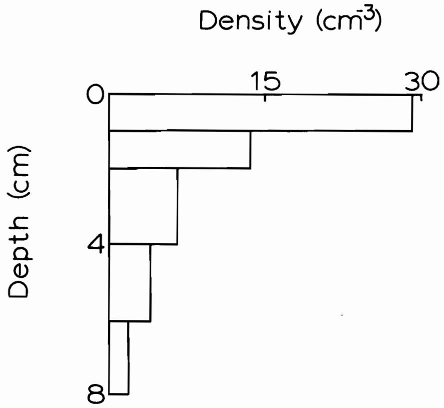


Fig. 17. Density of nematodes within the sediments of Mirror Lake, as a function of depth from the sediment surface. Data are lakewide means from the transect.

distinct set of nematode species (Jensen 1984). The benthic fauna is strongly dominated by *Monhystera* and *Ethmolaimus*, which together constitute 55% of the nematodes in the lake. Prejs (1977b) found that these two genera dominate the faunas of many oligotrophic lakes. The genus *Tobrilus* is conspicuous by its rarity in Mirror Lake. This genus is often abundant in lakes, most frequently in eutrophic

Table 7. Species richness (S) of nematodes in some lakes where they have been well studied, in comparison with Mirror Lake.

Lake	S	Notes	Source
Mirror	>20	based on the 1133 animals that I identified	this study
Rybinsk Reservoir, USSR	56	includes many terrestrial species	Gagarin 1978
Mikolajskie, Poland	52	eutrophic	Prejs 1977a
Geneva, Switzerland	>50		cited by Stefanski 1938
Bodensee, Germany	41		Muckle 1942
Quatre Cantons, Switzerland	40		cited by Stefanski 1938
Paajarvi, Finland	37	oligotrophic, mesohumic	Holopainen & Paasivirta 1977
Grosser Plöner See, Germany	36		cited by Stefanski 1938
Lunzer Untersee, Austria	33		cited by Stefanski 1938
Neuchatel, Switzerland	32	oligotrophic	Monard 1920
Balaton, Hungary	31	shallow, eutrophic	Biro 1973
Ivankovo Reservoir, USSR	26		Gagarin 1978
Neusiedlersee, Austria	26	shallow, oligohaline	Schiemer 1978
Morskie Oko, Poland	23	oligotrophic	Stefanski 1938
Char, Canada	21	oligotrophic, arctic	Prejs 1977a
Toporwy (Lower), Poland	18	dystrophic	Stefanski 1938
Zarnowieckie, Poland	16	mesotrophic	Prejs 1977a
Gro'kiy Reservoir, USSR	13		Gagarin 1978
Toporwy (Upper), Poland	13	dystrophic	Stefanski 1938
Vorderer Finstertalersee, Austria	10	oligotrophic, alpine	Bretschko 1973

lakes (Prejs 1977b), but also in some oligotrophic lakes like the Austrian Vorderer Finstertalersee (Bretschko 1973). Lakes usually contain 20–50 specimens of benthic nematodes (Table 7).

Although nematodes are very abundant in Mirror Lake, they constitute only 1% of zoobenthic biomass (Tables 6, 35). Higher values for biomass have been found in other lakes (Tables 6), and nematodes commonly contribute more than 10% of zoobenthic biomass in lakes. Nematode biomass presumably turns over rapidly. Nematode populations have high growth rates in culture (e. g., Prejs 1970; Schiemer et al. 1980; Banse 1982; Schiemer 1983), and I estimated an annual P/B of 23 by the modified Banse & Mosher (1980) regression. As a result, nematodes may be responsible for 5% to 10% of zoobenthic assimilation in Mirror Lake (Table 35), in spite of their relatively small biomass. In other lakes, where nematodes frequently account for a larger fraction of zoobenthic biomass, they may contribute much of zoobenthic metabolism. Especially in such lakes, the nematodes may be the dominant consumers of benthic bacteria and some algae.

Gastrotricha

Little is known of the ecology of freshwater gastrotrichs. There have been only a few major studies directed at these small animals (e.g., Voigt 1904; Praeobrajenskaja 1926; Brunson 1949, 1950; d'Hondt 1967; Kisielewski 1981), and gastrotrichs have received only incidental mention in surveys of the lacustrine microbenthos. Nonetheless, as shown below, gastrotrichs may be among the most abundant of benthic animals in lakes. Gastrotrichs are tiny, ciliated aschelminths that reproduce largely by parthenogenesis (but see Weiss & Levy 1979; Kisielewska 1981). They browse among sediment particles for bacteria and algae (Bennett 1979). I made all morphological measurements and taxonomic determinations on living animals.

Chaetonotus spp.

This genus contains many (perhaps 8–20) species in Mirror Lake, but I was not able to distinguish the individual species reliably. In fact, I found it difficult to distinguish short-spined species of *Chaetonotus* from species of *Heterolepidoderma,* which also may have been present in the lake. *Chaetonotus* is abundant and widely distributed in Mirror Lake (Figs. 18, 20), and was found commonly during all seasons. It is more abundant on the gyttja than elsewhere, and is commonly found under anoxic conditions.

Members of this genus have been reported from most lakes where the gastrotrich fauna has been studied. Moore (1939) and Cole (1955) reported only the taxon "*Chaetonotus* sp.", and some authors (e.g., Fehlmann 1912; Monard 1920) have found only a single species of *Chaetonotus* in a lake. However, Voigt (1904) found four species in the Grosser Plöner See, Varga (1949) reported 14 species from a shallow bay of Lake Balaton, and Praeobrajenskaja (1926) found 23 and 26 species of *Chaetonotus* in the Russian lakes Beloye and Tschernoe, respectively. Species richnesses comparable to those in Mirror Lake are therefore probably common. Given the present state of gastrotrich taxonomy and ecology, it is not even possible to name any particularly typical lacustrine species of *Chaetonotus.*

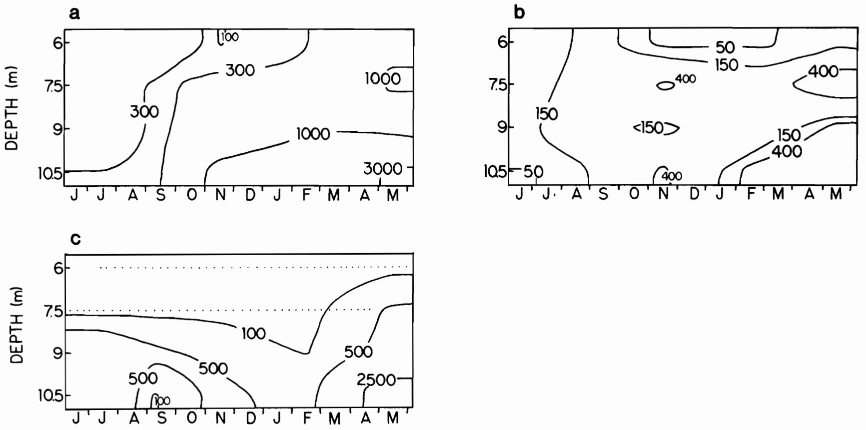


Fig. 18. Abundance (dm^{-2}) of gastrotrichs in Mirror Lake. (a) *Chaetonotus* spp., (b) *Lepidodermella trilobum,* (c) Gastrotricha sp. 1. Dotted lines show extended periods when the species was absent from the indicated station.

Lepidodermella trilobum

This species is abundant throughout Mirror Lake at all seasons (Fig. 18, 20), and occurs under anoxic conditions. It is apparently most abundant at the 7.5-m stations, but shows little other regularity in its distribution.

Specimens from Mirror Lake are 130- to 180-μm long ($\bar{x}$ = 144 μm, n = 16), with a body width of about 1/6 of the total length. The head is distinctly 3-lobed, the pharynx is about 1/4 of the total length, and the furca are about 1/9 of the total length. The scales are so small (<2-μm diameter) that I could not resolve their shape, and are arranged so that the body surface is smooth.

Since its description from a bog in Michigan (BRUNSON 1950), *L. trilobum* has been reported once, from Indiana (PFALTZGRAFF 1966).

Gastrotricha sp. 1

This species, either a *Chaetonotus* with very short, flat-lying spines, or a *Heterolepidoderma,* is the most abundant species of gastrotrich in Mirror Lake. It is most abundant on the deep profundal sediments, but is found in low numbers at the 5-m to 7.5-m stations (Figs. 18, 20). I frequently found it under anoxic conditions. This species reaches maximum population densities in spring and early summer.

Individuals of Gastrotricha sp. 1 are 170- to 220-μm long ($\bar{x}$ = 179 μm, n – 18) and about 1/6 as wide as long. The head is indistinctly 3-lobed. The pharynx is about 1/4 of the body length, and the furca are about 1/8 of the body length. The body is covered with scales that are difficult to resolve and that bear either a keel or a short (4- to 10-μm), flat-lying spine. The scales are about 4 × 3 μm.

I collected a single hermaphroditic individual of this species from a 9-m station in August, 1980 (Fig. 19). Until WEISS & LEVY (1979) found a few hermaphrodites in a laboratory culture of *Lepidodermella squammata,* it was thought that all freshwater gastrotrichs were obligate parthenogens. More recently, KISIELEWSKA (1981) reported that hermaphrodites occur occasionally in natural populations of six species of gastrotrichs in

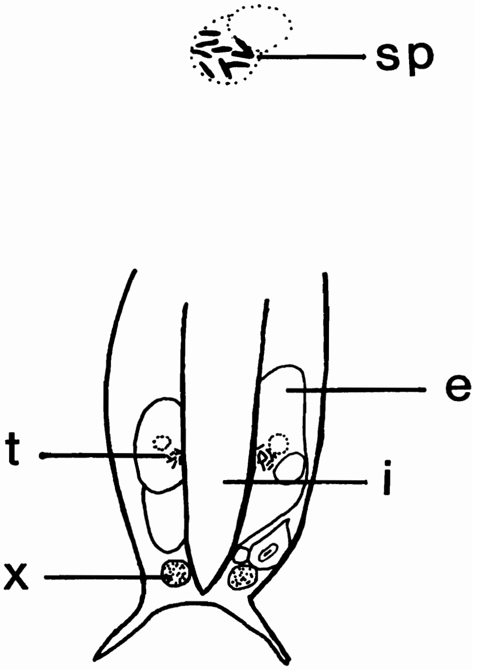


Fig. 19. Sketch of a hermaphrodite of Gastrotricha sp. 1. Posterior end of living animal (lower) and detail of testis (upper). e = egg, i = intestine, sp = sperm, t = testis, x = X-organ? Freehand.

Poland. Including my report from Mirror Lake, hermaphrodites are now known in four genera and eight species of freshwater gastrotrichs. As Kisielewska (1981) stated, it seems probable that hermaphroditism is widely distributed, but sporadic, in natural populations of freshwater gastrotrichs. However, we are presently ignorant of the frequency of this trait in nature, of the factors that control its appearance, and of its importance in the dynamics of natural populations.

Other Gastrotricha

I collected at least 10 other species of gastrotrichs from Mirror Lake (Table 8). *Ichthydium* spp. includes at least three species, and *Lepidodermella* spp. at least two. *Lepidodermella squammata* and the species of *Polymerurus* are all common, widely distributed taxa (Voigt 1960). *Aspidiophorus,* on the other hand, has not been reported previously from the fresh waters of North America, although various species of the genus are widespread in Europe and Japan (Kisielewski 1981).

Table 8. List of rare gastrotrichs in Mirror Lake.

Aspidiophorus sp. 1
Aspidiophorus sp. 2
Ichthydium spp.
Lepidodermella squammata
Lepidodermella spp.
Polymerurus cf. *callosus*
Polymerurus nodicaudatus

Aspidiophorus sp. 1 has the following morphology: trunk, 175- to 190-μm long and 28-μm wide at maximum; pharynx, 40- to 42-μm; head with five, distinct, subequal lobes and no oral bristles or cephalic shield; furca 19- to 20-μm. This species resembles *A. polonicus*. *Aspidiophorus* sp. 2 is a large species: 380-μm long by 50-μm maximum width; head 5-lobed; pharynx 110-μm; furca 30-μm.

Discussion

Gastrotrichs are among the most abundant and widespread of the benthic animals in Mirror Lake. I found them in almost every (97%) sample I collected, and the mean lakewide density (June–October) is 130,000 m^{-2}. Although I cannot state precisely the number of species present, there must have been 20–30 species in my samples. I found gastrotrichs at every season and in every habitat in Mirror Lake, but densities are distinctly higher on the gyttja sediments (Fig. 20), confirming previous statements (Fehlmann 1912; Monard 1920; Remane 1936) that gastrotrichs are especially abundant on highly organic sediments. Several species of gastrotrichs were collected under anoxic conditions; in fact, I found the highest densities of gastrotrichs at the seasonally anoxic 10.5-m station (Figs. 20, 21). Several other authors (e.g., Moore 1939; Cole 1955) have reported gastrotrichs from anoxic habitats. About 87% of the gastrotrichs in Mirror Lake live in the top 2 cm of sediment (Fig. 22).

From my limited observations (Fig. 18), it appears that individual species of gastrotrichs are present throughout the year. At least some species show definite depth distributions (Fig. 18).

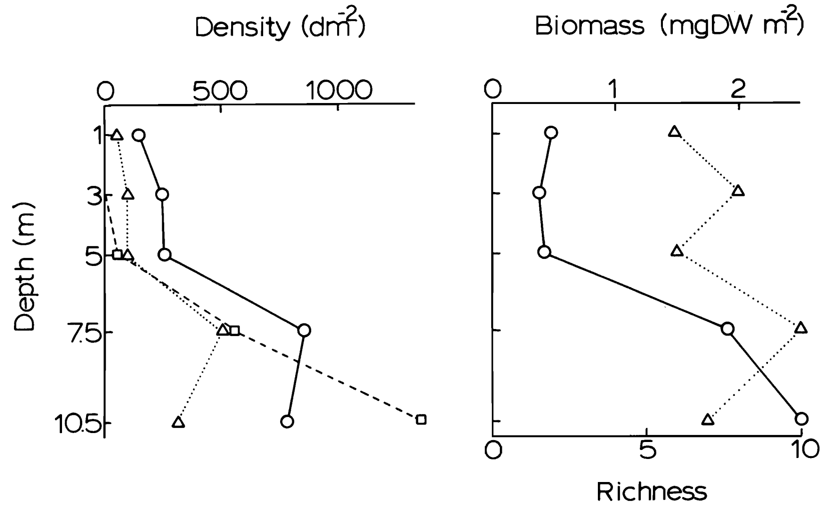


Fig. 20. Left: Density of gastrotrichs in Mirror Lake. *Chaetonotus* spp. (○), *Lepidodermella trilobum* (△), and Gastrotricha sp. 1 (□). Right: Biomass (○) and species richness (△) of gastrotrichs in Mirror Lake. All data from the transect.

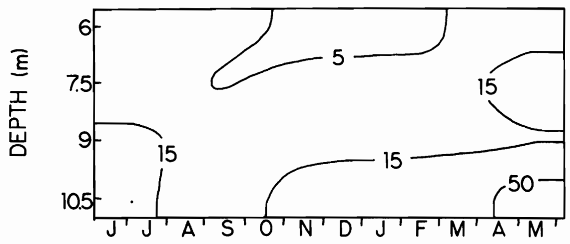


Fig. 21. Abundance (cm^{-2}) of gastrotrichs in Mirror Lake.

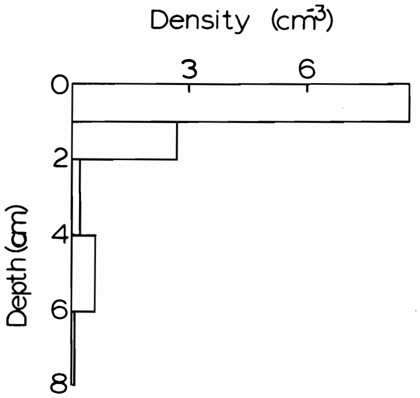


Fig. 22. Gastrotrich density within the sediments of Mirror Lake, as a function of depth from the sediment surface. Data are lakewide means from the transect.

Few data have been published about lacustrine gastrotrich assemblages. It is clear from previous work that *Chaetonotus* is the dominant genus in most lakes, although *Lepidodermella, Polymerurus, Ichthydium, Aspidiophorus,* and *Heterolepidoderma* often have been found as well. Authors have reported from 1 to 37 species in lakes (Table 9), but it is not clear how much of this variation is real and how much reflects variation in sampling intensity. Perhaps lakes typically contain 5 to 50 species of gastrotrichs.

Table 9. Species richness (S) of gastrotrichs in some lakes.

Lake	S	Source
Mirror	ca. 25	this study
Tschernoe, USSR	37	PRAEOBRAJENSKAYA 1926
Beloye, USSR	35	PRAEOBRAJENSKAYA 1926
bay of Balaton, Hungary	18	VARGA 1949
Grosser Plöner See, Germany	7	VOIGT 1904
Neuchatel, Switzerland	1	MONARD 1920
Luganer See, Switzerland	1	FEHLMANN 1912

Because gastrotrichs are not retained quantitatively even on sieves as fine as 37-µm mesh (HUMMON 1981), there are almost no quantitative data on gastrotrich population densities in lakes. In fact, the only acceptable data that I found are those of EVANS (1982), who found from 15,000 to 100,000 m^{-2} in the top 3 cm of sand in summer samples from three beaches on Lake Erie.

The biomass of gastrotrichs in Mirror Lake is very small: only 0.05% of zoobenthic biomass. Data from laboratory cultures (BRUNSON 1949; HUMMON 1974) suggest that natural populations of gastrotrichs may turn over rapidly, but I know of no field data to support this contention. Using the modified regression of BANSE & MOSHER (1980), I estimate P/B to be about 80 yr^{-1} for the Mirror Lake gastrotrich assemblage. Gastrotrichs may be responsible for about 1% of zoobenthic assimilation in Mirror Lake (Table 35).

The place of gastrotrichs in benthic food chains is uncertain. They may be important consumers of benthic bacteria, but nothing is known of the selectivity or feeding rates of gastrotrichs in nature. MOORE (1979) found gastrotrichs to be a dominant item in the diet of the chironomid *Procladius denticulatus* in Great Slave Lake. Other predators presumably eat gastrotrichs as well.

The gut walls of many gastrotrichs collected from the deepwater stations (9-m and 10.5-m) were lined with small but conspicuous, magenta-colored bodies of an unknown nature. I saw these bodies especially frequently in Gastrotricha sp. 1, but found them in other gastrotrich species as well. I noticed small inclusions of a similar color in the musculature lateral to the gut of the nematode *Monhystera* sp. In *Monhystera*, as in the gastrotrichs, I did not see such inclusions in animals collected from well-oxygenated, shallow-water sediments. The occurrence of these inclusions in diverse taxa living in a particular habitat suggests that they have some functional significance.

NUSS (1984; NUSS & TRIMKOWSKI 1984) recently investigated apparently similar inclusions in the nematode *Tobrilus gracilis*, a common species of anaerobic environments. These authors found that the inclusions were associated with mitochondria, and contained considerable elemental sulfur. NUSS presented other evidence to support the idea that these sulfur deposits are the end product of a sulfide detoxification system. A similar system has been reported from marine benthic animals (e. g., POWELL et al. 1979, 1980), and is an important adaptation allowing animals to cope with an anaerobic environment rich in H_2S.

If the inclusions that I observed in Mirror Lake result from a sulfide detoxification system, then such systems may be phylogenetically widespread in fresh water. It would be highly desirable to know more about the physiological mechanisms, ecological importance, and phylogenetic distribution of sulfide detoxification systems in the freshwater zoobenthos.

Monogononta

The class Monogononta contains all of the planktonic rotifers, a group that is well represented in lakes and well known to most limnologists (see RUTTNER-KOLISKO 1974, and WETZEL 1983, for introductions). Also belonging to the class are the so-called sessile rotifers, large and spectacular animals that have been the subject of the interesting studies of EDMONDSON (1944, 1945) and WALLACE (1980), among others. However, most monogonont species are small, free-swimming rotifers associated with sediment and vegetation. These animals have received little attention from limnologists. The benthic monogononts include bacteriovores, herbivores, carnivores, and parasites, some of them highly modified and specialized (e.g., POURRIOT 1965). Presumably, all monogononts are facultative parthenogens.

Cephalodella spp.

This is one of the most abundant genera of benthic monogononts in Mirror Lake, and is represented by at least 12 species. *Cephalodella* is found at all stations and at all seasons, but is absent from the 9-m and 10.5-m stations during periods of anoxia (Figs. 23, 24). Most members of this genus eat small algae or micrometazoans (MYERS 1941; POURRIOT 1965), but DODSON (1984) recently described a remarkable kind of bacteriovory in the tube-dwelling *C. forficula*. In Mirror Lake, *Cephalodella* often contains small diatoms, and sometimes appears to be very selective; for example, one individual contained 22 cells of one benthic diatom and nothing else.

Cephalodella is commonly a conspicuous part of the benthic rotifer fauna of lakes. KOCH-ALTHAUS (1963) found 23 species in the littoral of the Stechlinsee in Germany, BERZINS (1972) found 16 species in his brief study of the rotifer fauna of the margins of Lake Straken in Sweden, and ODEN (in litt.) found 21 species in Par Pond, South Carolina.

Colurella spp.

At least two species of this genus were collected from Mirror Lake. *Colurella* has a strongly seasonal occurrence in Mirror Lake (Fig. 23). The genus is found regularly from 6 m to 9 m where dissolved oxygen was plentiful. Because the transect samples were taken during the period of minimum population density, very few specimens were collected, and I have almost no information on the occurrence of this rotifer in the littoral zone.

Colurella has been found commonly in lakes. Previous studies have reported from three to six species per lake, of which *C. obtusa* and *C. uncinata* seem to be the most frequent (e.g., PEJLER 1962; KOCH-ALTHAUS 1963; BERZINS 1972).

Lecane spp.

This genus contains two easily distinguished subgenera in Mirror Lake. Each subgenus is represented by at least two species. *L. (Lecane)* is abundant throughout the year at the 6-m stations, but is found only occasionally at other depths (Fig. 23). *L. (Monostyla)*, less abundant than *L. (Lecane)*, is found commonly at 6-m and 7.5-m, and occasionally elsewhere (Fig. 23). It is most abundant in October and November.

Members of both of these subgenera are among the most abundant and widespread of the benthic monogononts (HARRING & MYERS 1926; KOCH-ALTHAUS 1963). Many species are found in the lacustrine fauna; for example, KOCH-ALTHAUS (1963) found 18 species in the Stechlinsee, and ODEN (in litt.) reported 60 species from the shallow waters of Par Pond.

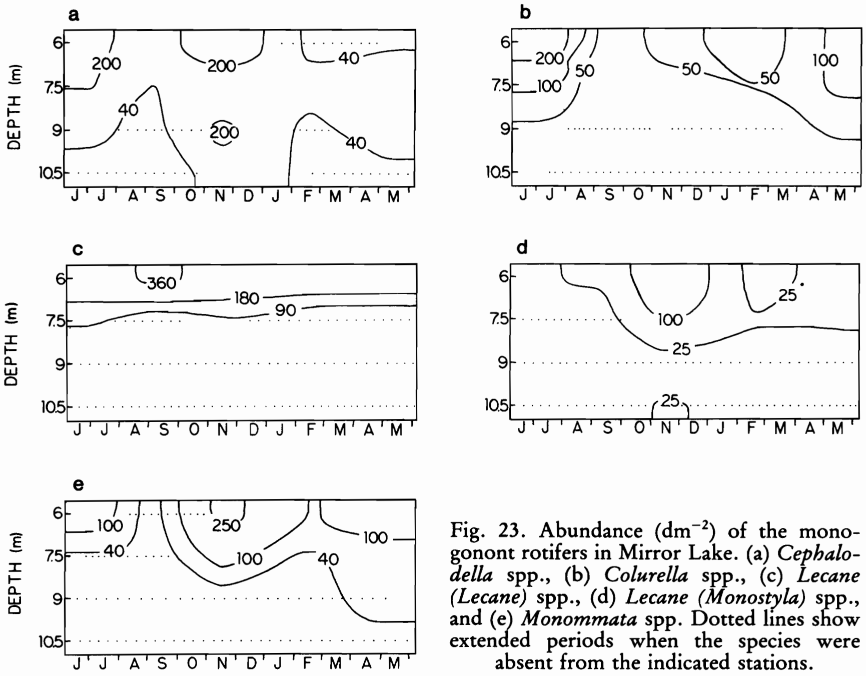


Fig. 23. Abundance (dm^{-2}) of the monogonont rotifers in Mirror Lake. (a) *Cephalodella* spp., (b) *Colurella* spp., (c) *Lecane (Lecane)* spp., (d) *Lecane (Monostyla)* spp., and (e) *Monommata* spp. Dotted lines show extended periods when the species were absent from the indicated stations.

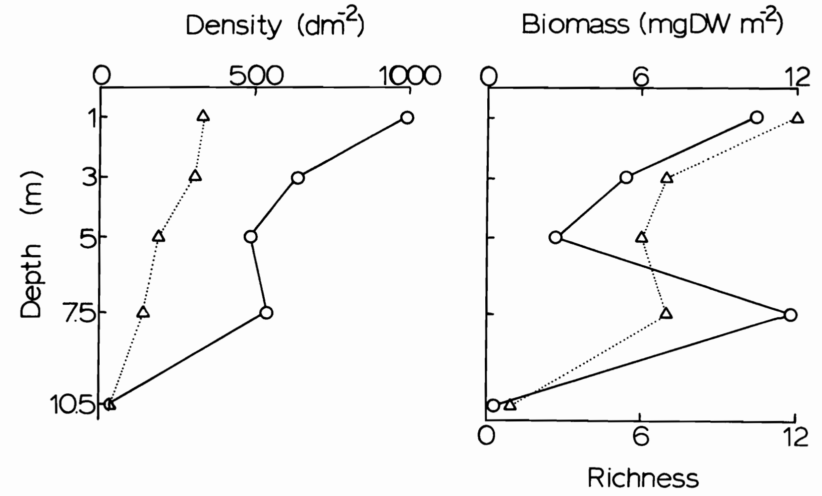


Fig. 24. Left: Density of all benthic Monogononta (○) and *Cephalodella* spp. (△). Right: Generic richness (○) and biomass (△) of benthic Monogononta. From transect data.

Monommata spp.

At least three species of *Monommata*, including *M. astia*, are found in Mirror Lake. I collected this genus at water depths of 1 m to 9 m, but it is distinctly more abundant at the shallower stations (Fig. 23). Like *Colurella*, it is not found in late summer. This genus is found commonly in lakes, but is especially abundant and species-rich in acid waters (Nogrady 1982).

Other monogononts

Many taxa of monogononts are too rare for me to describe their ecological distributions in Mirror Lake. I have summarized my records of these taxa in Table 10. See Strayer (1984) for sketches and brief descriptions of some of these taxa.

Table 10. List of rare monogonont rotifers in Mirror Lake. The number in parentheses is the minimum number of species in the genus present in the Mirror Lake zoobenthos.

Ascomorpha sp.
Collotheca sp.
Dicranophorus spp. (4)
Erignatha clastopis
Gastropus minor
Kellicottia longispina
Lepadella sp.
Macrochaetus spp. (2)
Microcodon clavus
Notommata spp. (2)
Polyarthra spp. (2)
Proales sp.
Proalinopsis spp. (2)
Scaridium longicaudum
Stephanoceras fimbriatus
Synchaeta sp.
Taphrocampa selenura
Taphrocampa sp. 2
Testudinella sp.
Tetrasiphon hydracora
Trichocerca spp. (4)
Trichotria sp.
Wierzejskiella sp.

My records of *Kellicottia longispina* are undoubtedly due to strays from the pelagic zone, where the species is abundant (Makarewicz & Likens 1975). *Polyarthra* includes at least one species in addition to *P. vulgaris* from the plankton. *Stephanoceras fimbriatus* lives on strands of *Nitella flexilis* in Mirror Lake. Individuals of *Tetrasiphon hydracora*, an acid-water species (Harring & Myers 1921; Pourriot 1965), had large desmids in their guts. In addition to the taxa listed in Table 10, I found single individuals of at least five genera of monogononts that I could not identify.

Discussion

I found at least 33 genera and 56 species of benthic monogononts in Mirror Lake. The fauna of the lake is undoubtedly much larger than this, and probably contains well in excess of 100 species. Lacustrine communities of benthic monogononts often contain more than 100 species (Table 11), and in soft waters very diverse faunas, exceeding 300 species, have been found (Harring & Myers 1928; Myers 1931; Oden 1979). Most of the taxa that I identified are common and

Table 11. Abundance (m^{-2}), biomass (mg DW m^{-2}), and species richness of benthic rotifers in some lakes.

Lake	MESH (μm)	Abundance	Biomass	Species richness Monogononta	Species richness Bdelloidea	Notes	Source
Mirror	–	150,000	15	56	8	lakewide mean, June–Oct.	this study
Par, USA	63	270,000	120	290[a]	41[a]	annual mean at reference site (z = 1 m)	ODEN 1979
Nine lakes, Canada	45	30,000	–	–	–	mean of single July samples from each lake	ANDERSON & DE HENAU 1980
Michigan, USA	45	9,000	2	–	–	z = 11 m to 23 m; May–Nov.	NALEPA & QUIGLEY 1983
Grosser Plöner See, Germany	–	–	–	59	9		VOIGT 1904
Stechlinsee, Germany	–	–	–	127	4	littoral zone only	KOCH-ALTHAUS 1963
Neusiedlersee, Austria	–	–	–	140	23	shallow, oligohaline	DONNER 1979

[a] ODEN (1979) reported 372 rotifer species, but the species list that she sent to me contains only 331 species

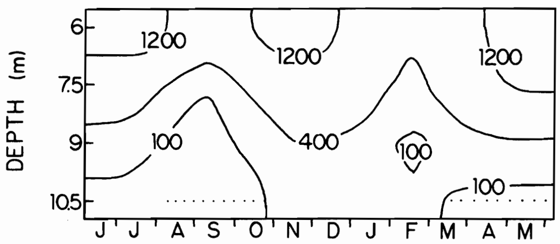


Fig. 25. Abundance (dm^{-2}) of all benthic monogonont rotifers on the gyttja sediments of Mirror Lake. Dotted lines show extended periods when these animals were absent from the indicated station.

widespread in lakes, but a few (e. g., *Monommata* spp., *Tetrasiphon hydracora*, and the dicranophorids) are characteristically found in soft waters.

Monogononts are most abundant in shallow water in Mirror Lake (Figs. 24, 25), but were collected from all stations. I found a single individual of *Synchaeta* under anoxic conditions, and occasionally found monogononts where the concentration of dissolved oxygen was less than 2 mg l^{-1}, but they are more plentiful where dissolved oxygen concentrations are higher. To my knowledge, there are no species of monogononts that are able to tolerate prolonged anoxia, as is the bdelloid rotifer *Rotaria tridens* (see below).

Monogononts live at the sediment surface; 79% of the monogononts live in the top centimeter of sediment in Mirror Lake (Fig. 26). NALEPA & ROBERTSON (1981a) found that 85% of the benthic rotifers (including bdelloids) lived in the top centimeter of sediments in the nearshore zone of Lake Michigan.

In Mirror Lake, the monogononts have two periods of minimum population density: in late summer, when many of my 1981 transect samples were taken, and during the winter (Fig. 25). ODEN (1979) also reported minimum population densities in July and August, but found winter to be the time of peak population densities in Par Pond, South Carolina. On the other hand, KOCH-ALTHAUS (1963)

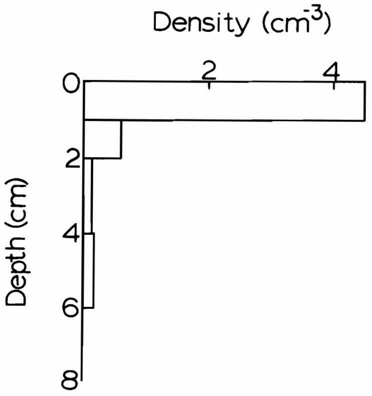


Fig. 26. Vertical distribution of monogonont rotifers within the sediments of Mirror Lake, as a function of depth below the sediment surface. Data are lakewide means from the transect.

reported species richness to be highest in July–October and lowest in November–December in the Stechlinsee, and Murray (1906) found the littoral rotifers of Loch Ness to have a winter maximum.

The mean lakewide density of monogononts in Mirror Lake is 57,000 m^{-2}; since the transect samples were taken in July–October, a period of low population densities (cf. Fig. 25), this number is probably an underestimate of the mean annual density. Authors of previous quantitative studies of benthic rotifers have lumped together the bdelloids and monogononts, so it is not possible to compare my results for monogononts with those from other lakes. Furthermore, unless extremely fine (or no) sieves are used, rotifer abundance may be severely underestimated (Hummon 1981). However, the density of all benthic rotifers in Mirror Lake compares well with the few results available from other lakes (Table 11).

Monogonont rotifers contribute a very small fraction (0.3%) of zoobenthic biomass in Mirror Lake. Benthic rotifers, including the bdelloids, have a mean lakewide biomass of 16 mg DW m^{-2} in Mirror Lake. This estimate lies between the only two values previously reported for the biomass of benthic rotifers (Table 11).

On a lakewide basis, the benthic monogononts do not appear to be important in the energetics of the zoobenthic community; they are responsible for only about 1–2% of zoobenthic assimilation (Table 35). Nonetheless, they may be important grazers of benthic algae, especially in the upper littoral zone, where their population densities are high (Fig. 24). The apparently great selectivity of some of the benthic monogononts (cf. Pourriot 1965, 1977) could amplify their influence on certain benthic algae. However, until we learn much more about the benthic algal community in Mirror Lake, and the selectivity and feeding rates of these rotifers, it is impossible to speculate further.

The apparent insignificance of the monogonont rotifers in the zoobenthos of Mirror Lake is in sharp contrast to their importance in the zooplankton. Although only a handful of rotifer species are represented in the Mirror Lake zooplankton, they account for 16% of the biomass and 40% of the secondary production of the zooplankton (Makarewicz & Likens 1979).

Bdelloidea

Bdelloid rotifers are creeping animals associated with soils, mosses, lichens, and aquatic substrata. They are collected occasionally in freshwater plankton samples (e. g., Klimowicz 1972), but all known freshwater species are benthic. Bdelloids are filter-feeders that consume bacteria and, secondarily, small algae (Pourriot 1965, 1977). Most of the previous work on this group has been taxonomic and has concentrated on the terrestrial and moss-dwelling species (see Bartos 1951, and Donner 1965, for an introduction to the literature). Little is known about the lacustrine bdelloids, even though they may be widespread and abundant in lakes.

Dissotrocha macrostyla

This is the most common and widely distributed bdelloid on the oxygenated sediments of Mirror Lake (Figs. 27, 28). In addition to typical specimens of *D. macrostyla,* I collected occasional individual of the "*tuberculata*" morph. These are included under *D. macrostyla* in Figures 27 and 28, as is the single specimen of *D. aculeata* found at 6-m in May, 1981. *D. macrostyla* is a cosmopolitan species found in mosses and in the littoral zone of ponds and lakes (Bartos 1951; Donner 1965). It is apparently common in lakes (Murray 1906; Moore 1939; Monard 1920; Cole 1955; Holopainen & Paasivirta 1977; Oden, in litt.).

Hablotrocha spp.

I was not able to assign a species name to either of the two species of *Hablotrocha* found in Mirror Lake. "Species 1" was found at the 1-m to 5-m stations and throughout the year at the 6-m and 7.5-m stations (Figs. 27, 28). I collected only two individuals of the second species. The genus *Hablotrocha* is a very large genus containing many terrestrial and moss-dwelling species (Bartos 1951; Donner 1965). Only a few species are known from truly aquatic habitats (Murray 1906; Oden, in litt.), and no species of the genus was found by Monard (1920), Moore (1939), or Cole (1955) in their surveys of lake microbenthos.

Macrotrachela sp.

Samples taken in the 1981 transects from 1- to 5-m depth contained a bdelloid apparently belonging to this large, mostly terrestrial genus. Although the most abundant bdelloid in the 1- to 5-m zone (Fig. 28), this species was never found at the 6-m to 10.5-m stations.

This oviparous rotifer is 325- to 450-µm long and lacks eyes. The dental formula is 2/2. The foot bears 24- to 30-µm long spurs and three toes, each about 10-µm long. The animal is brown and has a thin unornamented cuticle.

Neither Moore (1939) nor Cole (1955) reported *Macrotrachela* in their surveys of the microzoobenthos of lakes in the American Midwest, but Murray (1906) found members of this genus (as *Callidina,* in part) in Scottish lochs, and Oden (in litt.) found 5 species in Par Pond, South Carolina. *Callidina progonidia* Monard, a common species in the profundal of Lac Neuchatel, Switzerland, may belong to *Macrotrachela.*

Rotaria cf. *macrura*

The rarest of the species of *Rotaria* in Mirror Lake, this species is found year-round at the 6-m depth, but only at the vegetated station. Its mean annual density is 60 dm^{-2} there, and 6 dm^{-2} for the entire gyttja area. All but a single individual were collected in the top centimeter of sediment. This species apparently lives on or among plants in Mirror Lake.

R. macrura has been reported from Europe, North America, Greenland, and New Zealand, among aquatic plants and in the benthos (Bartos 1951). Pourriot (1965) classified the species as a warm stenotherm, and reported that it was most common in slightly acid waters in France.

Rotaria rotatoria

R. rotatoria is found in small numbers throughout the oxygenated sediments of Mirror Lake (Figs. 27, 28). Both eyeless specimens and specimens with eyes are found in Mirror Lake.

R. rotatoria has been found worldwide in a wide variety of habitats: ponds, lakes, streams, and on the cuticles of aquatic insects (Bartos 1951; Donner 1965; Pourriot 1965). Monard (1920, as *Rotifer vulgaris*), Moore (1939), Cole (1955) and Oden (in litt.)

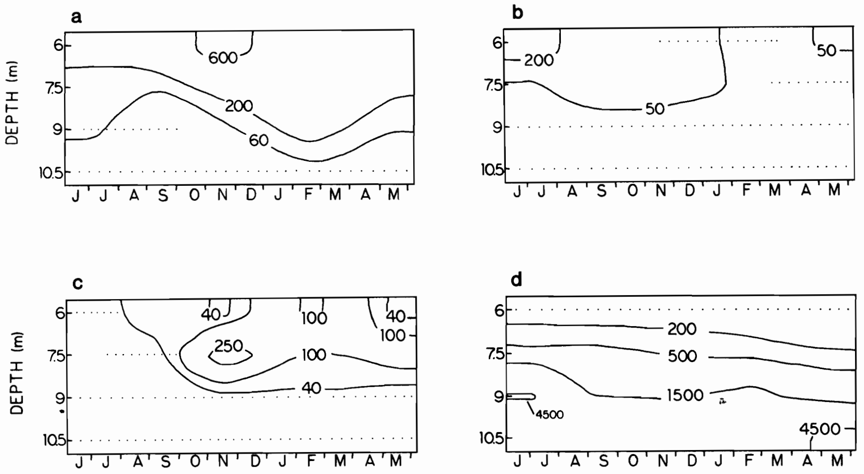


Fig. 27. Abundance (dm^{-2}) of bdelloid rotifers in Mirror Lake. (a) *Dissotrocha macrostyla*, (b) *Hablotrocha* sp. 1, (c) *Rotaria rotatoria*, (d) *Rotaria tridens*. Dotted lines show extended periods when the species were absent from the indicated stations.

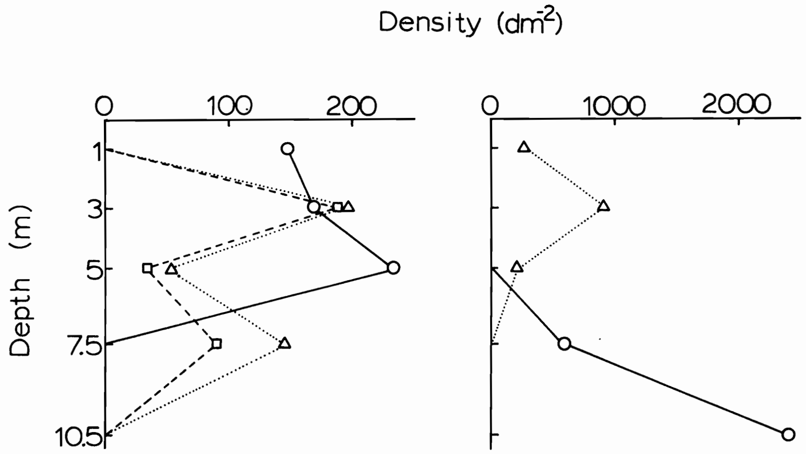


Fig. 28. Density of bdelloid rotifers in Mirror Lake, from transect data. Left: *Hablotrocha* sp. 1 (○), *Dissotrocha macrostyla* (△), and *Rotaria rotatoria* (□). Right: *Rotaria tridens* (○) and *Macrotrachela* sp. (△).

all have reported this species from the lake microbenthos, and GODDARD & MCDIFFETT (1983) found it to dominate the rotifer community of a freshwater marsh in Pennsylvania.

Rotaria tridens

This species is the most abundant benthic rotifer in Mirror Lake, constituting almost half of all individuals living on the gyttja. Its distribution (Figs. 27, 28) is unique among rotifers and very unusual for any benthic animal. *R. tridens* was never found in samples from less than 7.5-m depth, and reaches its greatest abundance (mean annual density of 270,000 m^{-2}) at the 10.5-m station. There is no apparent seasonal variation in its abundance; it is abundant even in anaerobic samples containing H_2S. Furthermore, *R. tridens* is frequently found several centimeters below the mud-water interface (Fig. 30). It seems likely that the same physiological adaptations that enable this species to tolerate prolonged anoxia also free it from any need to visit the sediment surface for respiratory exchange. No other species of rotifer in Mirror Lake is common at the 9-m or 10.5-m station or within the sediments.

Moore (1939) found that "*Rotaria* spp." (*R. tridens* and *R. rotatoria*) were present in the anaerobic profundal sediments of Douglas Lake, Michigan, where no other rotifer lived. Cole (1955) reported that *R. rotatoria* was found under anaerobic conditions in eutrophic Crystal Lake, Minnesota. Since this species resembles *R. tridens* closely (the species are distinguished by their dental formulas), it is possible that Cole confounded the two species, as did Moore. In view of the distributions of the two species in Mirror Lake (Figs. 27, 28), I would suggest that the records of Moore and Cole of a *Rotaria* living on anoxic sediments probably refer to *R. tridens* rather than *R. rotatoria*. From this evidence, it would appear that *R. tridens* may be particularly adapted to life on the anoxic sediments of lakes. However, the species has been reported from streams and macrophyte beds in Europe (e.g., Donner 1964), so it is apparently not an obligate anaerobe. It would be interesting to know what physiological mechanisms enable this species to tolerate prolonged periods of anoxia, and why it is absent from the 0- to 6-m zone of Mirror Lake (compare the distributions of *Nais communis* (Oligochaeta) and *Cypria turneri* (Ostracoda)).

Discussion

Bdelloid rotifers are widespread and abundant in the benthos of Mirror Lake (Figs. 28, 29), having a lakewide density of 100,000 m^{-2}. The distributions of individual species (Figs. 27–28) are related to water depth, all of the species except

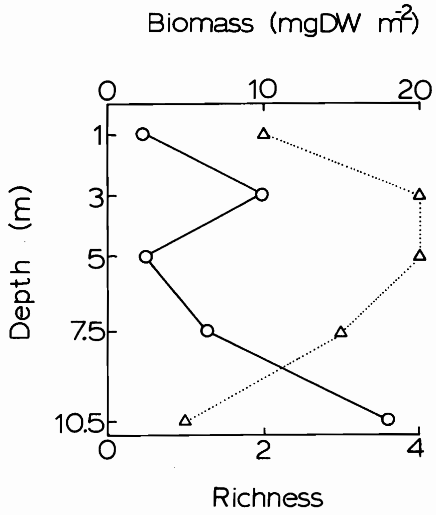


Fig. 29. Biomass (○) and species richness (△) of bdelloid rotifers in Mirror Lake, from transect data.

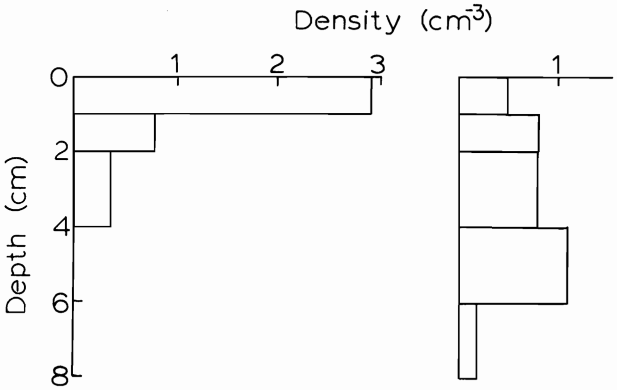


Fig. 30. Vertical distribution of *Rotaria tridens* (right) and all other bdelloid rotifers (left) within the sediments of Mirror Lake, as a function of distance from the sediment surface. Data are lakewide means from the transect.

Rotaria tridens being restricted to oxygenated sediments. *Rotaria tridens* also penetrates several centimeters into the Mirror Lake sediments, but the other bdelloids live at the sediment surface (Fig. 30). There is no evidence of seasonality in the bdelloid fauna of Mirror Lake, confirming MURRAY's (1905b) comment that "it is unusual for Bdelloids to have any seasonal limits". There are eight species of bdelloids in Mirror Lake, five of them common and widespread. In this respect, the fauna contrasts with the benthic monogonont rotifer taxocene of the lake, which consists of at least 56 species, none of them abundant.

There are very few studies of lacustrine bdelloids with which to compare my results, and essentially no quantitative data. MURRAY (1905b, 1906) reported that most species of bdelloids lived in ponds or along the margins of lakes, although *Dissotrocha macrostyla* (as *Philodina macrostyla*) was found at depths exceeding 75 m in Scottish lochs. MONARD (1920) found five species of bdelloids, including *Rotaria rotatoria* and *Dissotrocha macrostyla*, in the profundal sediments of Lac de Neuchatel. MOORE (1939) and COLE (1955) each found three species of bdelloids, including these two species, in the lakes that they studied. It seems clear that only a small fraction of bdelloid species (including *Dissotrocha macrostyla*, *Rotaria rotatoria* and *R. tridens*) are well adapted to life in lakes. However, these few species may be abundant, as they are in Mirror Lake. Although lakes may typically contain from two to ten species of bdelloids, ODEN (in litt.) found 41 species of bdelloids on the shallow-water sediments of Par Pond, South Carolina.

Because so little is known of the quantitative natural history of the bdelloids, it is difficult to assess their role in the Mirror Lake ecosystem. The bdelloids constitute a tiny fraction (0.3%) of zoobenthic biomass (Table 35). However, laboratory studies show that bdelloid populations may turn over very rapidly: RICCI (1978, 1983) found doubling times of 1.6 to 7 days for populations of nine species of bdelloids in culture. Using the modified equation of BANSE & MOSHER (1980), I predict a P/B of about 40 yr^{-1}. The bdelloids thus could account for about 2% of zoobenthic assimilation in Mirror Lake (Table 35). Bdelloids are eaten by predatory rotifers, chaetogastrine oligochaetes, and tanypod midge larvae in Mirror Lake.

Ectoprocta ("bryozoans")

I found the statoblasts of *Plumatella fruticosa* in the sediments of Mirror Lake. BUSHNELL (1966) found this species to frequent sites with slightly acid water in Michigan. WALTER (1985a) has reported two additional species of ectoproct from Mirror Lake, *Pectinatella magnifica* and *Fredericella sultana*.

Oligochaeta

Many of the "aquatic earthworms" are large enough to be collected by the coarse sieves that most limnologists use. As a result, the oligochaetes, along with the chironomid and chaoborid midges, are probably the best known animals in the lacustrine benthos. Several families of oligochaetes are represented in the freshwater zoobenthos. The Tubificidae and Lumbriculidae contain the large oligochaetes most frequently encountered by limnologists. These worms are primarily deposit feeding detritivores (e.g., BRINKHURST et al. 1969, 1972; MOORE 1981), but some species feed on benthic algae (MOORE 1978). Many important ecological and taxonomic studies have been carried out on the tubificids by BRINKHURST and others (see (BRINKHURST & JAMIESON 1971; BRINKHURST & COOK 1980; STIMPSON et al. 1982; and the references cited in these works for an introduction). The Tubificidae are especially important because their method of deposit feeding causes rapid mixing of lake sediments, a process of major importance to nutrient cycling, paleolimnology, and other fields (e.g., McCALL & FISHER 1980; ROBBINS 1982).

The other major family of freshwater oligochaetes is the Naididae, an ecologically diverse group of worms, many of them small. Some naidids are deposit feeders, but many others eat algae or small animals (e.g., STREIT 1977; LEARNER et al. 1978; MOORE 1981; FRENZEL 1981, 1983a; BOWHER et al. 1983). Reproduction in the Naididae is predominately asexual, in contrast to the sexually reproducing tubificids and lumbriculids. The Naididae often are overlooked by limnologists, even though they dominate the oligochaete communities of many lakes (see below). Other families of oligochaetes (Enchytraeidae, Dorydrilidae, Haplotaxidae) are usually of secondary importance in northern temperate lakes.

Naididae

Amphichaeta americana

This is the second most abundant oligochaete in Mirror Lake, having a mean density of 3800 m^{-2} for the transect and 8600 m^{-2} for the gyttja. It is widespread from 1-m to 7.5-m, but I never found it at 9-m or 10.5-m (Figs. 31, 32). Although it is present throughout the year, highest densities occur from October through May. I found the trophi of the bdelloid rotifer *Hablotrocha* in the gut of one animal; more commonly, though, *A. americana* feeds on benthic diatoms in Mirror Lake. FRENZEL (1981, 1983a) reported that another species of the genus, *A. leydigii,* fed almost exclusively on benthic diatoms in the Bodensee in Germany.

A. americana is known through only a few collections from Michigan, New Jersey, and the Carolinas (BRINKHURST & KATHMAN 1984). This paucity of records is probably due in part to the small size of this worm: I estimate that a 105-µm sieve retained only 70% of the individuals that I collected. Very little is known of the ecology of *A. americana.*

Chaetogaster diastrophus

This small oligochaete is the most abundant annelid in Mirror Lake, with a mean density of 15,000 m^{-2} lakewide and 8700 m^{-2} on the gyttja. It is also the dominant oligochaete in terms of biomass, constituting 20% of oligochaete biomass. *C. diastrophus* is abundant throughout the year at the 1-m to 7.5-m stations (Figs. 31, 32). I sometimes found this species at the 9-m and 10.5-m stations, but the densities were never high, and found this species only four times where the dissolved oxygen concentrations were less than 3 mg l^{-1}. The animals that I collected from Mirror Lake usually contained benthic diatoms, some 1/3 as long as the worm. A few contained the remains of benthic ploimate rotifers such as *Colurella.* Previous studies likewise have found diatoms and rotifers to form the bulk of the diet of *C. diastrophus* (WACHS 1967; STREIT 1977; SCHWANK 1981; FRENZEL 1981, 1983a).

C. diastrophus is common and widely distributed in lakes and streams (e.g., KASPRZAK 1977; LEARNER et al. 1978; HILTUNEN & KLEMM 1980; SCHWANK 1981; FRENZEL 1981, 1983a). Quantitative data on density are rare because of the small size of this worm. For example, in Mirror Lake, a 105-µm sieve retains only 50% of the individuals of this species. In some localities, *C. diastrophus* was most abundant in the summer (MCELHONE 1978; FRENZEL 1981), but in others, including Mirror Lake, it is abundant at all seasons (SCHWANK 1981; LODEN 1981).

Nais communis

This worm has an unusual distribution in Mirror Lake. It is abundant only during October through May, and only at the 7.5-m and 9-m stations (Fig. 31). I found only one example of *N. communis* in the 1-m to 6-m zone, and never found it where the water temperature was above 18 °C. Furthermore, unlike the other naidids, *N. communis* frequently burrows a few centimeters into the substratum (Fig. 38). I can confirm FRENZEL'S (1983) observation that the guts of these animals usually contain sediment particles and benthic algae.

If only the data from Mirror Lake were available, one might conclude that this species is a specialized deepwater stenotherm. In fact, the species is among the most eurytopic of the naidids, and has been recorded from the littoral zones of lakes (PIGUET 1906; MUCKLE 1942) and streams (LEARNER et al. 1978; SCHWANK 1981) throughout the world. A few authors (e.g., MUCKLE 1942; LEARNER et al. 1978) reported *N. communis* to be most abundant in the summer or autumn, while several others (PIGUET 1906; WACHS 1967; LODEN 1981) found it to be a winter species.

Given the broad environmental tolerances of this species, the question arises as to the factors restricting its distribution in Mirror Lake. It is likely that low concentrations of dissolved oxygen prevent *N. communis* from colonizing the 10.5-m station. Its absence from the littoral zone is more puzzling. Perhaps some interactions with other organisms keep this species out of the littoral zone.

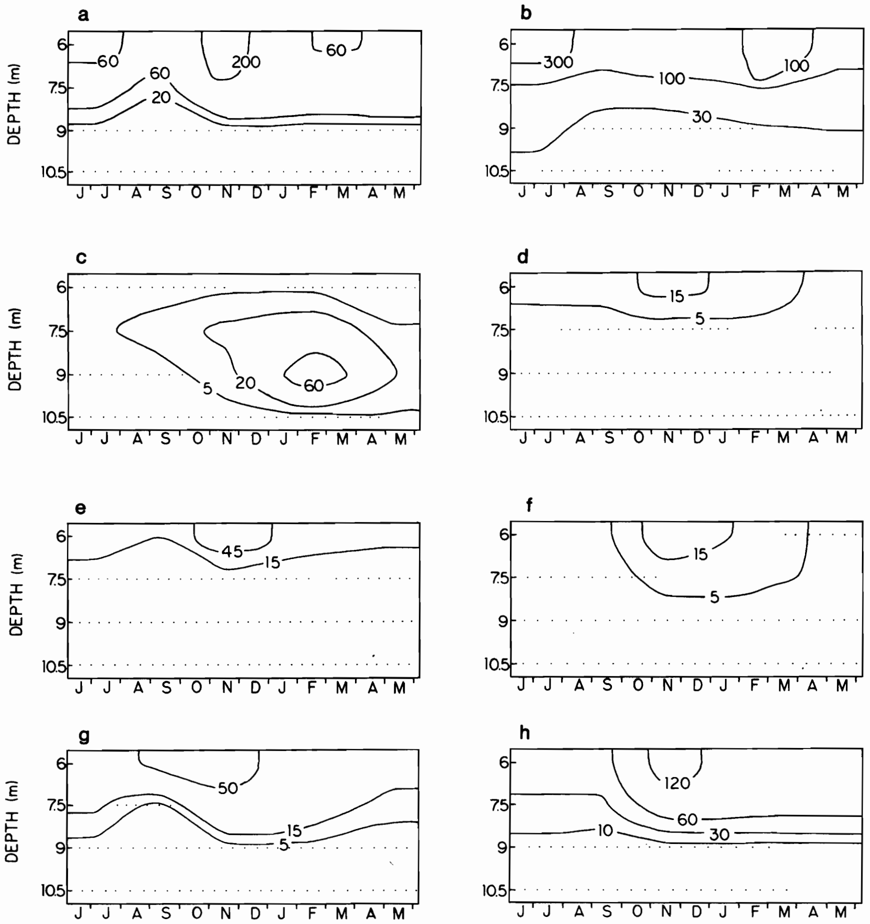


Fig. 31. Abundance (dm^{-2}) of naidid oligochaetes in Mirror Lake. (a) *Amphichaeta americana*, (b) *Chaetogaster diastrophus*, (c) *Nais communis*, (d) *Nais simplex*, (e) *Piguetiella blanci*, (f) *Slavina appendiculata*, (g) *Specaria josinae*, (h) *Vejdovskyella comata*. Dotted lines show extended periods when the species were absent from the indicated stations.

Nais simplex

This species is found in small numbers at the 1-m to 6-m stations (Figs. 31, 32). I collected *N. simplex* throughout the year, but there is a slight indication of a population maximum in October and November. Unlike its congener, *N. simplex* is a surface-dweller; 82% of the population lives in the top centimeter of sediment in Mirror Lake. This Holarctic species has been found frequently in the littoral zone of lakes, but it is usually rare (e. g., Piguet 1906; Kasprzak 1977; Hiltunen & Klemm 1980; Loden 1981).

Piguetiella blanci

This species is present, but uncommon, throughout the year at the 1-m to 6-m stations in Mirror Lake (Figs. 31, 32). As Frenzel (1983a) reported, *P. blanci* feeds on lake sediments.

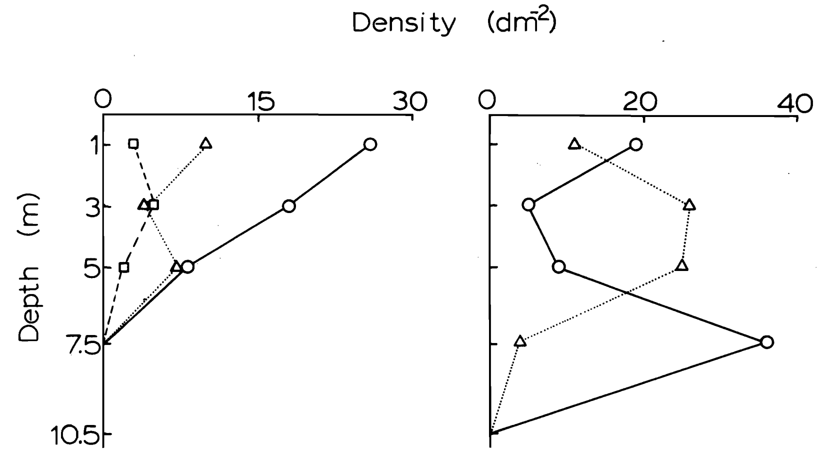


Fig. 32. Density of naidid oligochaetes in Mirror Lake, from transect data. Left: *Pristina* spp. (○), *Piguetiella blanci* (△), and *Nais simplex* (□). Right: *Vejdovskyella comata* (○) and *Specaria josinae* (△).

P. blanci lives in the littoral and sublittoral zones of lakes, especially on mud or muddy sand (PIGUET 1906; MONARD 1920; MUCKLE 1942; TIMM 1970; SARKKA 1979; FRENZEL 1983a). It is usually not abundant. Mirror Lake is the only known North American locality for this species (see STRAYER 1983, where I also gave data on the morphology of specimens of *P. blanci* from Mirror Lake).

Pristina spp.

Both species that live in Mirror Lake, *P. aequiseta* and *P. leidyi,* have similar distributions in the lake, so I have combined them in Fig. 32. *Pristina* spp. are fairly abundant at the 1-m to 5-m stations on the transect, and were found throughout the year at the 6-m stations on the gyttja. There is some evidence that densities were highest in the autumn. I found both the "*aequiseta*" and "*foreli*" morphs of *P. aequiseta* in Mirror Lake, but following LODEN & HARMAN (1980), I consider them both to be *P. aequiseta.*

Slavina appendiculata

This worm was collected in small numbers from 1-m to 7.5-m in Mirror Lake (Fig. 31). Population densities are somewhat higher during the autumn than during the rest of the year. *S. appendiculata* is a cosmopolitan species found in lakes and slow-moving streams, and particularly in bogs and marshes (PIGUET 1906; TIMM 1970; LEARNER et al. 1978; SCHWANK 1981; WHITESIDE & LINDEGAARD 1982).

Specaria josinae

S. josinae is present throughout the year at the 1-m to 7.5-m stations in Mirror Lake (Figs. 31, 32). Densities are somewhat higher during the autumn. Unlike most of the naidids, *S. josinae* burrows below the top centimeter of sediment (Fig. 38). The guts of individuals of this species in Mirror Lake are filled with sediments (see also FRENZEL 1983a). I have previously presented some notes on the morphology of specimens of this worm from Mirror Lake (STRAYER 1983).

S. josinae is known from lakes and streams in Europe and North America, where it is usually regarded as uncommon. It has been found most frequently in littoral and sublittoral sand and mud (TIMM 1970; JUGET & GIANI 1974; LEARNER et al. 1978; TUDORANCEA et al. 1979, FRENZEL 1983a).

Vejdovskyella comata

This is the most abundant of the large naidids in Mirror Lake (gyttja = 4900 m^{-2}; transect = 2100 m^{-2}), and was found throughout the year at the 1-m to 7.5-m stations (Figs. 31, 32). Peak densities occur in the autumn. *V. comata* feeds on sediment particles and benthic diatoms in Mirror Lake. FRENZEL (1983) reported that *V.* cf. *intermedia* had a similar diet in the Bodensee.

There are scattered records of *V. comata* from lakes, and occasionally streams, in Europe and North America (e. g., KASPRZAK 1977; LEARNER et al. 1978; HILTUNEN & KLEMM 1980; SCHWANK 1981). It often has been considered rare, but may be abundant in soft waters such as Mirror Lake (cf. TIMM 1970; WHITESIDE & LINDEGAARD 1982).

Other Naididae

I found four other species of naidids in Mirror Lake (Table 12). In addition, WALTER (1985a) listed *Stylaria fossularis,* which may be a synonym of *S. lacustris* (BRINKHURST & KATHMAN 1984), from Mirror Lake.

Table 12. List of rare oligochaetes in Mirror Lake.

Naididae	Tubificidae
Dero digitata	*Quistadrilus multisetosus*
Dero obtusa	*Rhyacodrilus montana*
Stylaria lacustris	*Spirosperma nikolskyi*
Uncinais uncinata	

Tubificidae

Seven species of Tubificidae were identified from Mirror Lake. Because immature individuals of most species cannot be identified with certainty, and because most of the tubificids that I collected were immature, I used the following approach to tentatively assign immature tubificids to species. All tubificids without hair chaetae and without any special distinguishing features were assigned to *Limnodrilus hoffmeisteri.* Immatures with hair chaetae were assigned to *Ilyodrilus templetoni* if the anterior ventral chaetae had obviously unequal teeth, or to *Tubifex tubifex* if the anterior ventral chaetae had subequal teeth.

Aulodrilus pigueti

This species is abundant only at the 1-m station (Fig. 33). In 1980–81, I found a few individuals of this species at 7.5-m in *Nitella* beds. According to STIMPSON et al. (1982), *A. pigueti* is a cosmopolitan species that prefers silty substrata in mesotrophic waters.

Ilyodrilus templetoni

I found this species only at 7.5-m in Mirror Lake (Fig. 33). It apparently has a very clumped distribution, since I found very high densities (>7000 m^{-2}) in three samples, low densities (ca. 1000 m^{-2}) in three others, and none in the remaining samples. *I. templetoni* has been found in low numbers in the sublittoral and profundal zones of European lakes (e.g., TIMM 1970; KASPRZAK 1977; FRENZEL 1983b). It is one of the most common tubificids in North America, where it prefers moderately enriched sites (STIMPSON et al. 1982).

Limnodrilus hoffmeisteri

This species is widely distributed in Mirror Lake, and most abundant at 9-m (Figs. 33, 34). I found the highest densities of this species in the autumn and winter. *L. hoffmeisteri* is one of the most abundant and widespread tubificids in the world. It is especially characteristic of polluted or enriched sites (e. g., STIMPSON et al. 1982). In lakes, *L. hoffmeisteri* is typically a species of sublittoral or upper profundal zone sediments (e. g., BRINKHURST 1964; SARKKA 1979; FRENZEL 1983b).

Tubifex tubifex

Worms that I assigned to this species are the most abundant of the tubificids in Mirror Lake, and are especially abundant at the 6-m to 9-m stations (Figs. 33, 34). *T. tubifex* is

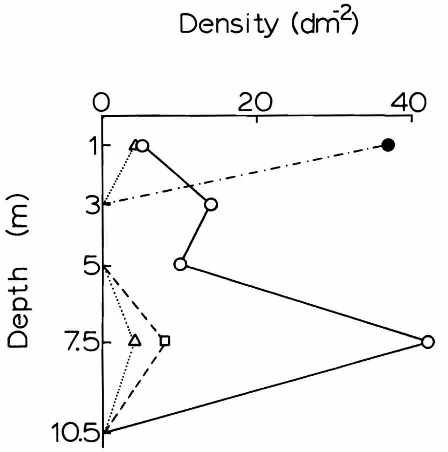


Fig. 33. Density of tubificid oligochaetes in Mirror Lake, from transect data. *Tubifex tubifex* (○), *Aulodrilus pigueti* (●), *Limnodrilus hoffmeisteri* (△), and *Ilyodrilus templetoni* (□).

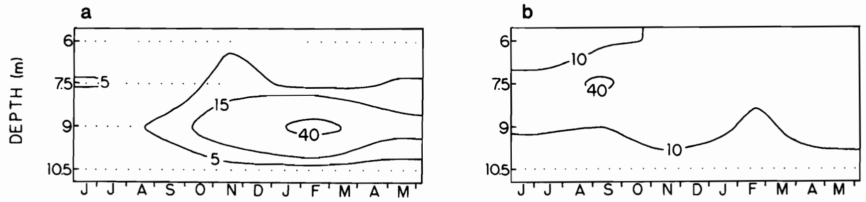


Fig. 34. Abundance (cm^{-2}) of tubificid oligochaetes in Mirror Lake. (a) *Limnodrilus hoffmeisteri*, and (b) *Tubifex tubifex*. Dotted lines show extended periods when the species were absent from the indicated stations.

well known as a species of grossly polluted habitats (e.g., BRINKHURST 1964, 1970; SARKKA 1979); it is also a characteristic species in oligotrophic and alpine lakes (e.g., MONARD 1920; BRINKHURST 1964; STIMPSON et al. 1982).

Other Tubificidae

Three other species of tubificids were collected from Mirror Lake (Table 12).

Enchytraeidae

Members of this taxonomically difficult family were fairly common in samples from the littoral sediments (Fig. 35). I found only a single enchytraeid in my survey of the gyttja. Although enchytraeids are often thought of as being terrestrial or semi-aquatic, they are in fact often collected in surveys of the lacustrine zoobenthos, and are sometimes abundant (Table 14). Other records of lacustrine enchytraeids have been given by MONARD (1920), MUCKLE (1942), JUGET & GIANI (1974), HARE & CARTER (1977), KASPRZAK (1977), DERMOTT (1978), SARKKA (1979, 1983), and FRENZEL (1983b).

Lumbriculidae

This family was represented in my collections by a single immature animal taken from 1 m. Lumbriculids are commonly prominent members of the lacustrine oligochaete fauna (Tables 13, 14).

Aeolosomatidae

These small worms (*Aeolosoma* spp.), now classified with the archiannelids rather than the oligochaetes, are abundant at the 6-m stations in Mirror Lake (Fig. 37). I found occasional specimens at 5-m and 7.5-m as well. Population densities are highest during October through

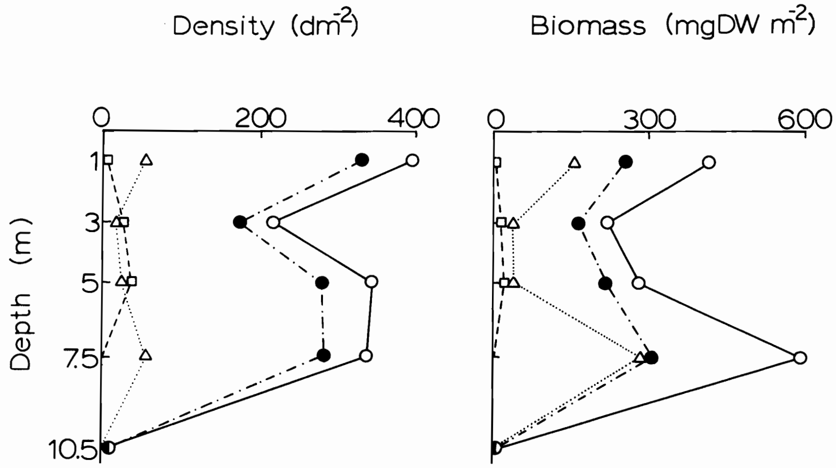


Fig. 35. Abundance and biomass of microannelids in Mirror Lake, from transect data. Total Microannelida (○), Naididae (●), Tubificidae (△), and Enchytraeidae (□).

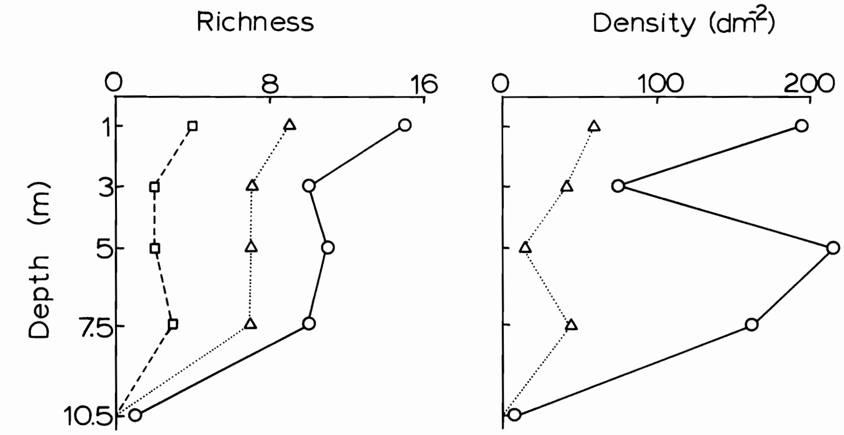


Fig. 36. Left: Species richness of microannelids in Mirror Lake. Total Microannelida (○), Naididae (△), and Tubificidae (□). Right: Abundance of naidid oligochaetes in Mirror Lake. *Chaetogaster diastrophus* (○) and *Amphichaeta americana* (△). All data from transect.

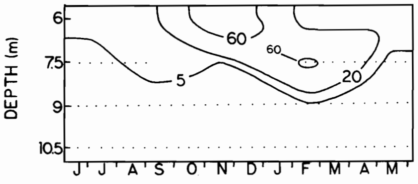


Fig. 37. Abundance (dm^{-2}) of the microannelids *Aeolosoma* spp. in Mirror Lake. Dotted lines show extended periods when the species were absent from the indicated station.

March, although my data are not detailed. At least two species are present in Mirror Lake. Aeolosomatids are too small to be found in most routine benthic surveys, but they are apparently common in many lakes (e.g., Monard 1920; Moore 1939; Cole 1955; Kasprzak 1977; Sarkka 1979). Most records are from the littoral zone, but Sarkka (1979) found *Aeolosoma* spp. in the profundal zone of the Finnish lake Paijanne.

Discussion

I found 25 species of microannelids in Mirror Lake. Because my sampling was not especially intensive, the fauna is probably actually larger than this. In Table 13, I have summarized the composition and species richness of oligochaete assemblages in lakes. It is possible to make a few generalizations about lacustrine oligochaete assemblages based on the information in this table. First, it is obvious that only lakes in the temperate zone have received much attention. Among the temperate lakes, there appears to be little variation in species richness or community composition at the familial level that can be related to environmental characteristics. All of the lakes in the table, whether productive or unproductive, hardwater or softwater, contain about 30–60 species of oligochaetes. Variation in species richness appears to be correlated only with intensity of sampling. Two families, the

Table 13. Total species richness (S), and familial composition of the microannelid fauna of some lakes where it has been studied, in comparison with Mirror Lake. Entries are the number of species reported; (–) indicates that the family was not studied.

Lake	S	Naididae	Tubificidae	Lumbriculidae	Enchytraeidae	Aeolosomatidae	Others	Source
Mirror	>25	14	7	1	>1	>2	0	this study
Ontario, USA/Canada	59	25	31	2	1	–	0	SPENCER 1980
Superior, USA/Canada	55	28	23	3	1	–	0	SPENCER 1980
Huron, USA/Canada	54	24	27	2	1	–	0	SPENCER 1980
Erie, USA/Canada	50	24	23	3	0	–	0	SPENCER 1980
Michigan, USA	46	16	27	2	1	–	0	SPENCER 1980
Goslawickie, Poland	44	21	10	2	9	2	0	KASPRZAK 1977
Cayuga, USA	>40	>15	22	1	>1	–	>1	SPENCER 1978
Mikorzynskie, Poland	39	19	11	1	3	5	0	KASPRZAK 1977
Neuchatel, Switzerland	>35	18	11	3	>1	>1	1	MONARD 1920
Patnowskie, Poland	34	20	7	1	3	3	0	KASPRZAK 1977
Slesinskie, Poland	34	15	12	2	3	2	0	KASPRZAK 1977
Paijanne, Finland	>33	18	9	3	>1	>1	1	SARKKA 1979
St. Clair, USA/Canada	33	16	15	2	0	–	0	SPENCER 1980
Lichenskie, Poland	30	16	7	1	4	2	0	KASPRZAK 1977
Parry Sound, Canada	>30	12	14	1	>1	>1	1	HARE & CARTER 1977
Bodensee, Germany, 1936/37	>29	18	7	3	>1	–	0	MUCKLE 1942
Bodensee, Germany, 1977/78	>28	14	11	1	>1	–	1	FRENZEL 1983 a, b

Tubificidae and the Naididae, contribute the bulk of the species in most lakes. The Laurentian Great Lakes contain more tubificids than do most other lakes, but this may be due to the widespread use of relatively coarse sieves, which retain few naidids, in the Great Lakes. I estimate a mean lakewide density of 30,000 oligochaetes m^{-2}, nine times higher than the value reported by WALTER (1985a), who used a 250-µm sieve in her study of the Mirror Lake macrobenthos. Naidids contribute 56% of the species, 83% of the individuals, and 56% of the biomass of the Mirror Lake oligochaete assemblage (Figs. 35, 36).

I found few comparable data on oligochaete densities in other lakes. Most previous workers have used sieves that are too coarse to retain the small naidids, enchytraeids, and aeolosomatids. In spite of statements to the contrary (e. g., LEARNER et al. 1978), the naidids are numerically dominant in most lakes that have been surveyed with fine sieves (Table 14). Tubificids, and less commonly lumbriculids and enchytraeids, are important in some lakes. Mirror Lake has the highest density of oligochaetes reported, but other lakes have similar densities.

Most naidids are abundant in the 1-m to 7.5-m zone in Mirror Lake (Figs. 31, 32) and are found only rarely at deeper stations. This distribution is consistent with the observation that the naidids are not usually found where dissolved oxygen is scarce or absent (e. g., LEARNER et al. 1978). The distribution of the tubificids is less easily explained. They are present throughout the 1-m to 9-m zone (Figs. 33, 34), but were never found deeper than 10-m, either by WALTER (1985a) or me. Tubificids may be very tolerant of low oxygen concentrations, and are in fact one of the characteristic inhabitants of grossly polluted, oxygen-free waters. It seems more likely that the tubificids are absent from the deepest sediments because of intense predation from the midge *Chaoborus,* an animal that is especially abundant in the profundal sediments of Mirror Lake (Figs. 60, 61). SWUSTE et al. (1973) reported that tubificids are a preferred prey of *Chaoborus,* and HOWMILLER (1977) found that tubificids were absent from the profundal sediments of lakes in Wisconsin where oxygen was absent and where *Chaoborus* densities were high.

The naidids and tubificids have very different vertical distributions within the Mirror Lake sediments (Fig. 38). Most of the naidids live in the top centimeter of sediment, although two species, *Specaria josinae* and *Nais communis,* were commonly found deeper. The tubificids burrow even more deeply, and are among the few benthic animals found more than 4 cm below the sediment surface in Mirror Lake. Several other authors have reported similar distributions of tubificids and naidids in lake sediments (e. g., MILBRINK 1973; NALEPA & ROBERTSON 1981a). The enchytraeids are restricted completely to the top 2 cm of sediment in Mirror Lake (Fig. 38).

Most oligochaete species are present throughout the year in Mirror Lake. However, many species, especially in the Naididae, show a distinct seasonality. Most of the naidids reach maximum population densities during the fall, often following a weak minimum in density in the late summer. *Nais communis,* an

Table 14. Microannelid abundance (m^{-2}), by family, in several lakes.

Lake	MESH (μm)	Total	Naididae	Tubificidae	Lumbriculidae	Enchytraeidae	Aeolosomatidae	Notes	Source
Mirror	–	30,000	25,000	4,100	120	810	90	lakewide mean, June–Oct.	this study
Mirror	–	33,000	27,500	3,700	0	90	1600	annual mean, gyttja	this study
Mirror	250	3,300	–	–	–	–	–	lakewide mean	WALTER 1985a
Neusiedlersee, Austria	507	23,000	23,000	700	0	0	a	near reed belt	SCHIEMER 1979
Loch Leven, Scotland	500	19,000	850	12,000	700	5,500	0		MAITLAND 1979
Bodensee, Germany	100	–	16,000	–	–	–	–	littoral + sublittoral	FRENZEL 1983a
Michigan, USA	45	15,000	6,200	4,200	3200	1,300	0	mean, Apr.–Nov., $z = 11–23$ m	NALEPA & QUIGLEY 1983
Grane Langsø, Denmark	100	6,200	2,700	1,700	420	1,500	0	lakewide mean, July	WHITESIDE & LINDEGAARD 1983

[a] "rarely encountered"

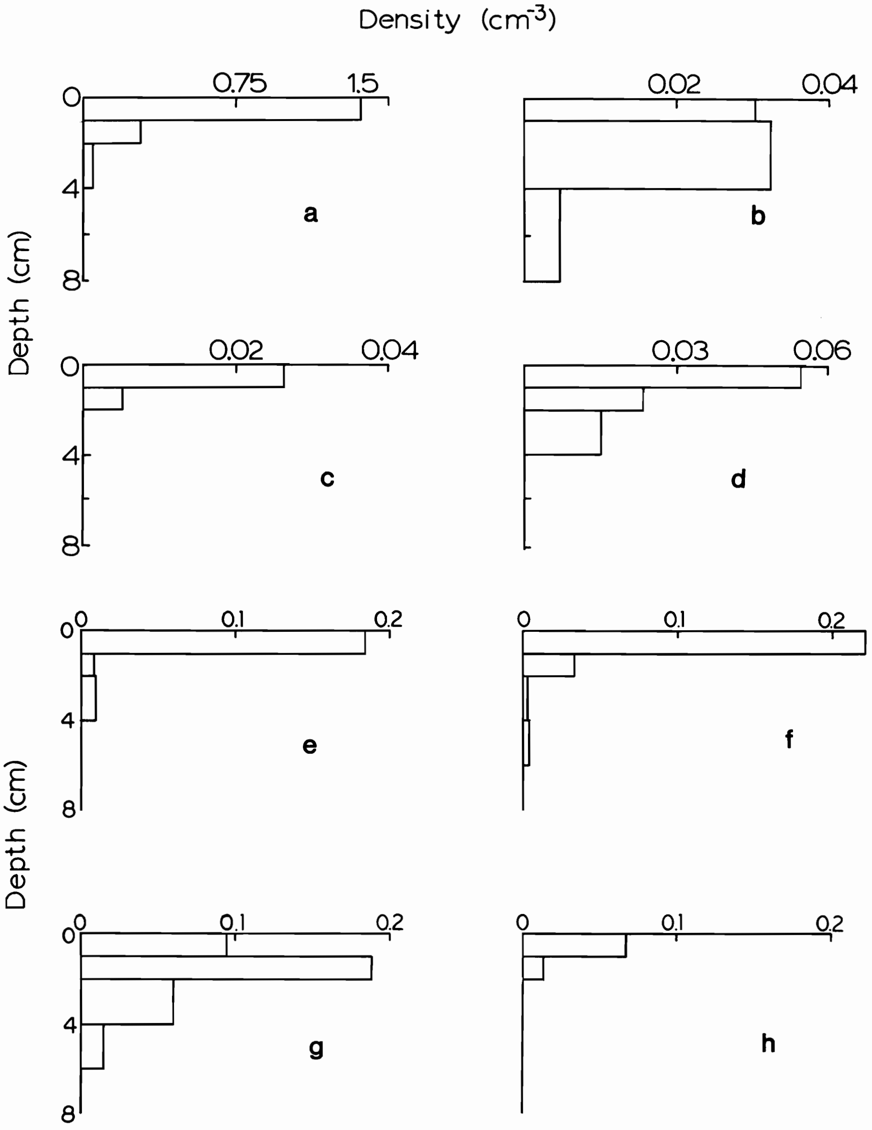


Fig. 38. Vertical distribution of oligochaetes within the sediments of Mirror Lake, as a function of depth from the sediment surface. (a) Chaetogastrinae, (b) *Nais communis*, (c) *Piguetiella blanci*, (d) *Specaria josinae*, (e) *Vejdovskyella comata*, (f) all other Naididae, (g) Tubificidae, (h) Enchytraeidae. Data are lakewide means from the transect, except for *Nais communis*, for which data from the gyttja survey were used.

exception to this pattern, is most abundant during January through March (Fig. 31). In the Tubificidae, I was unable to identify any seasonal trends with certainty.

The oligochaetes are one of the most prominent parts of the Mirror Lake zoobenthos. They contribute an estimated 16% of zoobenthic biomass, and about 15 to 20% of zoobenthic assimilation (Table 35). The algivorous naidids are probably responsible for a large fraction of the grazing pressure on benthic algae. In turn, the oligochaetes are eaten by predatory flatworms (personal observation; LUTHER 1960), cyclopoids (FRYER 1957a), chironomids (personal observation; LODEN 1974), and *Chaoborus* (SWUSTE et al. 1973). Furthermore, it seems likely that the tubificids cause much of the bioturbation that has been observed in the sediments of Mirror Lake (MOELLER 1985) by their feeding activities.

The modified BANSE and MOSHER regression predicts a P/B of 5 yr^{-1} for oligochaetes in Mirror Lake. Estimated P/B ratios for natural populations of tubificids vary widely, but average about 5 yr^{-1} (MASON 1977; WATERS 1977; KAJAK et al. 1980; ADREANI et al. 1981). Naidids reproduce very rapidly under favorable conditions in the laboratory (PODDUBNAYA 1972; STREIT 1978; LOCHHEAD & LEARNER 1983), suggesting that natural populations may turn over more rapidly than predicted by the BANSE and MOSHER equation. However, I know of no estimates of the turnover rates of naidid populations in nature.

Nematode parasites of oligochaetes

I found large (>1 mm long) parasitic nematodes in 13 individuals of six oligochaete species, viz: *Amphichaeta americana*, *Chaetogaster diastrophus*, *Piguetiella blanci*, *Specaria josinae*, *Limnodrilus hoffmeisteri*, and *Tubifex tubifex*. Most of the infested worms harbored one or two nematodes, but one animal of *L. hoffmeisteri* contained five large nemtatodes. I know nothing of the identity or life cycle of these nematodes. POINAR (1978), who reviewed the nematode parasites of oligochaetes, gave no records for naidids or tubificids, but JUGET (1958) reported that some of the oligochaetes in Lake Geneva contained parasitic nematodes.

Because these nematodes are so large, and because they often inhabit the reproductive segments of the oligochaetes, it seems likely that they do great harm to their hosts. The low infestation rate (0.6% for all oligochaetes combined) suggests that these parasites are of little importance in the population dynamics of the Mirror Lake oligochaetes. However, because only the largest nematodes would be visible in the mounting medium that I used for oligochaetes, I have certainly underestimated the true infestation rate. Until much more is known about the life cycle and actual population size of these parasitic nematodes in Mirror Lake, it is impossible to estimate the impact that they might have on the oligochaete populations.

Tardigrada (water bears)

Tardigrades are small metazoans that creep about on aquatic or terrestrial substrata. The terrestrial species, which constitute the majority of tardigrade species, are well known for their ability to withstand severe freezing and drying. Most tardigrades are herbivores, but a few carnivorous species are known (PENNAK 1978). The tardigrades have received much attention recently, especially from morphologists and systematists (RAMAZZOTTI 1972, 1974; HIGGINS 1975; NELSON 1982). Most of this work has been done on the terrestrial species, so we still know little about the lacustrine tardigrades (but see SCHUSTER et al. 1977).

Three species of tardigrades are found in Mirror Lake: *Dactylobiotus grandipes,* an unidentified species of *Macrobiotus,* and a species of *Pseudobiotus* which, according to Dr. DIANE NELSON (in litt.), belongs to a complex of species that are usually erroaneously referred to *Isohypsibius augusti* (Table 15). The three species have similar distributions in space and time at Mirror Lake, so I lumped them together in Figures 39 and 40.

Table 15. Mean weighted abundance (dm^{-2}) of tardigrades in Mirror Lake.

Species	Transect	Gyttja
Pseudobiotus sp.	50	110
Macrobiotus sp.	0	25
Dactylobiotus grandipes	20	15
Total Tardigrada	70	140

Tardigrades are found in small numbers throughout the year at stations where dissolved oxygen was present (Fig. 39). Although tardigrades are often thought of as animals of the beach zone and shallow water sediments, there is no indication in my data that they are more abundant in the shallows of Mirror Lake (Fig. 40). SCHUSTER et al. (1977) found marked seasonal changes in the tardigrade populations of the nearshore benthos of Lake Tahoe, but I found no evidence for any strong seasonal trends in Mirror Lake (Fig. 39). My data are too meager to describe the distribution of tardigrades within the sediments of Mirror Lake.

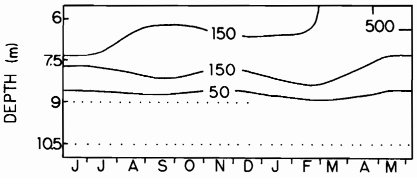


Fig. 39. Abundance (dm^{-2}) of tardigrades in Mirror Lake. Dotted lines show extended periods when tardigrades were absent from the indicated station.

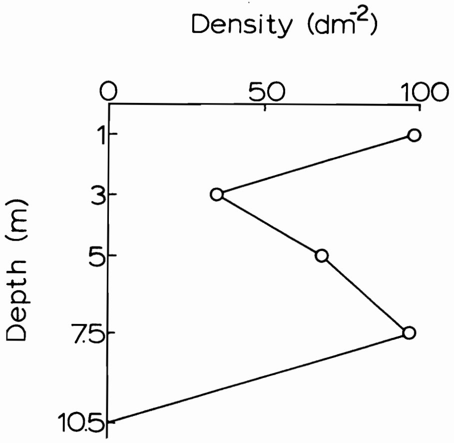


Fig. 40. Density of tardigrades in Mirror Lake, from transect data.

Knowledge of the lacustrine tardigrades is limited to the studies of MURRAY (1905a, 1907) and SCHUSTER et al. (1977) and to the incidental information reported in general surveys of the lacustrine meiobenthos. From these studies, it appears that the tardigrades are usually minor members of the lacustrine zoobenthos. Lakes usually contain only two to five species (Table 16), excluding stragglers from the lake's margin and watershed. The species most commonly reported belong to the genus *Dactylobiotus* (SCHUSTER et al. 1980) (formerly *Macrobiotus,* in part). These species include *D. grandipes* (SCHUSTER et al. 1977); this study), *D. macronyx* (MURRAY 1907; MONARD 1920; MUCKLE 1942), and *D. dispar* (HOLOPAINEN & PAASIVIRTA 1977). Other species belonging to *Macrobiotus, Hypsibius, Diphascon,* and *Isohypsibius* are found occasionally as well (e. g., MONARD 1920; MUCKLE 1942; SCHUSTER et al. 1977; ANDERSON & DE HENAU 1980).

Tardigrades are widely distributed in lakes on various substrata, and have been found from the shoreline to depths of 150 m (MONARD 1920). They have never been collected from sediments beneath anoxic waters, to my knowledge. However, NALEPA & ROBERTSON (1981a) found undetermined species of tardigrades to be among the few animals abundant within the reduced sediments of Lake Michigan. Their observations suggest that some species are able to tolerate anoxia, at least for short periods.

There are few quantitative data on densities of tardigrades in lakes (Table 16). From these data, it appears that tardigrade densities in lakes are often on the order of 10,000 m^{-2}. Much higher densities have been found on occasion; both ODEN (1979) and ANDERSON & DE HENAU (1980) found some samples to contain more than 100,000 tardigrades m^{-2}. However, such densities are probably exceptional.

The biomass of tardigrades in Mirror Lake is very low (Table 16); only about 0.6% of zoobenthic biomass. The few comparable data are listed in Table 16. Unless

Table 16. Species richness (S), abundance (m^{-2}), and biomass (mg m^{-2}) of tardigrades in some lakes.

Lake	MESH (µm)	S	Abundance	Biomass	Notes	Source
Mirror	–	3	7,500	2^b	lakewide means, June–Oct.	this study
Neusiedlersee, Austria	50?	1	33,000	–	annual mean for one site	SCHIEMER 1979
Michigan, USA	45	–	34,000	10^b	z = 11–23 m; Apr.–Nov.	NALEPA & QUIGLEY 1983
Paajarvi, Finland	100	–	1,200	1^c	annual lakewide mean	HOLOPAINEN & PAASIVIRTA 1977
Tahoe, USA	44	4^a	–	–	detailed study of one site (z = 0–6 m)	SCHUSTER et al. 1977
Bodensee, Germany	–	2	–	–	z = 0–30 m	MUCKLE 1942
Neuchatel, Germany	–	2	–	–	profundal samples	MONARD 1920

[a] excludes semi-aquatic species restricted to the lake margin
[b] dry weight
[c] ash-free dry weight

tardigrades are much more abundant than these observations suggest, it is not likely that they are of any great importance in community or ecosystem dynamics in lakes (cf. Table 35).

Cladocera

The order Cladocera contains many species that live on the sediments, among vegetation, and in the pelagic zone of lakes. The planktonic cladocerans, including such genera as *Daphnia* and *Bosmina,* have been the subject of an enormous amount of ecological study, some of which was reviewed by HUTCHINSON (1967) and KERFOOT (1980). However, as is the case with the rotifers and copepods, the majority of cladoceran species are associated with sediments or vegetation. These species are very diversified morphologically and ecologically (see the outstanding work of FRYER 1968, 1974, for some examples). Most benthic cladocerans are bacterivorous or herbivorous filter-feeders, like their planktonic counterparts, and most are facultative parthenogens.

The benthic cladocerans have received much less study than the planktonic species, but one family, the Chydoridae, has attracted considerable attention from ecologists. Since the discovery of large numbers of chydorid remains in lake sediments, ecologists have tried to understand the taxonomy and ecology of living chydorids, so that the chydorid remains can be used as an interpretative tool in paleolimnology (see FREY 1960, 1964, 1979; GOULDEN 1964, 1969; and WHITESIDE 1970, for some examples). Because of the many studies on chydorid ecology done in the past 20 years (e. g., FLÖSSNER 1964; FRYER 1968; WHITESIDE 1970, 1974; GOULDEN 1971; KEEN 1973, 1976; WHITESIDE et al. 1978; WILLIAMS & WHITESIDE 1978; DOWNING 1981; CHENGALATH 1982; FREY 1982c; WILLIAMS 1983), we now know more about the chydorids than about most meiobenthic animals, although our knowledge is hardly complete. Other cladoceran families, for example the Macrothricidae, have received much less study from ecologists (but see FLÖSSNER 1964; SERGEEV 1970; FRYER 1974; CHENGALATH 1982; FRENZEL 1982).

Ilyocryptus sordidus

This mud-dwelling cladoceran is abundant along a narrow band of the gyttja sediments in Mirror Lake (Figs. 41, 42). Although present throughout the year, the population exhibits a distinct maximum in the late fall, when I found densities in excess of 10,000 m^{-2}. It seems likely that the lower limit of distribution of *I. sordidus* in Mirror Lake is set by low concentrations of dissolved oxygen; I found the species only once where the dissolved oxygen concentration was less than 5 mg l^{-1}, and never where it was below 2 mg l^{-1}. Unsuitable substrata may prevent *I. sordidus* from living on the shallow-water sediments, since the species usually reaches its greatest abundance in mud or detritus, and is found in small numbers on other substrata (MONARD 1920; MOORE 1939; MUCKLE 1942; COLE 1955; REY & DUPIN 1973a; HOLOPAINEN & PAASIVIRTA 1977).

Ilyocryptus sordidus has been reported from the benthos of many lakes in Europe and North America (BROOKS 1959; SMIRNOV 1976; CHENGALATH 1982; and references cited above). FRYER (1974) described in detail the structure and habits of this cladoceran.

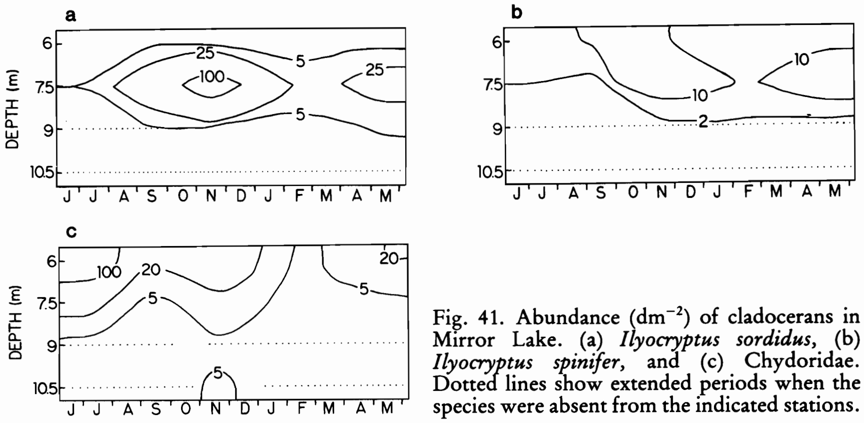


Fig. 41. Abundance (dm^{-2}) of cladocerans in Mirror Lake. (a) *Ilyocryptus sordidus,* (b) *Ilyocryptus spinifer,* and (c) Chydoridae. Dotted lines show extended periods when the species were absent from the indicated stations.

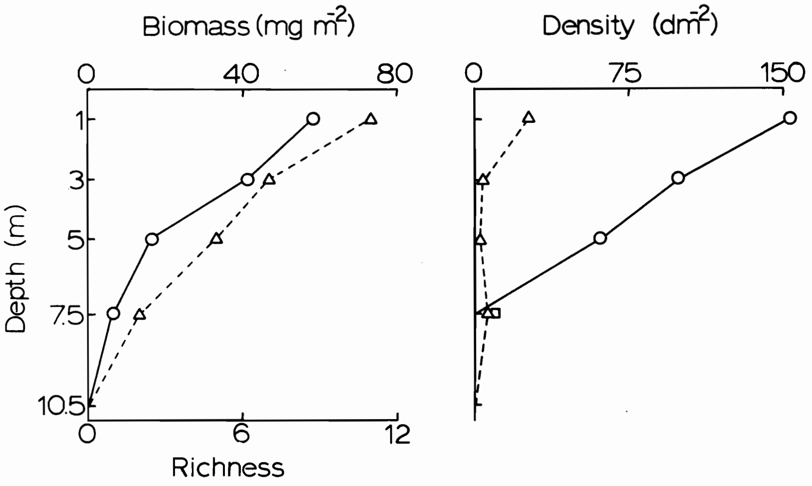


Fig. 42. Left: Biomass (○) and species richness (△) of benthic cladocerans in Mirror Lake. Right: Density of benthic cladocerans in Mirror Lake. Chydoridae (○), *Ilyocryptus spinifer* (△), and *Ilyocryptus sordidus* (☐). All data from transect.

Ilyocryptus spinifer

This species is widely distributed on the oxygenated sediments, both sand and gyttja, of Mirror Lake (Figs. 41, 42), but is less abundant than *I. sordidus*. There is a suggestion of a population maximum in the fall, but it is far less pronounced than the fall maximum of *I. sordidus*. *I. spinifer* is found in lakes of the tropics and middle latitudes throughout the world (SMIRNOV 1976: fig. 20). It is known from lakes throughout eastern North America (BROOKS 1959; WILLIAMS 1978; CHENGALATH 1982).

Chydoridae

Although found occasionally on the deeper sediments of Mirror Lake, the chydorids reach their greatest abundance in the littoral zone (Figs. 41, 42). The chydorids show a strong

Table 17. Records of benthic cladocerans from Mirror Lake.

Species	Weighted mean density (dm^{-2}) Gyttja	Transect
Chydoridae		
Alonella nana	3	2
Alona affinis	0.5	5
Alona cf. *barbulata*	2	0
Alona quadrangularis	7	5
Alona rustica	0.7	7
Chydorus bicornutus	0.6	0
Chydorus brevilabris gr. sp.	0.5	0
Chydorus piger	0.8	20
Chydorus sp.	0.3	0
Disparalona acutirostris	0	5
Eurycercus longirostris	0.1	0
Monospilus dispar	a	a
Rhynchotalona falcata	0	5
Other families		
Latona parviremis	0.2	0
Latona setifera	0	0.4
Macrothrix laticornis	0	0.4
Ophryoxus gracilis	0.6	0.4
Polyphemus pediculus	a	a
Sida crystallina	0	0.4

[a]not taken during the main survey, but collected in preliminary samples

seasonality in Mirror Lake, and are absent entirely from January through March. There also may be a slight minimum in population density in the late summer.

I identified 13 species from the lake (Table 17). More species are undoubtedly present, since many chydorids frequent the weedy habitats that I did not sample well. GOULDEN & VOSTREYS (1985) reported that 28 species of chydorids have lived in Mirror Lake since the glacial retreat, 21 since European development of the watershed about 150 years ago.

A few of the records in Table 17 merit brief comment. *Chydorus bicornutus* is a species of softwater lakes in northeastern North America (CHENGALATH 1982; FREY 1982a). CHENGALATH (1982) reported that this species favors vegetation-free sediments, but I found only 1 of 27 specimens on vegetation-free sediments. According to FREY (in litt.), *Chydorus brevilabris* group sp. is an undescribed species that is widespread in the eastern United States. Until recently, species of the *brevilabris* group were not distinguished from *C. sphaericus* (FREY 1980), so this may be the taxon, reported as *C. sphaericus* by GOULDEN and VOSTREYS (1985), that has been abundant throughout much of Mirror Lake's history. *Chydorus piger*, the most abundant benthic chydorid in Mirror Lake, is widespread in North American lakes, where it favors the sandy, vegetation-free sediments that are so common in the littoral zone of Mirror Lake. DUMONT (1983) recently put *C. piger* into the genus *Pleuroxus*. "*Chydorus* sp." is a large animal (440- to 520-μm long) that does not match *C. canadensis*, *C. gibbus*, or *C. ovalis* (FREY, in litt.). *Latona parviremis* is a rare species that has been found only a few times since its description in 1910 (MARGARITORA et al. 1975). Both LIKENS (1972) and BURTON (1977) reported *Alonella excisa,* a vegetation-dwelling species that I did not collect, from the lake.

Other Cladocera

The six other species of benthic cladocerans found in my study are listed in Table 17. *Polyphemus pediculus* is sometimes abundant just above the sediments in shallow water, but I did not collect it as part of my survey. LIKENS (1972) also recorded *Scapholeberis kingi* (probably actually a different species of the genus – cf. DUMONT & PENSAERT 1983) for the lake.

Discussion

Twenty-three species of benthic cladocerans, including two reported by previous workers and not found in the present study, have been collected in Mirror Lake. Since I largely ignored the vegetated habitats, which although scarce (MOELLER 1975) probably harbor many cladocerans, it is likely that 30–50 species of non-planktonic cladocerans actually live in the lake. Lakes typically contain 10–50 species of non-planktonic cladocerans (Table 18), with the greatest diversity occurring in clear, softwater lakes of pH 4–5 (CHENGALATH 1982; FREY 1982b). In contrast, CONFER et al. (1982) found that the species richness of planktonic crustacean assemblages declines with decreasing pH in some lakes of the northeastern United States. The Chydoridae dominate the fauna in most lakes (Table 18); in Mirror Lake, they contribute 61% of the species, 77% of the individuals, and 63% of the biomass of the benthic cladocerans.

Cladocerans form an important part of many lacustrine zooplankton communities; for example, in Mirror Lake, they constitute 28% and 41% of zooplanktonic biomass and secondary productivity, respectively (MAKAREWICZ & LIKENS 1979). They are a much less prominent part of benthic communities, though: in Mirror Lake, less than 1% of the individuals and biomass belong to the Cladocera. Similar figures have been reported from other lakes (Table 19).

Most of the benthic cladocerans in Mirror Lake are animals of the shallow-water sediments. Both abundance and species richness decline sharply with increasing depth (Fig. 42). A few species have different distributions, though. *Ilyocryptus sordidus,* a species known to favor soft, organic sediments, was collected only from the gyttja (Figs. 41, 42). Its congener, *I. spinifer,* is widely distributed in the lake, and appears to be relatively indifferent to water depth (Figs. 41, 42). The absence of benthic cladocerans from the deepwater sediments is probably due to the low concentrations of dissolved oxygen that occur there. I found cladocerans in one sample where the dissolved oxygen concentration was 2.1 mg l^{-1}, but these animals were otherwise restricted to sites having more than 5.5 mg l^{-1}. In lakes where hypolimnetic oxygen levels are high, the benthic cladocerans may occur to great depth: MONARD (1920) reported 25 species from the profundal zone ($z = 11–144$ m) of the Lac de Neuchatel, and seven from depths exceeding 100 m.

Table 18. Species richness of non-planktonic Cladocera in some representative well studied lakes, in comparison with Mirror Lake.

Lake	Total Cladocera	Chydoridae	Notes	Source
Mirror	23	14	no study of weed-dwelling species	this study
Neuchatel, Switzerland	45	–	oligotrophic	Monard 1920
Stechlinsee, Germany	41	32	oligotrophic	Flössner 1964
Nehmitzsee, Germany	40	29		Flössner 1964
Gerlinsee, Germany	37	25		Flössner 1964
Bodensee, Germany, 1936/37	27	20		Muckle 1942
Reelfoot, USA	24	15	shallow, weedy lake in Tennessee	Hoff 1943
Bodensee, Germany, 1977/78	23	16	after eutrophication	Frenzel 1982
Paajarvi, Finland	>22	>17	oligotrophic, mesohumic	Holopainen & Paasivirta 1977
Grane Langsø, Denmark	20	19	oligotrophic, softwater	Whiteside 1970; Whiteside & Lindegaard 1982
Balaton, Hungary	11	8	shallow, eutrophic	Ponyi 1969
Port-Bielh, France	11	8	oligotrophic, alpine	Rey & Dupin 1973 a

Table 19. Abundance (m^{-2}) and biomass ($mg\ m^{-2}$) of non-planktonic cladocerans in lakes where they have been well studied, in comparison with Mirror Lake.

Lake	MESH (µm)	Abundance	Biomass	Notes	Source
Mirror	–	6,400	20[c]	lakewide mean, June–Oct.	this study
Mirror	–	4,900	20[c]	annual mean, gyttja	this study
Par, USA	63	37,000	260[c]	annual mean at reference site (z = 1 m)	ODEN 1979
Bodensee, Germany	100	18,000	–	z = 0–15 m	after table 3 of FRENZEL 1982
Grane Langsø, Denmark	100	4,900[a]; 39,000[b]	–	lakewide mean, July	WHITESIDE & LINDEGAARD 1982
Paajarvi, Finland	100	3,100	12[d]	annual lakewide mean	HOLOPAINEN & PAASIVIRTA 1977
Michigan, USA	45	2,400	14[c]	z = 11–23 m; Apr.–Nov.	NALEPA & QUIGLEY 1983

[a] Kajak sampler; probably too low

[b] funnel sampler

[c] dry weight

[d] ash-free dry weight

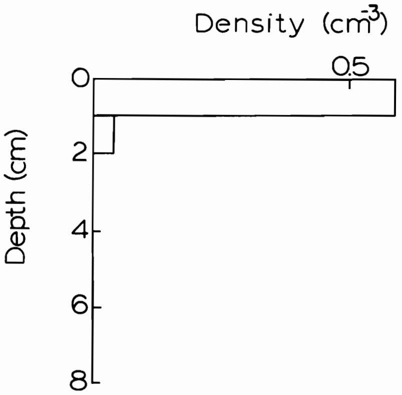


Fig. 43. Vertical distribution of benthic cladocerans within the sediments of Mirror Lake, as a function of depth from the sediment surface. Data are lakewide means from the transect.

Even though the cladoceran fauna of Mirror Lake is dominated by species that are specialized to a benthic existence (*Chydorus piger* and *Ilyocryptus* spp.), few cladocerans penetrate more than 1 cm into the Mirror Lake sediments (Fig. 43). Other studies (Cole 1955; Nalepa & Robertson 1981a) likewise have found the benthic cladocerans to be essentially restricted to the sediment surface, although Cole (1953, 1955) collected a few specimens of *Ilyocryptus sordidus* 8–10 cm below the sediment surface.

The Cladocera are among the most strongly seasonal animals of the Mirror Lake zoobenthos. The chydorids are absent during the winter, and may have a weak mid-summer minimum in population density (Fig. 41). A similar seasonal pattern has been reported for the Chydoridae of many other lakes (e.g., Flössner 1964; Goulden 1971; Keen 1973, 1976; Whiteside 1974; Whiteside et al. 1978; Williams & Whiteside 1978; Frenzel 1982). *Ilyocryptus sordidus* exhibits a strong seasonality of a different kind, with a single population maximum during fall overturn (Fig. 41). Rey & Dupin (1973b) found the same species to reach its maximum density early in fall overturn in the alpine lake Port-Bielh.

Because the benthic cladocerans are relatively rare in Mirror Lake, it hardly seems likely that they play an important role in community or ecosystem dynamics. Where their abundance is especially great – in the upper littoral zone during summer, and on the gyttja during the population maximum of *Ilyocryptus sordidus* – the cladocerans may possibly exert some influence on the abundance of their food items, bacteria and benthic algae. Even there, though, they are likely to be overshadowed by other more abundant animals that feed on the same items; rotifers, oligochaetes, and chironomids, for example.

Cladocerans are an important item in the diet of some benthic predators such as carnivorous oligochaetes (Green 1954), cyclopoid copepods (Fryer 1957a), and tanypod midges (Goulden 1971). Burton (1977) found that benthic cladocerans constitute 38% (by weight) of the diet of adult red-spotted newts *(Notophthalmus* *viridescens)* in Mirror Lake during June through October, and they may likewise be an important food of small fish.

Benthic cladocerans are probably not important in overall benthic metabolism in Mirror Lake. According to the modified BANSE and MOSHER equation, P/B is about 7 yr^{-1} for the benthic cladocerans of Mirror Lake. Accordingly, the Cladocera are probably responsible for about 1% of zoobenthic assimilation (Table 35).

Copepoda

The planktonic calanoid and cyclopoid copepods are well known to limnologists, and have been the subject of many ecological studies (see HUTCHINSON 1967, and KERFOOT 1980, for an introduction). However, the majority of cyclopoid species and all of the freshwater harpacticoid copepods are benthic in habit, and have received little attention, particularly in North America. Aside from a few basic taxonomic works (summarized by YEATMAN 1959; WILSON & YEATMAN 1959; SMITH & FERNANDO 1978) and a few preliminary ecological and faunistic surveys (e.g., DAGGETT & DAVIS 1974, 1975; SMITH & FERNANDO 1977; EVANS & STEWART 1977; ROBERTSON & GANNON 1981) very little work has been done on North American benthic freshwater copepods. Members of two suborders of copepods, the Cyclopoida and the Harpacticoida, have been found in Mirror Lake sediments.

Cyclopoida

Benthic cyclopoids, like their planktonic relatives, are good swimmers and raptorial feeders. Various species feed on small invertebrates, algae, or detritus (FRYER 1957a, b). All species reproduce sexually, although males are relatively scarce in some situations (e.g., COLE 1955). Cyclopoids (and other copepods) have a complicated life history: six naupliar states and five copepodid stages precede the adult instar. It is often difficult or impossible to identify these immature forms to species. Figure 44 is based only on adult densities, but I used my tentative identifications of late instar copepodids to produce Table 20.

Diacyclops nanus

D. nanus is a common deepwater species in Mirror Lake (Fig. 44). With a mean lakewide density of 1600 adults m^{-2}, it is the most abundant cyclopoid taken on my transect. Even from the limited data at hand, it is apparent that *D. nanus* has a seasonal life cycle in Mirror Lake (Table 20). Of the adults that I collected, 44% were males. I found the trophi of a dicranophorid rotifer in the gut of one animal.

D. nanus has been regarded as a rare animal in North America, with records only from a lake in North Carolina (YEATMAN 1944), three boggy sites in Newfoundland (DAGGETT & DAVIS 1975), Georgian Bay (HARE & CARTER 1976), and Lake Erie (EVANKO 1977). DUSSART (1969), writing about the distribution of the species in Europe, called it a summer species that is most common in softwater lakes and bogs. There is evidence, though, that *D. nanus* is a characteristic benthic copepod of profundal lake sediments. In addition to my records from Mirror Lake, HARE & CARTER (1976) found it in abundance (ca. 1000 m^{-2})

Table 20. Lakewide proportion of adults in cyclopoid populations in Mirror Lake (transect data). Figures are based on tentative identifications of late-instar copepodids only, and do not include nauplii or early instar copepodids.

Taxon	Dates		
	VI.23–VII.16	VII.28–IX.4	X.6–X.27
Diacyclops nanus	0.53	0.19	0
Microcyclops spp.	0.36	0.18	0
Paracyclops affinis	0.69	0.55	0.46

at depths of 30 to 100 m in Georgian Bay, and HOLOPAINEN & PAASIVIRTA (1977) called it a dominant species throughout the depth profile (z = 1–65 m) of the oligotrophic lake Paajarvi in Finland. As HARE & CARTER (1976) suggested, it is likely that further sampling in appropriate habitats will reveal this small species to be widespread in North America.

Eucyclops agilis

This species (= *E. serrulatus*) occurs in small numbers in the littoral zone of Mirror Lake (Fig. 44). *E. agilis* is probably the most common and widespread of the benthic cyclopoids, and has been found in nearly every lake where benthic copepods have been studied (e. g., YEATMAN 1959; DUSSART 1969; REY & DUPIN 1975a; DAGGETT & DAVIS 1974, 1975; SMITH & FERNANDO 1978). It feeds on various benthic algae, especially diatoms (FRYER 1957a).

Macrocyclops albidus

This is another littoral species in Mirror Lake (Fig. 44), although I did find one of its copepodids at 7.5-m. *M. albidus*, which feeds on microcrustaceans, oligochaetes, and dipteran larvae (FRYER 1957a), is widespread and common among vegetation in lakes and ponds (e. g., MUCKLE 1942; DUSSART 1969; DAGGETT & DAVIS 1974, 1975; SMITH & FERNANDO 1978; WHITESIDE & LINDEGAARD 1982).

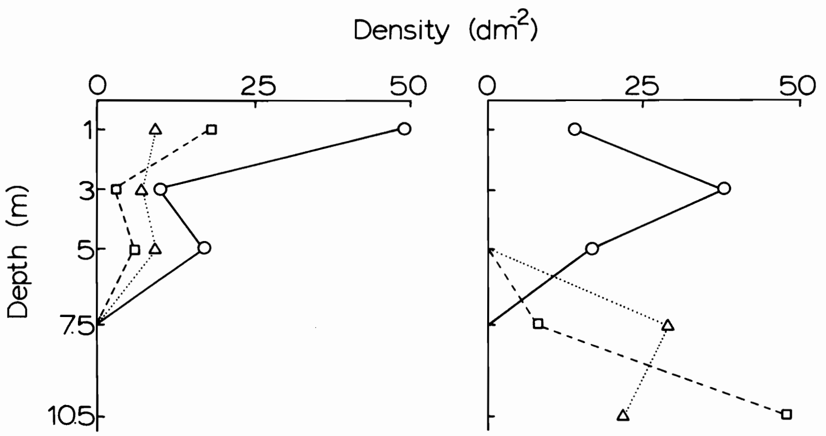


Fig. 44. Density of benthic cyclopoid copepods in Mirror Lake, from transect data. Left: *Paracyclops affinis* (○), *Macrocyclops albidus* (△), and *Eucyclops agilis* (□). Right: *Microcyclops* spp. (○), *Diacyclops nanus* (△), and *Mesocyclops edax* (□).

Mesocyclops edax

M. edax is one of the common zooplankters in Mirror Lake (MAKAREWICZ & LIKENS 1975, 1979). Its occurrence on the sediments (Fig. 44) is apparently seasonal, since I found almost no specimens in June through September, 1981. Although *M. edax* is one of many planktonic cyclopoids known to have a benthic resting stage (e. g., ELGMORK 1967, 1980; SARVALA 1979), I did not find any diapausing cyclopoids, of this or any other species, in the Mirror Lake sediments. *M. edax* is a common and widespread plankter in North America, and is probably also common in the benthos of many lakes (e.g., MOORE 1939; COLE 1955; NALEPA & QUIGLEY 1980).

Microcyclops spp.

Two species of this genus, *M. varicans* and *M. rubellus*, are present in approximately equal numbers (500 adults m^{-2} lakewide) in Mirror Lake. Both are confined to the littoral zone (Fig. 44). As was the case with *Diacyclops nanus*, the proportion of adults in the population declines through the summer (Table 20). Only 8% of the adults that I collected were males.

Both species of *Microcyclops* live among weeds and debris in ponds and in the shallow water of lakes. *M. rubellus* is common and widely distributed in North America (YEATMAN 1959; DAGGETT & DAVIS 1975; SMITH & FERNANDO 1978). According to DUSSART (1969), it is rare in Europe, and prefers acid waters. Both DUSSART (1969) and DAGGETT & DAVIS (1974) found it to reach its peak abundance in the summer. *M. varicans* is known from North America only from scattered sites in Ontario (SMITH & FERNANDO 1978). FRYER (1957a) reported that some African species of *Microcyclops* are primarily herbivorous.

Paracyclops affinis

This is a another common littoral species in Mirror Lake (Fig. 44). I collected adults throughout the duration of the transect study (Table 20); 23% of the adults were males. *P. affinis* has been found from only a few localities in North America: the leaves of pitcher plants in Quebec (YEATMAN 1959), and a few sites in Ontario (SMITH & FERNANDO 1978) and Quebec (LEBLANC et al. 1981). Here, as in Europe, it is regarded as a rare species of ponds and lake margins (cf. MONARD 1920; MUCKLE 1942; DUSSART 1969). MONARD and MUCKLE thought *P. affinis* to be a warm stenotherm.

Other Cyclopoida

Cyclopoid copepodids (immatures) are abundant in Mirror Lake (11,000 m^{-2} lakewide), and follow a depth profile like that of the adult cyclopoids (Fig. 45). I also found three species of cyclopoids to be uncommon in Mirror Lake (Table 21). *Acanthocyclops vernalis*, which is actually a complex of species (PRICE 1958), is one of the most widespread and abundant of the benthic cyclopoids (e. g., YEATMAN 1959; EVANS & STEWART 1977;

Table 21. List of rare copepods in Mirror Lake.

Cyclopoida	Harpacticoida
Acanthocyclops vernalis	*Canthocamptus assimilis*
Paracyclops sp.	*Parastenocaris brevipes*
Cyclopoida indet.	

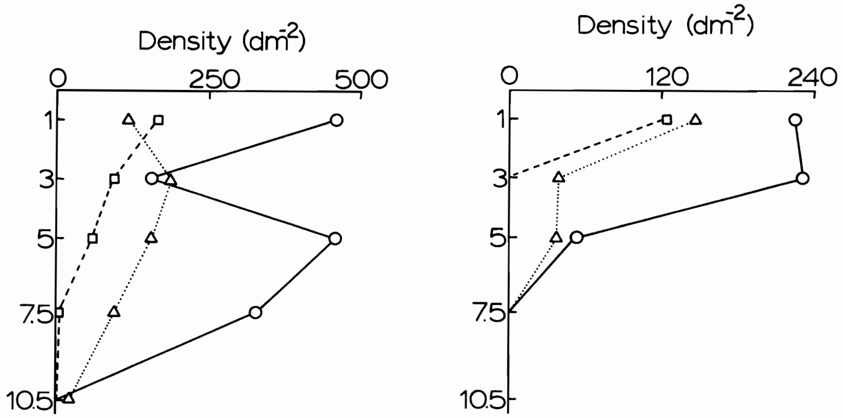


Fig. 45. Left: Density of immature copepods in Mirror Lake. Nauplii (○), cyclopoid copepodids (△), and harpacticoid copepodids (□). Right: Density of harpacticoid copepods in Mirror Lake. *Bryocamptus minutus* gr. sp. (○), *Attheyella obatogamensis* (△), and *Bryocamptus zschokkei* (□). All from transect data.

Smith & Fernando 1978). The animal from Mirror Lake is "Isolate B", according to Price's (1958) key. The single immature specimen of "*Paracyclops* sp." has a 10-segmented first antenna and a longitudinal row of spinules on the caudal ramus. It may represent an undescribed species. "Cyclopoida indet." has a 10-segmented first antenna, swimming legs with 2-segmented exopods and endopods, a 2-segmented fifth leg, and a caudal ramus that is more than twice as long as wide.

Harpacticoida

The freshwater harpacticoids are strictly benthic animals that feed on algae and detritus. Harpacticoids are found commonly in lakes, streams, bog mats, and subterranean waters; some of the subterranean species, such as the vermiform *Parastenocaris*, are strikingly modified to interstitial life. Reproduction is normally sexual, with separate sexes, but at least a few species may reproduce by parthenogenesis (Sarvala 1979). As with many other groups of benthic animals, most of the investigations of the freshwater harpacticoids had been made by European workers. Lang (1948) and Dussart (1967) summarized this work. I was not able to assign immature harpacticoids to species; the depth distribution of harpacticoid copepodids is shown in Fig. 45.

Attheyella obatogamensis

This species is abundant on the littoral sediments of Mirror Lake (Fig. 45). Of the adult specimens that I collected, 43% were males. I collected egg-bearing females in June and August. *A. obatogamensis*, which is closely allied to or a synonym of *A. wierzejskii* of European lakes (Lang 1948; Borutsky 1952), has been collected previously only in Quebec and western New York State (Wilson & Yeatman 1959). Almost nothing is known of its ecology.

Bryocamptus minutus group species

My specimens do not match any of the species in the works of LANG (1948) or WILSON & YEATMAN (1959), but definitely belong to the *B. minutus* group. This is the most abundant harpacticoid in Mirror Lake, contributing 50% and 60% of harpacticoid numbers and biomass, respectively. It is restricted to the 1- to 5-m zone (Fig. 45). I found egg-bearing females in October, and 38% of the adults that I collected were males. Members of the *B. minutus* group are common in lakes in Europe and North America (e.g., MONARD 1920; LANG 1948; DUSSART 1967).

Bryocamptus zschokkei

B. zschokkei is restricted to the 1-m stations in Mirror Lake, where it is abundant (Fig. 45). The species is widely distributed in Eurasia and North America north of the Carolinas, where it lives in the littoral zone of unproductive lakes, as well as in streams and subterranean waters (LANG 1948; WILSON & YEATMAN 1959; DUSSART 1967; REY & DUPIN 1973a). Previous authors have considered it to be a cold stenotherm, but I found it in greatest abundance (30,000 m^{-2}) in a sample having a water temperature of 26 °C.

Other Harpacticoida

I found scattered specimens of two other species of harpacticoids in Mirror Lake (Table 21). *Canthocamptus assimilis,* which is widely distributed in standing waters in North America (WILSON & YEATMAN 1959), was found in small numbers only at the 7.5-m station. I found *Parastenocaris brevipes* regularly, but in small numbers, at the 1-m stations. *P. brevipes* is one of the few members of its genus commonly found in epigean waters, and has been collected from bog mats and sandy lake beaches in Europe and North America (PENNAK 1949; LANG 1948; WILSON & YEATMAN 1959; DUSSART 1967). NALEPA & QUIGLEY (1980) reported "*Parastenocaris* spp." from relatively deep-water sediments ($z = 11-23$ m) in Lake Michigan.

Discussion

I found 15 species of benthic copepods in Mirror Lake. Since this figure is based on the relatively few samples from the transect, it is probable that the fauna actually contains 20–25 species of copepods. Previous studies of lacustrine benthic copepod assemblages have revealed faunas of 7–25 species, split roughly evenly between the cyclopoids and the harpacticoids (Table 22). Of the 15 species found in Mirror Lake, perhaps three are new to science, and another four or five are very poorly known ecologically. These figures are indicative of the paucity of studies on the North American fauna.

Copepods are one of the most abundant groups in the zoobenthos of Mirror Lake, constituting 6 and 3% of zoobenthic numbers and biomass, respectively (Table 35). The few comparable data on benthic copepods in other lakes are similar (Table 23).

The copepods are widely distributed in Mirror Lake, and cyclopoids are found even under anoxic conditions (Figs. 44, 46, 47). The harpacticoids are much more restricted in distribution (Figs. 45, 46, 47) and are essentially animals of the littoral

Table 22. Species richness of benthic copepods in lakes where they have been well studied, in comparison with Mirror Lake.

Lake	Cyclopoids	Harpacticoids	Notes	Source
Mirror	10	5	transect data only	this study
Leman, Switzerland	12	13		DUSSART 1966
Bodensee, Germany	16	7	littoral and sublittoral zones (z = 0–30 m)	MUCKLE 1942; FRENZEL 1980
Neuchatel, Switzerland	10	7	profundal sediments only	MONARD 1920
Michigan, USA	8	8	Apr.–Nov.; z = 11–23 m	NALEPA & QUIGLEY 1983
Tiberias, Israel	6	5[a]	oligohaline lake	POR 1968
Paajarvi, Finland	>3 23 - Sarvala 1986 -	7 13	oligotrophic, mesohumic lake	HOLOPAINEN & PAASIVIRTA 1977; SARVALA 1977
Port-Bielh, France	4	3	oligotrophic alpine lake	REY & DUPIN 1973a

[a] excludes two species that are restricted to the supralittoral zone

Table 23. Abundance (m^{-2}) and biomass ($mg\ m^{-2}$) of benthic copepods in some lakes[a].

Lake	MESH (µm)	Cyclopoida		Harpacticoida		Notes	Source
		Abundance	Biomass	Abundance	Biomass		
Mirror	–	17,000[b]	44[b,c]	20,000[b]	32[b,c]	lakewide mean, July–Oct.	this study
Mirror	–	34,000[b]	90[b,c]	1,300[b]	2[b,c]	annual mean, gyttja	this study
Paajarvi, Finland	100	41,000[b]	49[d,e]	30,000[b]	30[d,e]	lakewide mean	Holopainen & Paasivirta 1977
Michigan, USA	45	9,000[f]	26[c,f]	7,700[b?]	15[b?,c]	Apr.–Nov.; z = 11–23 m	Nalepa & Quigley 1983
Bodensee, Germany	100	3,000[g]	–	3,400[g]	–	littoral zone	est. from fig. 2 of Frenzel 1980
Grane Langsø, Denmark	100	………… 7,400 m^{-2} [f,h,i] …………				lakewide mean, July	Whiteside & Lindegaard 1982
Tiberias, Israel	?	………… 520 m^{-2}, 1.6 $mg\ m^{-2}$ [c,i,j] …………				lakewide mean	Por & Eitan 1970

[a] all studies except for that of Whiteside & Lindegaard (1982) apparently exclude nauplii, which represent 31,000 m^{-2} and 6 mg DW m^{-2} on the transect and 62,000 m^{-2} and 14 mg DW m^{-2} on the gyttja in Mirror Lake

[b] adults plus copepodids

[c] dry weight

[d] includes diapausing planktonic cyclopoids, which Sarvala (1979) found to represent 28,000 m^{-2} and 19 mg C m^{-2} in the lake Paajarvi

[e] ash-free dry weight

[f] includes some calanoids

[g] adults only

[h] adults, copepodids, plus nauplii

[i] cyclopoids plus harpacticoids

[j] converted from wet weight by multiplying by 0.15

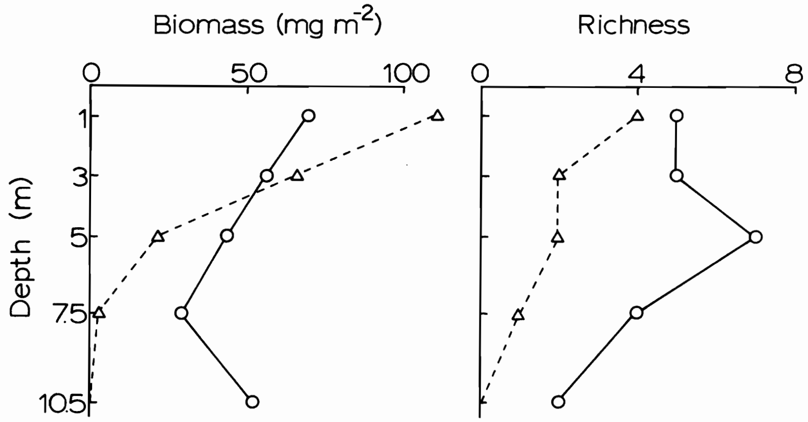


Fig. 46. Biomass and species richness of benthic copepods in Mirror Lake, from transect data. Cyclopoids (O) and harpacticoids (△).

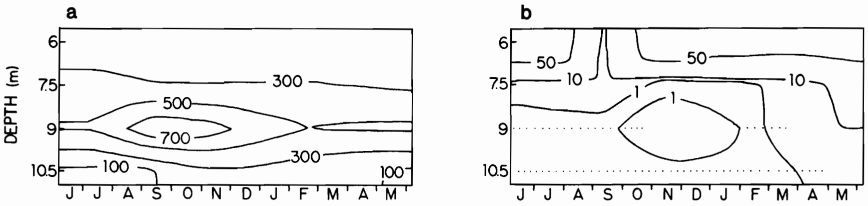


Fig. 47. Abundance (dm^{-2}) of (a) cyclopoids, and (b) harpacticoids in Mirror Lake. Dotted lines show extended periods when these animals were absent from the indicated stations.

zone. As with most benthic animals in Mirror Lake, the benthic copepods have well defined depth distributions. The density of most of the benthic copepods peaks in the shallow littoral zone, but at least two species (*Diacyclops nanus* and *Mesocyclops edax*) are restricted to the gyttja, and two other species (*Microcyclops* spp.) may be most abundant at mid-depths (Fig. 44). Since I did not identify the specimens collected in my survey of the gyttja, I cannot comment extensively on the seasonality of copepod species. No distinct seasonality is apparent in Fig. 47, but at least some of the cyclopoid species have a seasonal reproductive cycle (Table 20).

A change in the trophic structure of the benthic copepod community also occurs with depth. In the littoral zone ($z = 1-5$ m), the copepod community is dominated by the harpacticoids and by *Paracyclops affinis*, *Microcyclops* spp., *Eucyclops agilis*, and *Macrocyclops albidus* among the cyclopoids. All of these species, except for the predatory *M. albidus*, feed on algae and detritus. However, on the deep-water sediments ($z = 7.5-10.5$ m), the only herbivorous species is the uncommon harpacticoid *Canthocamptus assimilis*. The other copepod species

(*Diacyclops nanus*, *Mesocyclops edax*, *Macrocyclops albidus*, and *Acanthocyclops vernalis*) are without exception predators. There is thus a shift in the copepod community from herbivores and detritivores to predators with increasing water depth.

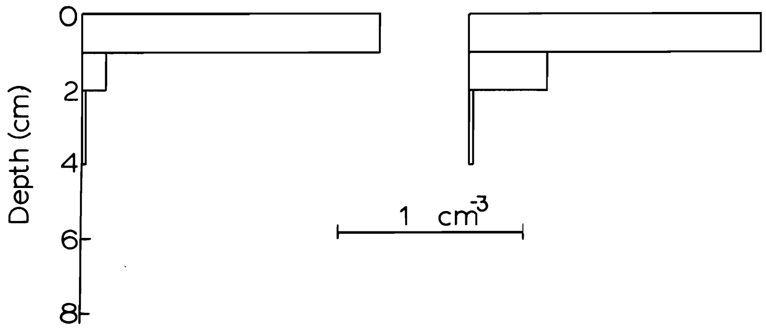


Fig. 48. Vertical distribution of cyclopoids (left) and harpacticoids (right) within the sediments of Mirror Lake, as a function of depth from the sediment surface. Data are lakewide means from the transect.

Copepods live in the surface sediments of Mirror Lake (Fig. 48). More than 90% of the cyclopoids and 75% of the harpacticoids live in the top 1 cm of sediment. MOORE (1939) and NALEPA & ROBERTSON (1981a) likewise reported that 80–90% of the active benthic copepods live in the top 2 cm of sediment, although diapausing animals frequently were found 5 to 20 cm below the sediment surface.

Some harpacticoids and many planktonic cyclopoids have a benthic resting stage, usually in the fourth copepedid states (e.g., ELGMORK 1967, 1980; SARVALA 1979). These diapausing copepods are often found in great numbers (on the order of 10^4-10^5 m^{-2}) in lake sediments (e.g., MOORE 1939; COLE 1955; HOLOPAINEN & PAASIVIRTA 1977), so I was surprised not to find them in Mirror Lake. I have no explanation for their absence, since *Cyclops scutifer* and *Mesocyclops edax*, the dominant planktonic cyclopoids in the lake (MAKAREWICZ & LIKENS 1979), are both known to have benthic resting stages in other lakes (ELGMORK 1962, 1967).

By virtue of their abundance and wide distribution in Mirror Lake, the copepods might be expected to have an important influence on benthic community structure and dynamics. The predatory copepods, which have a combined density of about 7,000 m^{-2} lakewide, may be major predators of small metazoans, such as rotifers, microcrustaceans, and chironomids (FRYER 1957a). The harpacticoids and herbivorous cyclopoids reach densities in excess of 80,000 m^{-2} at some stations in Mirror Lake, and may therefore contribute a significant fraction of the grazing pressure on benthic algae. Until further studies are done on the feeding rates and selectivity of the benthic copepods, a more definite role cannot be assigned to them.

Benthic copepods are probably responsible for about 10% of zoobenthic assimilation (Table 35). The modified BANSE & MOSHER (1980) equation predicts P/B ratios of 8 yr^{-1} for the cyclopoids and 12 yr^{-1} for the harpacticoids of Mirror Lake. These values are similar to those reported for natural populations of copepods, although almost all of the published studies refer to planktonic species. P/B values for planktonic cyclopoid populations in the temperate zone range from 0.24 yr^{-1} to 19 yr^{-1}, with a mean value of about 7 yr^{-1} (WATERS 1977; MAKAREWICZ & LIKENS 1979; WETZEL 1983). FELLER (1983) found the P/B ratio of a marine harpacticoid to be about 4 yr^{-1}. Thus, the BANSE & MOSHER regression seems to give reasonable results, although more data on benthic copepods certainly are needed.

Ostracoda

Ostracods are small bivalved crustaceans that live among sediments and vegetation in lakes and streams. Some species burrow into the substratum, some are free-swimming at the sediment surface, and a few are planktonic. Ostracods browse on bacteria, algae, and detritus, although some are scavengers. Reproduction may be parthenogenetic or sexual, depending on the species. Ostracods have great potential as indicators of paleoenvironments, a potential that has not been realized because we know so little about the ecology of living ostracods (but see DELORME 1969; STARK 1976; DELORME et al. 1977).

Candona sp.

I found a few scattered individuals of this genus of burrowing ostracods in Mirror Lake (Fig. 49), but was not able to assign a species name to them. Dozens of species of this genus have been reported from lakes, and it is common to find five to ten species of *Candona* in a single lake (e. g., MONARD 1920; MUCKLE 1942; KOSMAL 1968; MCGREGOR 1972; DELORME 1978).

Cypria turneri

This ostracod has a very sharply defined depth distribution in Mirror Lake (Figs. 49, 50). The population is essentially restricted to the zone at and below 7.5 m, where it is abundant (mean annual density of 24,000 m^{-2} at 7.5 m). I occasionally found *C. turneri* under anoxic conditions, as other workers have (e. g., MOORE 1939), but population densities are low at the seasonally anoxic stations. I doubt *C. turneri* can tolerate anoxia for an extended period. I found small diatoms and detritus in the guts of individuals of *C. turneri* in Mirror Lake.

The taxonomy of this species is not clear. Early workers in North America (e. g., FURTOS 1933; DOBBIN 1941) recorded it as *C. elegantula,* but noted differences between the North American specimens and those previously described from Europe. HOFF (1942) believed these differences to merit specific recognition, and described the American taxon as *C. turneri.* Some later authors (e. g., COLE 1955; MCGREGOR 1972) have used the name *C. turneri* in reference to this species, but DELORME (1970) put HOFF's species into the

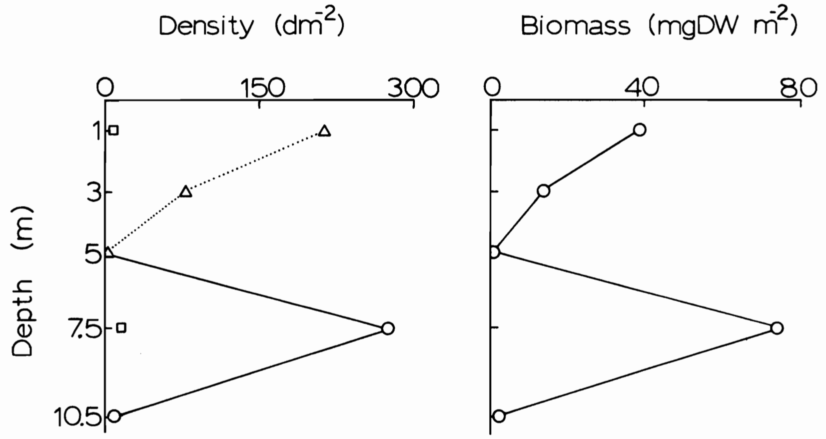


Fig. 49. Left: Density of ostracods in Mirror Lake. *Cypria turneri* (○), *Candona* sp. (□), and *Darwinula stevensoni* (△). Right: Biomass of ostracods in Mirror Lake. All data from transect.

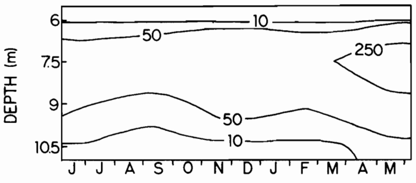


Fig. 50. Abundance (dm^{-2}) of ostracods in Mirror Lake. Most of these animals are probably *Cypria turneri* (cf. Fig. 49).

synonomy of the widespread European species *C. opthalmica.* I am tentatively recognizing *C. turneri* until a detailed comparison of *C. turneri* and *C. opthalmica* is made.

The distribution of *C. turneri* in Mirror Lake suggests that the species has a strict requirement for the deepwater environment (i. e., it is a mud-loving cold stenotherm). MOORE (1939) also found it (as *C. exsculpta*) to be restricted to the sublittoral and profundal muck in Douglas Lake, Michigan, furthering the impression that it is a stenotopic species. In fact, *C. turneri* is a widely distributed and extremely tolerant species. HOFF (1942) found the species in all kinds of lentic habitats, both permanent and temporary, in Illinois, and FURTOS (1933) and DOBBIN (1941) found it in many localities in Ohio and Washington, respectively. MCGREGOR (1972) collected the species at all depths in Gull Lake, Michigan, and wrote "No other ostracod was a uniformly dispersed, geographically or with depth, as *C. turneri*". *C. opthalmica* likewise has one of the broadest ecological tolerances of any European freshwater ostracod (NUCHTERLEIN 1969; HILLER 1972), although MALLWITZ (1984) claimed that the species is a cold stenotherm in some German lakes. It therefore seems very unlikely that environmental conditions are responsible for the absence of *C. turneri* from the littoral sediments of Mirror Lake and Douglas Lake. I have pointed out other examples of widely distributed species that are restricted to the deepwater sediments of Mirror Lake (the bdelloid rotifer *Rotaria tridens* and the oligochaete *Nais communis*). I have no idea what is keeping these animals out of the littoral zone, but the subject is an intriguing area for further research.

Darwinula stevensoni

This species is abundant in the upper littoral zone in Mirror Lake (Fig. 49). All of the mature animals that I found were females, as has been the case in other localities (McGregor 1969; Ranta 1979). The gut contents of this species in Mirror Lake are very fine particles.

McGregor (1969, 1972) reported that the populations of *D. stevensoni* and *D. pagliolii* in Gull Lake, Michigan, were heavily "parasitized" by an unidentified bdelloid rotifer, although he presented no evidence that the rotifer actually harmed its ostracod host. After reading McGregor's papers, I reexamined my specimens, and found that two individuals of *D. stevensoni* from Mirror Lake harbored a bdelloid rotifer on the hind margin of the carapace. The rotifer was unfortunately badly contracted and overcleared by the mounting medium, so I can describe it only as a bdelloid with numerous fine teeth in its trophi.

D. stevensoni has been found in many lakes throughout the world (McGregor 1969). It is ecologically tolerant (Hiller 1972), but is restricted to permanent waters, and is not usually found in more than 10 m of water (e. g., Moore 1939; Fox 1963; Por 1968; McGregor 1969; Stark 1976; Holopainen & Paasivirta 1977; Sywula 1977; Ranta 1979).

Discussion

I found only three species of ostracods, all widely distributed taxa, in Mirror Lake. Even allowing for my relatively sparse sampling, it appears that Mirror Lake

Table 24. Species richness (S) of ostracods in lakes where they have been well studied, in comparison with Mirror Lake.

Lake	S	Notes	Source
Mirror	>3	softwater, oligotrophic	this study
Mikorzynskie, Poland	40	eutrophic, heated	Sywula 1977
Slesinskie, Poland	32	eutrophic, heated	Sywula 1977
Lichenskie, Poland	29	eutrophic, heated	Sywula 1977
Kisjano, Poland	26		Kosmal 1968
Erie, USA/Canada	26[a]	eu-/mesotrophic, hardwater	Delorme 1978
Gull, USA	24	mesotrophic, hardwater	McGregor 1972
Patnowskie, Poland	24	eutrophic, heated	Sywula 1977
Goslawickie, Poland	23	eutrophic, heated	Sywula 1977
Luttauersee, Germany	22	hardwater, $z = 0.2-0.7$ m	Mallwitz 1984
Elk, USA	21	hardwater, Minnesota	Stark 1976
Neuchatel, Switzerland	18	oligotrophic	Monard 1920
Manitoba, Canada	15	shallow, eutrophic, hardwater	Tudorancea et al. 1979
Bodensee, Germany	13		Muckle 1942
Tiberias, Israel	>9	oligohaline	Por 1968
Paajarvi, Finland	>6	oligotrophic, mesohumic	Holopainen & Paasivirta 1977
Reelfoot, USA	6	shallow, eutrophic	Hoff 1943
Port-Bielh, France	2	oligotrophic, alpine	Rey & Dupin 1973 a

[a] some represented only as dead shells

has an impoverished ostracod fauna (Table 24). This impoverishment may be due in part to the soft water in Mirror Lake, since ostracods use calcium carbonate in their shells, and many species require fairly hard water (HOFF 1942; DELORME 1969). Furthermore, some species (e.g., *Cypriodopsis vidua* – see STARK 1976) live among aquatic plants, and would be expected to be rare or absent on the largely barren sediments of Mirror Lake. In fact, the most diverse lacustrine ostracod assemblages have been reported from hardwater lakes with an abundance of aquatic vegetation (e. g., Gull, Kisjano, Erie).

Ostracods are abundant throughout most of the 0-m to 9-m depth zone in Mirror Lake, although the two dominant species have very different depth distributions (Fig. 49). Many other workers have noted the importance of water depth in determining ostracod distributions. Both density and species richness are usually highest in the littoral zone (e. g., MCGREGOR 1972; STARK 1976; SYWULA 1977). Although ostracods are usually rare or absent from the profundal sediments of eutrophic lakes (MCGREGOR 1972; STARK 1976; SYWULA 1977), presumably because of insufficient dissolved oxygen, they may penetrate to great depths in oxygen-rich oligotrophic waters. Thus, FOX (1965) found three species regularly at a depth of 311 m in Lago Maggiore, Italy, and TRESSLER (1957, cited by MCGREGOR 1972) found ostracods on sediments under 600 m of water in Great Slave Lake, Canada.

Ostracods are abundant in Mirror Lake (Table 25), constituting 2% of zoobenthic density and biomass. The few comparable data that have been published indicate an extraordinary range of ostracod densities in lakes (Table 25). Since ostracods are quantitatively retained on a mesh of about 60–100 µm (HUMMON 1981; NALEPA & ROBERTSON 1981b), it does not appear that methodological differences can account for the range shown in Table 25. From the limited data at hand (Table 25), it appears that ostracods constitute from 0.2% (Lake Michigan) to 9% (Paajarvi) of zoobenthic biomass.

Most ostracods live at or near the sediment surface. I found 97% and 62% of the population of *D. stevensoni* and *C. turneri*, respectively, to live in the top 2 cm of sediment in Mirror Lake (Fig. 51). MOORE (1939) found 79% of the population of *Cypria* spp. in Douglas Lake in the top 2 cm of sediment, and MCGREGOR (1969) found 97% of the *D. stevensoni* population to occupy the top 5 cm of sediments in Gull Lake. NALEPA & ROBERTSON (1981a) reported that 89% of the ostracods in the near-shore zone of southeastern Lake Michigan lived in the top 2 cm of sediment. Nonetheless, some ostracods, notably the species of *Candona,* do burrow deeply into sediments. MOORE (1939) found that *Candona* spp. penetrated the sediments to at least 17 cm in Douglas Lake, and 37% of the population lived below 5 cm. It is obvious that long cores will be required to sample some ostracod communities quantitatively.

The modified BANSE & MOSHER (1980) regression predicts an average P/B ratio of 9 yr^{-1} for the Mirror Lake ostracods. However, there is evidence that ostracod populations turn over more slowly than this. HERMAN et al. (1983) used

Table 25. Abundance (m^{-2}) and biomass (mg m^{-2}) of ostracods in some lakes.

Lake	MESH (μm)	Abundance	Biomass	Notes	Source
Mirror	–	18,000	40[a]	lakewide mean, July–Oct.	this study
Mirror	–	12,000	30[a]	annual mean for gyttja	this study
Par, USA	63	110,000	110[a]	annual mean at reference site (z = 1 m)	Oden 1979
Paajarvi, Finland	100	39,000	70[b]	annual lakewide mean	Holopainen & Paasivirta 1977
Schmalsee, Germany	?	26,000	–	annual mean, z = 0.2–0.7 m	Mallwitz 1984
Manitoba, Canada	200	8,400	540[a]	mean of 7 stations, May–Jan.	Tudorancea et al. 1979
Gull, USA	202	5,200	–	annual lakewide mean	data of McGregor 1972
Luttauersee, Germany	?	3,000	–	annual mean, z = 0.2–0.7 m	Mallwitz 1984
Michigan, USA	45	600	10[a]	z = 11–23 m, Apr.–Nov.	Nalepa & Quigley 1983
Tiberias, Israel	?	150	–	annual lakewide mean	Por & Eitan 1970
Grane Langsø, Denmark	100	30	–	lakewide mean, July	Whiteside & Lindegaard 1982

[a] dry weight
[b] ash-free dry weight

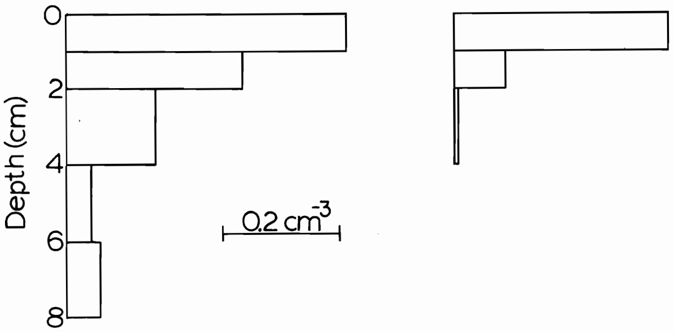


Fig. 51. Vertical distribution of ostracods within the sediments of Mirror Lake, as a function of depth from the sediment surface: *Cypria turneri* (left) and *Darwinula stevensoni* (right). Data are lakewide means from the transect.

the age distribution of ostracod shells preserved in the sediments of a brackish pond in Belgium to construct a survivorship curve for *Cypideis torosa*. From this curve, they estimated a P/B ratio of only 2.7 yr^{-1}. According to KAJAK et al. (1980), *Candona candida* has a P/B ratio of 3.2 yr^{-1} in Lake Krivoye, USSR.

Furthermore, ostracods may have long life cycles. I believe that *C. turneri* produces only one generation per year in Mirror Lake. *D. stevensoni* takes an entire year to mature in Gull Lake, Michigan (MCGREGOR 1969), and two years in the Finnish lake Paajarvi (RANTA 1979), and adults may live for at least one additional year in each of these lakes. FERGUSON (1944) found that three species of ostracods living in a pond in Missouri produced two or three generations per year.

If ostracods take four months to two years to complete a life cycle, and if WATERS' (1977) estimate of P/B = 5 per cohort applies, we would expect P/B to be in the range of 2 to 15 yr^{-1}, with the lacustrine species perhaps occupying the lower end of the range. Using P/B = 5 yr^{-1} as the most reasonable estimate for Mirror Lake, I calculate a secondary production of ostracods of about 200 mgDW m^{-2} yr^{-1}. Thus, about 4% of zoobenthic assimilation is due to the ostracods (Table 35).

Little is known of the quantitative role of ostracods in benthic food webs. Where population densities are high, as at 7.5 m in Mirror Lake, it is tempting to speculate that grazing by ostracods might regulate microbial populations. However, we simply know too little about the rates and selectivity of feeding by these animals to evaluate such a speculation.

Ostracods are eaten by many predators: fish, salamanders, tanypodine midges (ROBACK 1969), cyclopoids (FRYER 1957a), oligochaetes (GREEN 1954), and *Hydra* among them (see pp. 151–154 of MCGREGOR 1972, for a review). It is not clear how important ostracods are in the diets of these predators, nor how important predation is in regulating ostracod populations.

I have suggested that ostracod populations turn over more slowly than those of other small invertebrates. If this is so, then mortality rates of ostracods must be unusually low. It may be relevant that some predators apparently find ostracods to be distasteful (e. g., Swuste et al. 1973). The possibility that ostracods have predator defenses, such as repellent chemicals, that reduce mortality rates in nature deserves further investigation.

Acari (mites)

Representatives of three major groups of mites live on the sediments of Mirror Lake. Because these three groups, the Oribatida, the Halacaridae, and the Parasitengona, differ biologically, I will treat each one separately.

Oribatida

The oribatids are small mites that are abundant in soil and leaf litter, where they feed on fungi and detritus (Wallwork 1983). Many species are parthenogenetic. Little is known of the few species of oribatids that have adapted to freshwater habitats (but see Newell 1945, 1959; Strenzke 1952; Walgram 1976).

I found two species of oribatids in Mirror Lake, *Hydrozetes lacustris* and *Trimalaconothrus novus.* Both species are restricted to the littoral sediments (Fig. 53), although I found a single specimen of *H. lacustris* at 9 m in 1980. The oribatids are the numerical dominants in the mite community of Mirror Lake, constituting 50% of all mite individuals.

Several species of *Hydrozetes,* especially *H. lacustris,* have been found in lakes and ponds in Europe and North America (e. g., Newell 1945; Strenzke 1952; Berg & Peterson 1956; Modlin & Gannon 1973; Walgram 1976). Members of the genus are among the most truly aquatic of the oribatids and are notable for their ability to regulate their buoyancy and position in the water column by producing an internal gas bubble (Newell 1945; Hutchinson 1967: 254–255).

Strenzke (1952) found *Trimalaconothrus novus* from *Sphagnum* mats and sandy beaches in softwater lakes in Germany, which fits nicely with its occurrence in the upper littoral of Mirror Lake. I have not seen any other reports of this species from lakes.

Oribatids may be fairly abundant in lakes (Table 26), although quantitative data are scarce. However, relatively few species of oribatids have been successful in invading lakes, and none of them seem to have been able to colonize the deep-water sediments. In all of the lakes that have been studied, the oribatids were absent from the sublittoral and profundal sediments (Moore 1939; Holopainen & Paasivirta 1977; Whiteside & Lindegaard 1982). The oribatids therefore form a regular, but minor, part of littoral benthic communities in lakes.

Table 26. Species richness (S), abundance (m^{-2}), and biomass ($mg\ m^{-2}$) of oribatid mites in some lakes.

Lake	MESH (μm)	S	Abundance	Biomass	Notes	Source
Mirror	–	2	1600	12[a]	lakewide mean, July–Oct.	this study
Grane Langsø, Denmark	100	1	1200	–	lakewide mean, July	Whiteside & Lindegaard 1982
Paajarvi, Finland	100	–	450	3[b]	annual lakewide mean	Holopainen & Paasivirta 1977
Bodensee, Germany	–	0	–	–		Muckle 1942
Neuchatel, Switzerland	–	0	–	–	oligotrophic	Monard 1920

[a] dry weight
[b] ash-free dry weight

Halacaridae

These tiny mites are a characteristic part of the marine meiofauna (Newell 1947), and have been studied in Europe as a part of the subterranean and interstitial faunas (e. g., Teschner 1963; Husmann & Teschner 1970). They have received almost no attention from North American freshwater biologists, and are often considered to be rare in freshwater. However, when appropriate sampling techniques are used, the halacarids have been found in fair numbers in lakes (e.g., Paasivirta 1975).

Halacarids do not swim. The single larval and two nymphal stages are free-living, and along with the adult, may feed on small metazoans (Bartsch 1981a). Males are rare in many species of freshwater halacarids (e. g., Bartsch 1981b).

In Mirror Lake, the halacarids are abundant on the littoral sediments and along the edge of the gyttja (Figs. 52, 53). I collected halacarids throughout the year, but found greatest densities (>5000/m^2) during spring and autumn turnovers.

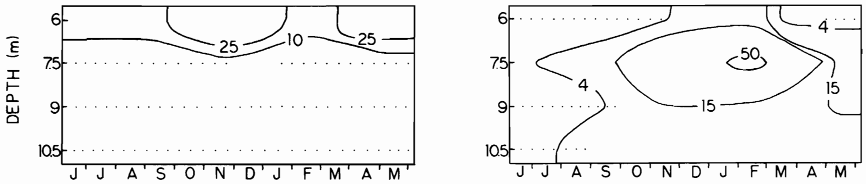


Fig. 52. Abundance (dm^{-2}) of halacarid mites (left) and the larvae of *Piona* sp. (right) in Mirror Lake. Dotted lines show extended periods when these animals were absent from the indicated stations.

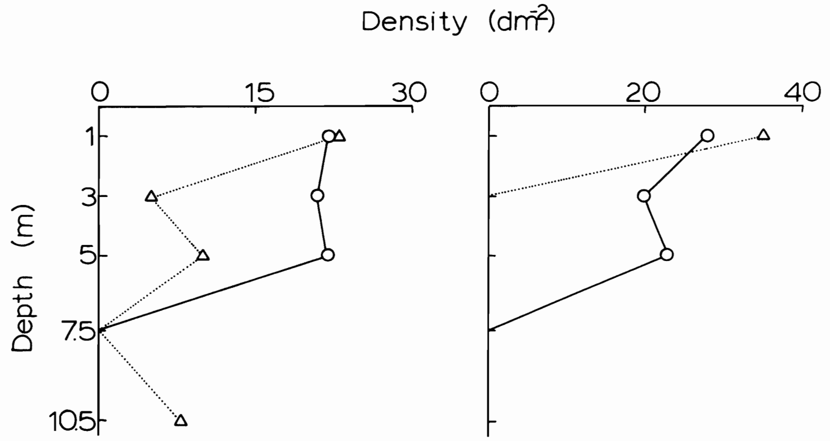


Fig. 53. Density of mites in Mirror Lake, from transect data. Left: Halacaridae (○) and larval Parasitengona (△). Right: *Hydrozetes lacustris* (○) and *Trimalaconothrus novus* (△).

PAASIVIRTA (1975) found halacarid densities to peak in late autumn in Lake Paajarvi, Finland. Almost all of the halacarids in Mirror Lake live in the top 2 cm of sediments, as they do in Paajarvi (PAASIVIRTA 1975).

The four species of halacarids that I found in Mirror Lake all have similar depth distributions, and are treated together in Figs. 52 and 53. All four of the species are eurytopic, widely distributed species that have been reported from many lakes elsewhere (e. g., MONARD 1920; MUCKLE 1942; RAMAZZOTTI & NOCENTINI 1960; NOCENTINI 1961; PAASIVIRTA 1975; BARTSCH 1975, 1981b, 1982). *Porolohmanella violacea,* the dominant species (Table 27), is the only one on which I have enough data to describe its life history. In Mirror Lake, all of the life stages of this mite are present throughout the year, suggesting overlapping generations. PAASIVIRTA (1975) also noted that the immature instars of most of the species in Paajarvi were present throughout the year.

Table 27. Mean weighted densities (dm^{-2}) of halacarid mites in Mirror Lake.

Species	Gyttja	Transect
Porolohmanella violacea	5	5
Lobohalacarus weberi	0.5	4
Porohalacarus alpinus	1	0.6
Soldanellonyx monardi	a	a

[a]not found during the main study, but collected in preliminary samples

I have summarized some records of halacarids in lakes in Table 28. In other lakes, as in Mirror Lake, most of the halacarids have been found in the littoral zone, with highest densities at depths of less than 5 m. However, one species, *Soldanellonyx chappuisi,* is restricted to the profundal sediments in Paajarvi and Lago Maggiore, and has been found at depths of 65 m. Also, MODLIN & GANNON (1973) collected two genera of halacarids from the neuston of Lake Michigan.

It is apparent that a few species of the Halacaridae are well adapted and characteristic members of the freshwater meiofauna. While it seems unlikely that these mites will prove to be quantitatively important in the ecology of lakes, they are probably widespread and common in many lakes.

Parasitengona

These mites are the familiar "water mites" frequently encountered by freshwater biologists. The adults and nymphs of the parasitengone mites are usually predaceous on small metazoans (BÖTTGER 1970), and the larvae are parasitic on aquatic insects, although variations on this basic pattern exist (e. g., SMITH 1976: 95–101). Usually, all stages of the life history are associated with sediments or

Table 28. Species richness (S), abundance (m^{-2}), and biomass (mg m^{-2}) of halacarid mites in some lakes.

Lake	MESH (µm)	S	Abundance	Biomass	Notes	Source
Mirror	–	4	950	0.7[a]	lakewide mean, July–Oct.	this study
Paajarvi, Finland	100	6	3400	1.6[b]	annual lakewide mean	Paasivirta 1975; Holopainen & Paasivirta 1977
Maggiore, Italy	?	6	–	–		Nocentini 1961
Mergozzo, Italy	?	4	–	–		Ramazzotti & Nocentini 1960
Neuchatel, Switzerland	–	3	–	–		Monard 1920
Bodensee, Germany	–	1	–	–		Muckle 1942

[a] dry weight
[b] ash-free dry weight

vegetation, but a few species have planktonic nymphs and adults (e. g., RIESSEN 1982). There have been many studies of lacustrine assemblages of Parasitengona in Europe (e. g., VIETS 1924a,b, 1930, 1931; NOCENTINI 1960; MOTHES 1964; PIECZYNSKI 1976; BIESIEDKA 1977; K.O.VIETS 1979), but I am aware of only one study in North America (HOFF 1944).

A species of *Piona* is the only abundant parasitengone mite in Mirror Lake. I found only three adults or nymphs of *Piona* sp. but the larvae are abundant, especially during the winter, when I found densities greater than 5000 m^{-2} (Fig. 52). The relative scarcity of adults and nymphs of this species in benthic collections from Mirror Lake leads me to believe that they are planktonic. Some species of *Piona* have planktonic nymphs and adults (RIESSEN 1982), and I have seen water mites in collections of zooplankton from Mirror Lake. Judging from Figure 52, *Piona* sp. is univoltine in Mirror Lake, and the nymphs and adults would be expected to appear in the pelagic zone in spring and early summer. The larvae might be free-living (cf. SMITH 1976), or they might be parasitic, for example on the dipterans that emerge in large numbers from Mirror Lake in May and June (WALTER 1976). To my knowledge, this is the first example of a parasitengone life cycle where the overwintering stage is a long-lived larva.

Table 29. Parasitengona collected from Mirror Lake.

Arrenurus sp.	*Limnesia* sp.
Forelia sp.	*Piona* sp.
Hygrobates sp.	*Unionicola* sp.
Lebertia sp.	

Table 30. Species richness (S) of parasitengone mites in some lakes where they have been well studied, in comparison with Mirror Lake.

Lake	S	Notes	Source
Mirror	7	based on only 17 adults and nymphs	this study
Mikorzynskie, Poland	67	productive lake	BIESIADKA 1977
Slesinskie, Poland	64	productive lake	BIESIADKA 1977
Patnowskie, Poland	53	productive lake	BIESIADKA 1977
Bodensee, Germany	50		K. O. VIETS 1979
Goslawickie, Poland	49	productive lake	BIESIADKA 1977
Maarsseveen, Netherlands	48		DAVIDS et al. 1981
Mergozzo, Italy	43		NOCENTINI 1960
Reelfoot, USA	42	shallow productive lake	HOFF 1944
Lichenskie, Poland	42	productive lake	BIESIADKA 1977
Neuchatel, Switzerland	20	oligotrophic	MONARD 1920
47 North German lakes	1–43	mean = 16	VIETS 1924a

Table 31. Abundance (m^{-2}) and biomass ($mg\ m^{-2}$) of Parasitengona in some lakes.

Lake	MESH (µm)	Abundance	Biomass	Notes	Source
Mirror	–	550^{a}	$0.4^{a,c}$	lakewide mean, July–Oct.	this study
Mirror	–	140^{b}	$3^{b,c}$	lakewide mean, July–Oct.	this study
Mirror	–	1500^{a}	$1^{a,c}$	annual mean, gyttja	this study
Mirror	–	180^{b}	$4^{b,c}$	annual mean, gyttja	this study
Par, USA	63	$160{,}000^{a,b?}$	$1200^{a,b?,c}$	annual mean at reference site (z = 1 m)	ODEN 1979
Paajarvi, Finland	100	$260^{b?}$	$16^{b?,d}$	annual lakewide mean	HOLOPAINEN & PAASIVIRTA 1977
Grane Langsø, Denmark	100	$70^{b?}$	–	lakewide mean, July	WHITESIDE & LINDEGAARD 1982

[a] larvae
[b] adults and nymphs
[c] dry weight
[d] ash-free dry weight

Other Parasitengona are scarce in Mirror Lake (Fig. 53). Because I collected only 17 adult or nymphal parasitengones, the seven species represented (Table 29) are probably only a small fraction of the parasitengone fauna of the lake. In lakes where the water mites have been well studied, the fauna typically contains 20–50 species (Table 30). I would expect that Mirror Lake contains a similar number of species.

There are few quantitative data on parasitengone densities in lakes. The published data indicate that water mites usually are a minor component of the zoobenthos (Table 31). I have no explanation for the extraordinarily high densities found in Par Pond, South Carolina, by ODEN (1979), nor do I know of other sites where such densities occur. In Par Pond, the water mites must play an important part in community dynamics, since the predation pressure from such a large mite population must be intense. However, in the other lakes listed in Table 31, including Mirror Lake, the water mites are probably insignificant in determining community structure.

Amphipoda (scuds)

Amphipods are abundant on the littoral sediments of Mirror Lake, but their density falls off sharply with increasing depth (Fig. 54). In my survey of the gyttja, I found amphipods only at the 6 m stations, and there at fairly low density (mean annual density = 2000 m^{-2}). In Mirror Lake, amphipods are responsible for about 2% of zoobenthic biomass and metabolism (Table 35). I did not identify the amphipods that I collected, but WALTER (1976, 1985a) reported *Hyallela azteca* to be the only species in her samples.

H. azteca is commonly found in lakes, and population densities often exceed those found in Mirror Lake. Further information about this species is available in papers by COOPER (1965) and LINDEMAN & MOMOT (1983), and in literature cited therein.

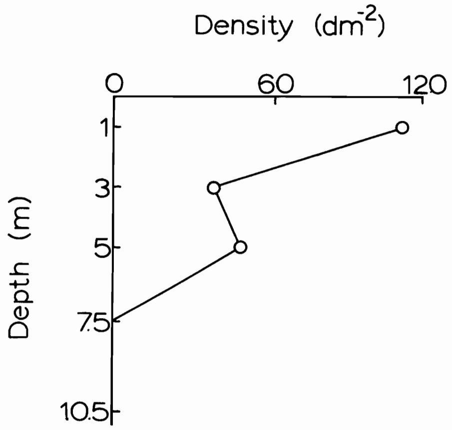


Fig. 54. Abundance of amphipods in Mirror Lake, from transect data.

Chironomidae

The chironomid midges are, by most measures, the most important animals in the lacustrine zoobenthos. They are abundant in most lakes, and commonly constitute upwards of 50% of zoobenthic biomass (WALTER 1985a). The chironomids are an important food for many species of fish (e.g., GERKING 1962; MASZA 1973; WELCH 1976), and thus form an important trophic link between the microflora and vertebrates. The burrowing and feeding activities of chironomid larvae affect the exchange of nutrients across the sediment-water interface (e.g., GRANELI 1979, 1980), and alter sediment stratigraphy (ROBBINS 1982). Chironomids have had a central role in the lake classification schemes of THIENEMANN, LENZ, BRUNDIN, and others (see the review of BRINKHURST 1974).

The family Chironomidae includes tremendous taxonomic and ecological diversity. As a result, it is difficult to generalize about the biology of chironomids. The larvae usually live in sediments of fresh water environments, although marine and terrestrial species are known. The first of four larval instars may be planktonic in lakes, and is the stage when much dispersal occurs. The short-lived aerial adult usually does not feed. In favorable conditions, chironomids may pass through several generations in a year, but life cycles are longer in more rigorous environments. Arctic species commonly take from two to seven years to complete their life cycle (WELCH 1976; BUTLER 1982). Most species reproduce sexually, but a few parthenogenetic species are known. See the review of OLIVER (1971), from which the above account was summarized, for further information.

The chironomids have diversified trophically as well. Various species feed on detritus and bacteria, phytoplankton, benthic algae, macrophytes, or any of many small animals (e. g., BERG 1950; WALSHE 1951; PROVOST & BRANCH 1959; ARMITAGE 1968; ROBACK 1969; IZVEKOVA 1971; MCLACHLAN & DICKINSON 1977; TITMUS & BADCOCK 1981). A few parasitic species are known as well (e. g., GORDON et al. 1979).

Because many chironomids are retained on coarse sieves (e.g., 0.5-mm mesh), they are often considered to be a part of the macrofauna. However, small species and early instar larvae pass such coarse sieves, and are retained quantitatively only on sieves as fine as about 100-µm mesh (JONASSON 1958; NALEPA & ROBERTSON 1981b; HUMMON 1981; STRAYER 1985a).

I identified only the chironomids that I collected during the transect study, so I cannot remark on the phenology of the various species. My statements about the diets of chironomids in Mirror Lake are based on my observations of the gut contents of slide-mounted animals. The genera are arranged by subfamily in the following account.

Tanypodinae

The tanypodines are free-living mobile animals. They are often considered to be predatory, and they do feed heavily on oligochaetes, microcrustaceans, and other chironomids, but they also consume large quantitites of benthic diatoms and desmids (e. g., HAMILTON 1965; ROBACK 1969; TARWID 1969; ARMITAGE 1968). I found three species of Tanypodinae in Mirror Lake in addition to the three species discussed below (Table 32).

Ablabesmyia sp.

This midge is fairly abundant on the littoral sediments of Mirror Lake (Fig. 55). WALTER (1976, 1985a) reported *A. mallochi* from Mirror Lake, but the larvae that I collected are not of this species. *Ablabesmyia* sp. feeds on diatoms and chironomids in Mirror Lake. Several species of this genus are common on the littoral sediments of lakes (e.g., HAMILTON 1965; REISS 1968; RADDUM & SAETHER 1981; WHITESIDE & LINDEGAARD 1982).

Larsia canadensis

This species lives on the littoral sediments of Mirror Lake, where it is moderately abundant (Fig. 55). *Larsia* sp. feeds largely on diatoms in Mirror Lake, but I found one individual to contain a rotifer and another a chironomid. HAMILTON (1965) found *Larsia acrocincta* to feed on diatoms, plant fragments, and detritus in Marion Lake, British Columbia, so there is evidence that *Larsia* is more herbivorous than are most of the tanypodines. *Larsia* has been reported from a few other lakes in North America (HAMILTON 1965; MOORE 1979).

Procladius sp.

This genus is the most abundant of the tanypodines in Mirror Lake, and is found throughout the depth profile (Fig. 55). WALTER (1976, 1985a) collected *P. denticulatus* and an undescribed species of *Procladius* from Mirror Lake, and ROBACK (1980) reported *P. denticulatus* from the lake. Presumably, at least some of the larvae that I collected belong to *P. denticulatus*, but I was not able to verify such a determination. *Procladius* sp. is markedly predatory in Mirror Lake; animals contained (in order of frequency) algae, chironomids, chydorid cladocerans, rotifers, oligochaetes, ostracods, and shelled amoebae.

Procladius is one of the most abundant and widespread of the lacustrine chironomids. Several species have been reported from lakes, from the littoral zone to the profundal zone (e.g., REISS 1968; PAASIVIRTA 1974; POTTER & LEARNER 1974; MAITLAND 1979; WHITESIDE & LINDEGAARD 1982; VODOPICH & COWELL 1984).

Orthocladiinae

Members of this large, taxonomically difficult subfamily are common in lakes, particularly at high latitudes and high altitudes (OLIVER 1971). Most species feed on detritus or algae. Four relatively rare genera of orthoclads were collected from Mirror Lake (Table 32) in addition to the three genera treated below.

Heterotanytarsus sp.

This species is restricted to the upper littoral zone in Mirror Lake, where it is fairly abundant (Fig. 55). *Heterotanytarsus* sp. feeds on unrecognizable detritus and sand grains in Mirror Lake. This genus is not especially common in lakes. However, it has been reported from the littoral zone in several lakes, especially from sandy substrata (PAASIVIRTA 1974; SAETHER 1975; MCGARRIGLE 1980; RADDUM & SAETHER 1981; SARKKA 1983). *H. apicalis*, the species most frequently reported, is very small; almost 100% of the population in the Finnish lake Paajarvi passed a 0.4-mm mesh sieve (PAASIVIRTA 1974).

Heterotrissocladius sp.

This species is widely distributed in Mirror Lake, but is not especially abundant (Fig. 55). It feeds on detritus and diatoms in Mirror Lake. Several members of this genus have been reported from lakes, usually in meso- or oligotrophic waters (REISS 1968; PAASIVIRTA 1974; SAETHER 1975, 1979; MOORE 1979; RADDUM & SAETHER 1981; WIEDERHOLM 1981). It is frequently a dominant genus in arctic or alpine lakes (e. g., BRETSCHKO 1974; WELCH 1976).

"*Parakiefferiella* sp."

This species is the most abundant of the orthoclads in Mirror Lake, and is especially abundant in the upper littoral zone (Fig. 55). It feeds on diatoms and detritus. This larva resembles *Parakiefferiella,* but has a weak cardinal beard, which is atypical for this genus (K. SIMPSON, pers. comm.; but see CRANSTON et al. 1983). Members of this genus are fairly common in lakes, in both littoral and profundal habitats (HAMILTON 1965; REISS 1968; MOORE 1979; BUTLER et al. 1980; RADDUM & SAETHER 1981; SARKKA 1983).

Chironominae

This subfamily is divided into three tribes, the Chironomini, the Tanytarsini, and the Pseudochironomini. The former two tribes dominate the lacustrine fauna throughout much of the world (OLIVER 1971; cf. Tables 33, 34). Many members of the Chironominae live in cases, some of which are portable. Seven species of the Chironominae, all Chironomini, were collected from Mirror Lake in addition to the nine taxa discussed below (Table 32).

Chironomus anthracinus

This midge is restricted to the gyttja sediments in Mirror Lake (Fig. 55). Although not abundant numerically, it dominates the biomass of chironomids in Mirror Lake, and is in fact responsible for about 20% of zoobenthic biomass lakewide. *C. anthracinus* feeds on detritus in Mirror Lake, as it does in other localities (WALSHE 1951; IZVEKOVA 1971). *C. anthracinus* is commonly found in the profundal sediments of lakes (e. g., REISS 1968; JOHNSON & BRINKHURST 1971a; CHARLES et al. 1974; MCGARRIGLE 1980). Although it is often thought of as a species of meso- or eutrophic waters (SAETHER 1975, 1979; WIEDERHOLM 1981), it is sometimes dominant in oligotrophic lakes as well (this study; WHITESIDE & LINDEGAARD 1982).

Cladotanytarsus sp.

This is the most abundant species of chironomid in the littoral zone of Mirror Lake, but is absent from the gyttja (Fig. 55). It feeds on detritus and, to a lesser extent, algae, in Mirror Lake. Other authors have likewise found species of *Cladotanytarsus* to be detritivores (ARMITAGE 1968; IZVEKOVA 1971). Members of this genus, especially *C. mancus,* are abundant in lakes, particularly in sandy littoral sediments (e. g., MUNDIE 1955; REISS 1968; POTTER & LEARNER 1974; SAETHER 1975; MCGARRIGLE 1980).

Cryptotendipes sp.

This chironomid is abundant in the upper littoral zone in Mirror Lake (Fig. 55). It feeds largely on diatoms in Mirror Lake, although some detritus is consumed, too. REISS (1968) found *C. pflugfelderi* and *C. usmaensis* to be fairly abundant in the upper littoral zone of the Bodensee in Germany.

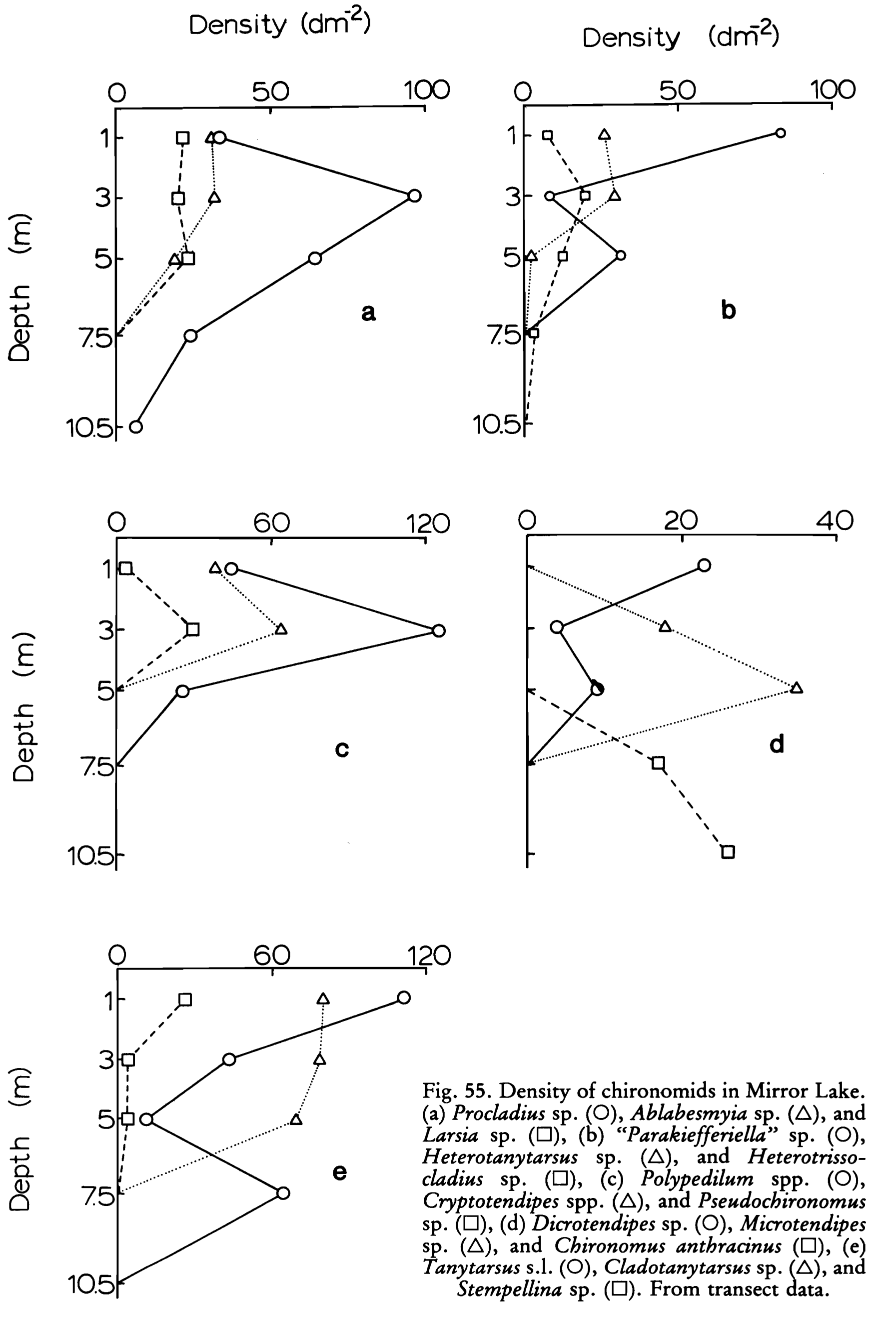


Fig. 55. Density of chironomids in Mirror Lake. (a) *Procladius* sp. (○), *Ablabesmyia* sp. (△), and *Larsia* sp. (□), (b) "*Parakiefferiella*" sp. (○), *Heterotanytarsus* sp. (△), and *Heterotrissocladius* sp. (□), (c) *Polypedilum* spp. (○), *Cryptotendipes* spp. (△), and *Pseudochironomus* sp. (□), (d) *Dicrotendipes* sp. (○), *Microtendipes* sp. (△), and *Chironomus anthracinus* (□), (e) *Tanytarsus* s.l. (○), *Cladotanytarsus* sp. (△), and *Stempellina* sp. (□). From transect data.

Dicrotendipes sp.

This species was found in low numbers throughout the littoral zone in Mirror Lake (Fig. 55). It feeds on diatoms and detritus in the lake. Several species of *Dicrotendipes* (= *Limnochironomus*) are common in lakes, especially in the littoral sediments (e.g., Reiss 1968; Maitland 1979; McGarrigle 1980; Whiteside & Lindegaard 1982). Members of this genus are said to be detritivores (Izvenkova 1971; Moore 1979).

Microtendipes sp.

Although not found at the 1-m station, this species is fairly plentiful in the lower littoral zone (Fig. 55). This species eats detritus and diatoms in Mirror Lake. Several species of *Microtendipes* are common in lakes (Hamilton 1965; Maitland 1979; McGarrigle 1980; Raddum & Saether 1981). Although most species live in the littoral zone, at least one species, *M. pedellus,* may live in profundal sediments as well (Reiss 1968). Most species are apparently detritivorous (Walshe 1951; Izvekova 1971), but *M. pedellus* may filter-feed on plankton (Leathers 1922, cited by Berg 1950).

Polypedilum spp.

This is one of the most abundant chironomids in the littoral zone of Mirror Lake (Fig. 55). Walter (1976, 1985a) reported *P. haltere* and *P. tritum* from Mirror Lake, but I could not distinguish the species in the larval stage. The genus feeds primarily on detritus in Mirror Lake, but eats diatoms as well. *Polypedilum* is very common in lakes, particularly in the littoral zone in fairly productive lakes (e.g., Hamilton 1965; Reiss 1968; Paasivirta 1974; Saether 1975, 1979; McGarrigle 1980). Species of the genus are generally considered to be detritivores, but may feed on diatoms, macrophytes, or small animals as well (Berg 1950; Walshe 1951; Izvekova 1971; Titmus & Badcock 1981).

Pseudochironomus sp.

This genus was collected in small numbers in the upper littoral zone of Mirror Lake (Fig. 55). It feeds on detritus in Mirror Lake. A few species of *Pseudochironomus* are found on the littoral sediments of lakes, but they are rarely abundant (Mundie 1955; Reiss 1968; Raddum & Saether 1981; Whiteside & Lindegaard 1982; Sarkka 1983).

Stempellina sp.

This small chironomid is uncommon on the littoral sediments of Mirror Lake (Fig. 55). I also found it on the gyttja at 6 m in 1980–81. The few specimens that I collected contained detritus and diatoms in their guts. *S. bausei* is the only species of this genus that has been found regularly in lakes. It lives in the littoral zone of oligo- to mesotrophic lakes (Hamilton 1965; Saether 1975; McGarrigle 1980; Wiederholm 1981), and may be a detritivore (Walshe 1951).

Tanytarsus s.l.

This taxon certainly contains more than one genus, but I did not distinguish among them. Simpson (pers. comm.) found both *Tanytarsus* and *Paratanytarsus* in the larvae that I collected. Walter (1976, 1985a) reported two species of *Tanytarsus* and a species of *Micropsectra* in her material. Although none of my larval specimens had the tubercular spur usually used to identify *Micropsectra,* this character is no longer considered to be reliable (Pinder & Reiss 1983). Furthermore, the depth distribution of *Tanytarsus* s. l. (Fig. 55) strongly suggests that at least two species are involved. Members of this complex of species feed on detritus and diatoms in Mirror Lake. *Tanytarsus, Micropsectra,* and *Paratanytarsus* all contain many species that are abundant in lakes (e. g., Hamilton 1965; Reiss 1968; Johnson & Brinkhurst 1971a; Potter & Learner 1974; Bretschko 1974; Saether 1975, 1979; Jonasson & Lindegaard 1979; McGarrigle 1980; Whiteside & Lindegaard 1982). Most species are detritivores (Walshe 1951; Armitage 1968; Izvekova 1971; Moore 1979).

Other Chironomidae

I found 17 other species of chironomids in Mirror Lake (Table 32). Most of these taxa are common and widely distributed in lakes. The species of *Psectrocladius* feed on detritus and diatoms in Mirror Lake. *Pagastiella* spp. may be fairly strict algivores. Hamilton (1965) found that an undetermined species of this genus fed almost exclusively on large diatoms in Marion Lake, British Columbia. *P. orophila* likewise subsists almost entirely on diatoms, according to Armitage (1968). In Mirror Lake, the three animals of *P. ostansa* that I collected all contained diatoms and nothing else. Walter (1976, 1985a) found eight genera of chironomids in Mirror Lake that I did not collect (Table 32).

Table 32. List of rare chironomids in Mirror Lake. Taxa marked with * were reported by Walter (1976, 1985a), but not found in the present study.

Tanypodinae
Clinotanypus pinguis
Conchapelopia sp.
Labrundinia sp.

Diamesinae
**Protanypus* sp.

Prodiamesinae
**Monodiamesa* sp.

Orthocladiinae
Hydrobaenus sp.
Nanocladius (Plecopteracoluthus) sp.
Psectrocladius sp. 1
Psectrocladius sp. 2
**Rheocricotopus* sp.
Zalutschia zalutschicola
Zalutschia sp. 2
Zalutschia sp. 3

Chironomini
Cladopelma sp.
Cryptochironomus sp.
**Glyptotendipes* nr. *lobiferus*
Lauterborniella sp.
Nilothauma sp.
Pagastiella ostansa
Parachironomus sp.
**Paracladopelma* sp.
**Paralauterborniella* sp.
**Phaenopsectra* sp.
Stichtochironomus sp.

Tanytarsini
**Micropsectra* sp.

Discussion

Walter (1985a) has already reviewed the ecology of the chironomids of Mirror Lake and made comparisons with other lakes, so the following review will be brief. Brundin (1949), Thienemann (1954), and Oliver (1971) also have written general reviews of chironomid biology and ecology.

Table 33. Species richness of major taxa of chironomids in some well studied lakes, in comparison with Mirror Lake.

Lake	Total[a]	Tany-podinae	Ortho-cladiinae	Chirono-mini	Tany-tarsini	Notes	Source
Mirror	48	7	14	18	6	small oligotrophic lake	this study
Bodensee, Germany	168	17	43	67	33	intensive study	Reiss 1968
Innaren, Sweden	140	–	–	–	–		cited by Reiss 1968
Chad, Chad	93	16	1	65	11	large, shallow tropical lake	Dejoux 1968
Grosser Plöner See, Germany	86	–	–	–	–		cited by Reiss 1968
Erken, Sweden	82	–	–	–	–	meso- to eutrophic	Sandberg 1969
Lunzer Untersee, Austria	77	–	–	–	–		cited by Reiss 1968
Costello, Canada	>75	>7	>12	39	15	dystrophic	Miller 1941
Konnevesi, Finland	>65	>5	>21	18	>18	oligotrophic lake	Sarkka 1983
Marion, Canada	56	16	14	16	9	shallow	Hamilton 1965
Bay of Quinte, Canada	43	7	7	22	7	productive bay of L. Ontario	Johnson & Brinkhurst 1971a
Barrow Ponds, Alaska	>37	4	>20	7	5	small arctic ponds	Butler et al. 1980
Eglwys Nunydd, Wales	34	4	6	17	7	eutrophic reservoir	Potter & Learner 1974
Michigan, USA	24	1	4	14	3	based on one site	Nalepa & Quigley 1980
Thingvallvatn, Iceland	21	3	11	2	3	large oligotrophic lake	Lindegaard 1980
Federsee, Germany	17	6	4	6	1	shallow hypereutrophic lake	Frank 1982
Myvatn, Iceland	12	4	5	2	1	shallow lake	Jonasson & Lindegaard 1979
Vorderer Finstertalersee, Austria	11	1	6	0	3	small alpine lake	Bretschko 1974
Blaxter Lough, Britain	11	2	4	3	2	small bog lake	McLachlan & McLachlan 1975
Manitoba, Canada	8	1	0	6	1	shallow productive lake	Tudorancea et al. 1979

[a] totals include Diamesinae, Prodiamesinae, Pseudochironomini, and Podonominae, in addition to listed taxa

Forty-eight species of chironomids have been collected from Mirror Lake. An intensive study would undoubtedly reveal many more species. The Mirror Lake chironomid fauna is dominated by the Chironomini, Tanytarsini, and the Orthocladiinae (Table 33, Fig. 57). Both the species richness and the composition of the chironomid fauna of Mirror Lake are typical for a lake in the temperate zone that has received moderate study (Table 33). Detailed studies of the Chironomidae have usually shown lakes to contain 50 to 200 species (Table 33). Arctic and alpine lakes tend to be species-poor, and have faunas dominated by the Orthocladiinae (Tables

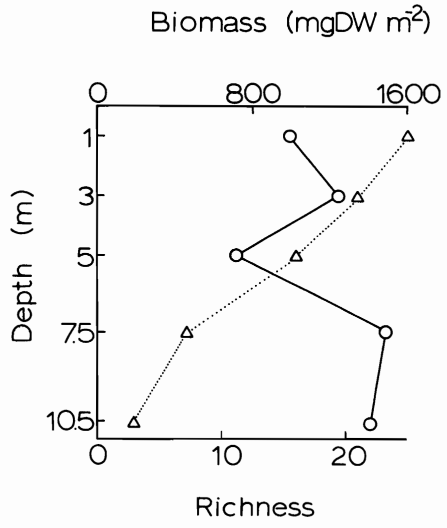


Fig. 56. Biomass (○) and species richness (△) of chironomids in Mirror Lake. All data from transect.

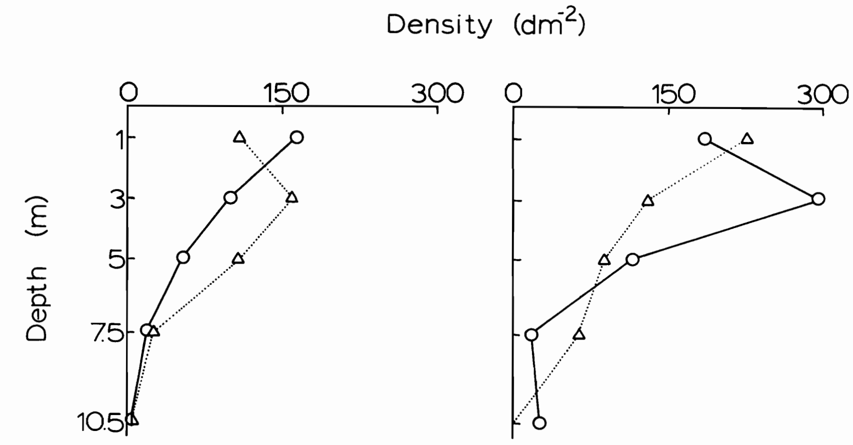
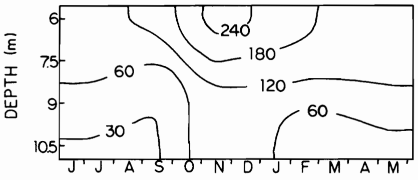


Fig. 57. Abundance of the various subfamilies and tribes of the Chironomidae in Mirror Lake. Left: Tanypodinae (○) and Orthocladiinae (△). Right: Chironomini + Pseudochironomini (○) and Tanytarsini (△).

33, 34; Oliver 1971). The single tropical lake included in Table 33 (L. Chad) has a rich fauna that is dominated by the Chironomini.

Chironomids are widely distributed in Mirror Lake, but are most abundant and species-rich in the littoral zone (Figs. 55–58). During June through October, most (66%) of the chironomids live in the top 1 cm of sediment in Mirror Lake (Fig. 59). Nalepa & Robertson (1981a) found that 75% of the chironomid population lived in the top 1 cm of sediments in Lake Michigan. However, some other authors have shown chironomid larvae to penetrate lake sediments much more deeply. Berg (1938), Cole (1953), and Frank (1982) all found that chironomid larvae may live more than 10 cm below the sediment surface. In fact, Frank found larvae more than 35 cm below the sediment surface, and showed that the degree of penetration varied among the larval instars of *Chironomus plumosus* in the eutrophic Federsee, Germany.

Fig. 58. Abundance (dm^{-2}) of chironomids in Mirror Lake.



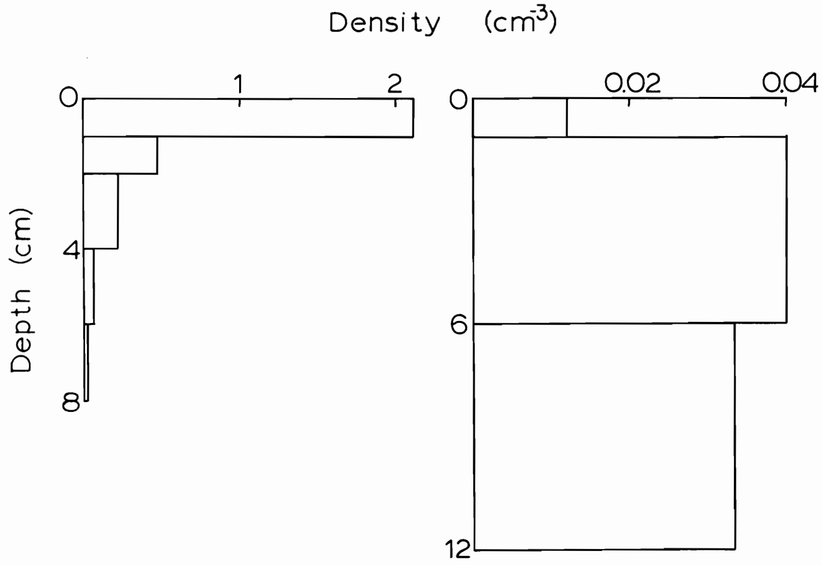


Fig. 59. Vertical distribution of dipteran larvae within the sediments of Mirror Lake, as a function of depth from the sediment surface. Left: Chironomidae (lakewide means from the transect). Right: Chaoboridae (annual means from the gyttja survey).

Table 34. Abundance (m^{-2}) of major taxa of chironomids in some representative lakes.

Lake	MESH (µm)	Total	Tany-podinae	Ortho-cladiinae	Chirono-mini[b]	Tany-tarsini	Notes	Source
Mirror	–	32,000	6,500	5,900	9,700	9,700	lakewide mean, July–Oct.	this study
Mirror	250	9,800	–	–	–	–	lakewide mean	Walter 1985 a
Myvatn, Iceland	?	59,000	400	1,200	6,000	51,000		Jonasson & Lindegaard 1979
Eglwys Nunydd, Wales	150	29,000	11,000	0	4,700	13,000	annual mean	Potter & Learner 1974
Leven, Scotland	500	16,000[a]	2,900	200	6,800	6,600	lakewide mean, Oct.	Maitland 1979
Grane Langsø, Denmark	100	14,000	1,200	4,300	6,700	2,000	lakewide mean, July	Whiteside & Lindegaard 1982
Char, Canada	67	7,800	0	7,700	0	0	annual lakewide mean	Welch 1976
Manitoba, Canada	200	5,600	2,600	0	2,900	80	mean of 7 stations, May–Jan.	Tudorancea et al. 1979
Thingvallvatn, Iceland	100	4,100	10	3,700	300	20		Lindegaard 1980
Michigan, USA	45	1,700	0	300	1,000	350	z = 11–23 m; Apr.–Nov.	Nalepa & Robertson 1981a
Vorderer Finstertalersee, Austria	100	500	–	–	–	–	4 year mean	Bretschko 1974

[a] probably an underestimate because of the coarse sieve used

[b] including *Pseudochironomus*

Although I do not have any information on the phenology on individual chironomid species, there is a clear maximum in total chironomid density in late autumn in Mirror Lake (Fig. 58). This maximum is undoubtedly due to the appearance of juveniles hatching from eggs laid during the summer.

The mean lakewide density of chironomids in Mirror Lake is 32,000 m^{-2}, compared with a figure of 9,800 m^{-2} reported by WALTER (1985a), who used a 250-µm sieve (Table 34). The former value is fairly high when compared to other lakes where chironomids have been sampled quantitatively (Table 34). I estimate a mean lakewide biomass of 1.25 g DW m^{-2}, which is very similar to WALTER's estimate of 1.1 g DW m^{-2}. Chironomid biomass is somewhat lower than that reported for other lakes (WALTER 1985a).

The chironomids dominate the zoobenthic community of Mirror Lake (Table 35). They account for about half of zoobenthic production (Table 35), and are probably major consumers of benthic bacteria and algae. The Tanypodinae may be important predators of such animals as oligochaetes, microcrustaceans, and other chironomids. As a result, the chironomids may be significant in regulating community structure in the benthos (cf. KAJAK et al. 1968).

Chaoboridae

This family is represented by a single genus, *Chaoborus,* in Mirror Lake. The larvae of *Chaoborus* live in the sediments during the day and in the pelagic zone at night. They are predaceous, feding both on zooplankton and zoobenthos such as oligochaetes (e.g., SWUSTE et al. 1973). WALTER (1976, 1985a) described the distribution and biology of *Chaoborus* spp. in Mirror Lake in detail, so the following section is brief.

Two species of *Chaoborus, C. punctipennis* and *C. flavicans,* have been found in Mirror Lake. The latter species is dominant (WALTER 1976). Both species live on

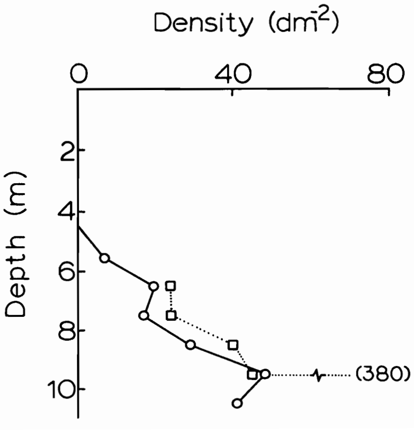


Fig. 60. Abundance of *Chaoborus* spp. in Mirror Lake, in July (○) and January (☐). Data from WALTER (1976).

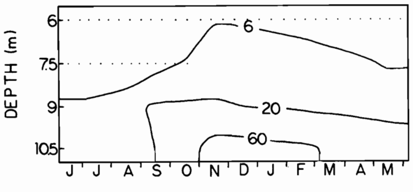


Fig. 61. Abundance (dm^{-2}) of *Chaoborus* spp. in Mirror Lake. Dotted lines show extended periods when the species were absent from the indicated station.

the gyttja in Mirror Lake, and are most abundant in the deepest parts of the lake (Figs. 60, 61). These animals burrow deeply into the sediments (Fig. 59), so the data in Fig. 61, which are based on 8- to 12-cm long cores, are probably underestimates. *Chaoborus* spp. account for about 10% of zoobenthic biomass and metabolism in Mirror Lake (Table 35).

Other Insecta

WALTER (1985a) listed 41 additional species of benthic insects from Mirror Lake; probably many more species are present. None of these species is, however, abundant enough for WALTER or me to describe its distribution or abundance in the lake. Nonetheless, some of these relatively rare animals play important ecological roles in Mirror Lake. The large insects, especially the odonates, are an important part of the diet of the fish in the lake (MASZA 1973). Furthermore, some of the insects may have a significant impact on populations of their food items. For example, larvae of the lepidopteran *Eoparargyractis plevie* feed on the macrophytes *Lobelia dortmanna* and *Isoetes tuckermani* in Mirror Lake, and may severely damage or kill many of these plants (FIANCE & MOELLER 1977). Other insects may play similarly important roles in community dynamics, but too little information is available to speculate further.

Mollusca

Six species of mollusks have been reported from Mirror Lake (WALTER 1985a). The only abundant mollusks are the sphaeriid bivalves *Sphaerium* sp. and *Pisidium* sp. (Fig. 62). We know little about the distribution of these two species, since WALTER did not distinguish between them and I did not collect many of them. However, all of the 48 sphaeriids that I collected on the gyttja were *Pisidium*, and all of the 3 sphaeriids that I collected from the littoral zone were *Sphaerium*. STRAYER et al. (1981) studied the unionid bivalve *Elliptio complanata* in Mirror Lake. This animal is rare in the lake (0.03 adults m^{-2} lakewide), and is restricted to the littoral zone. Of the remaining species of mollusks listed by WALTER, I have seen only *Campeloma decisum; Helisoma* sp. and *Lymnaea* sp. must be rare. In all, about 10% of zoobenthic biomass and much less of zoobenthic metabolism in Mirror Lake can be attributed to the mollusks (Table 35).

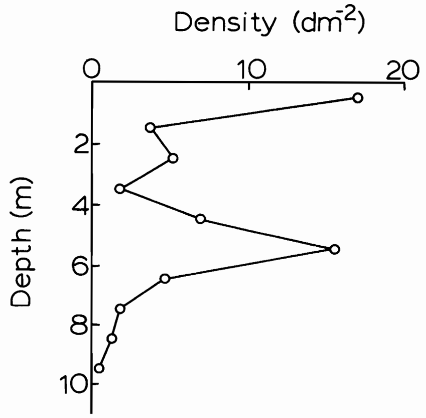


Fig. 62. Abundance of the Sphaeriidae in Mirror Lake, from the data of WALTER (1985a).

General discussion

General description of the zoobenthos of Mirror Lake

The zoobenthic community of Mirror Lake is very diverse; the incomplete species list resulting from WALTER's (1985a) work and the present study contains 322 species belonging to 12 phyla (Table 35). WALTER (1985a) presented a listing of these 322 species. About 65% of these species belong to the meio- or microfauna. Throughout my discussions of the various taxonomic groups, I have made crude estimates of the actual number of species that inhabit the lake. These estimates, which are probably almost all too conservative, suggest that Mirror Lake probably contains about 600 species of benthic metazoans (Table 35). Many groups are well represented in the zoobenthos in Mirror Lake, but the monogonont rotifers and insects are especially speciose, together contributing about half of the benthic animal species in the lake.

I have tried to show throughout the preceding pages that the fauna of Mirror Lake is not extraordinary. In fact, there seems to be surprisingly little variation among lakes in the species richness of various taxonomic groups. The two major exceptions to this generalization are the monogonont rotifers, which are especially diverse in softwater lakes such as Mirror Lake, and the ostracods, which are especially species-poor in Mirror Lake (Table 24). It is very likely that the zoobenthos of most lakes contains several hundred species and at least ten phyla (Table 36).

It seems worthwhile to mention in passing an observation that may be obvious to most freshwater biologists, but struck me as interesting. There are 16 phyla of free-living animals (including the protozoans and chordates) known from the world's fresh waters. Fourteen of these phyla have already been reported from Mirror Lake. Of the remaining phyla, the nematomorphs have been collected

Table 35. Profile of the zoobenthos of Mirror Lake. All figures except for species richness are lakewide means based on transect data. Observed species richness includes species actually collected by WALTER or me; predicted species richness is the number of species that I suspect to occur in the lake.

Taxon	Species richness Observed	Species richness Predicted	Abundance (m^{-2})	Biomass (mgDW m^{-2})	Production (mgDW $m^{-2}yr^{-1}$)	Respiration (mgC $m^{-2}yr^{-1}$)
Porifera	4^{a}	4	–	–	–	–
Coelenterata	2	2	500	50	100^{d}	200^{g}
Turbellaria	23	40	27,000	24	300^{d}	300^{g}
Nemertea	1	1	–	–	–	–
Nematoda	20	35	680,000	32	700^{d}	700^{g}
Gastrotricha	ca. 25	30	130,000	1	100^{d}	50^{g}
Monogononta	56	200	57,000	8	200^{d}	100^{g}
Bdelloidea	8	10	97,000	7	300^{d}	200^{g}
Tardigrada	3	5	7,500	2	40^{d}	30^{g}
Ectoprocta	2^{a}	2	–	–	–	–
Annelida	25	30	30,000	410	2,000^{d}	1,900^{g}
Cladocera	23	40	6,400	20	100^{d}	200^{g}
Copepoda	15	22	37,000	76	700^{d}	1,200^{g}
Ostracoda	3	5	18,000	42	200^{e}	400^{g}
Amphipoda	1	1	2,100^{a}	40^{a}	200^{f}	200^{a}
Decapoda	1^{a}	1	–	–	–	–
Parasitengona	7	40	700	3	10^{d}	30^{g}
Halacaridae	4	5	1,000	1	6^{d}	10^{g}
Oribatida	2	3	1,600	12	100^{d}	100^{g}
Chironomidae	48	60	32,000	1,250	6,600^{f}	1,800^{a}
Chaoboridae	2^{a}	3	2,700^{a}	280^{a}	1,400^{f}	600^{a}
Other Insecta	41^{a}	75	400^{a}	14^{a,c}	70^{c,f}	–
Mollusca	6^{a}	6	600^{a}	200^{a,b}	300^{d}	100^{a}
Total metazoa	322	ca. 600	1,150,000	2,500	14,000	8,000
% meio- and microfauna	65	68	98	ca. 25	ca. 35	ca. 65

[a] from WALTER (1976, 1985a)
[b] from STRAYER et al. (1981)
[c] probably several-fold too low
[d] from P/B ratios predicted by the modified BANSE & MOSHER (1980) regression
[e] see text
[f] after P/B ratios of WATERS (1977)
[g] after BANSE's (1982) regression

Table 36. Composition of the zoobenthos in three well studied lakes. Most of these figures are probably underestimates.

Taxon	Reported species richness		
	Mirror[a]	Neuchatel[b]	Bodensee
Porifera	4	0	1[c]
Coelenterata	2	1[d]	2[c]
Turbellaria	23	36	27[e]
Nemertea	1	2[d]	0[c]
Nematoda[f]	20	33	42[c]
Gastrotricha	ca. 25	2[d]	[g]
Rotatoria	64	33	57[h]
Tardigrada	3	3[d]	2[c]
Ectoprocta	2	1[d]	2[c]
Oligochaeta	25	35	28[c]
Hirudinea	0	7[d]	4[c]
Cladocera	23	35	35[c]
Copepoda	15	17	23[c]
Ostracoda	3	18	13[c]
Isopoda	0	0	1[c]
Amphipoda	1	3[d]	3[c]
Decapoda	1	0	0[c]
Acari	13	25[d]	51[c,i]
Chironomidae	48	7[d]	168[j]
Other Insecta	43	8[d]	46[c]
Mollusca	6	43	27[c]
Total metazoa	322	309	532[k]

[a] Walter 1985a, and this study
[b] Monard 1920
[c] Muckle 1942
[d] estimated from tables on pp. 185 and 202 of Monard 1920
[e] Rixen 1968
[f] excludes Mermithidae
[g] data not available
[h] Koch-Althaus 1962
[i] K.O. Viets 1979
[j] Reiss 1968
[k] excludes Gastrotricha

from streams less than 1 km from Mirror Lake, and probably live in the lake itself. Only the Entoprocta are likely to be absent from Mirror Lake.

Thus, a small, geologically young lake in the temperate zone, a lake that does not possess a particularly wide range of habitats, probably contains 15 of the 16 phyla of freshwater animals. Many other lakes and streams very likely contain 14 or 15 phyla, as well (cf. Table 36). These observations show that every phylum of animals that has been successful in coping with freshwater environment (except the Entoprocta) has also dispersed and diversified to such an extent as to be found in most permanent fresh waters, regardless of location or limnology.

According to my results from the transect, the mean lakewide density of benthic metazoans in Mirror Lake is 1,150,000 m^{-2}. The mean annual density of

Table 37. Biomass (g m^{-2}) of micro- and meiobenthic metazoans in some lakes. Data are only approximately comparable because of differences among studies in the definitions of micro- and meiofauna. Most workers used sieve mesh sizes to define these groups; I have listed the upper and lower mesh sizes that they used to circumscribe the fauna under "LIMITS" below.

Lake	Limits (μm)	Biomass	Ratio[a]	Notes	Source
Mirror	0–250	0.6[b]	0.3	lakewide mean from transect	this study
Par, USA	63–500	3.7[b]	–	annual mean from reference site (z = 1 m)	Oden 1979
Nine Canadian lakes	45–425	0.2–2.4[b]	0.2–2.7 (x=0.8)	single sample from each lake	Anderson & de Henau 1980
Paajarvi, Finland	100–400	0.3[c]	0.75	lakewide annual mean	Holopainen & Paasivirta 1977
Michigan, USA	f	0.3[b]	0.07	z = 11–23 m; Apr.–Nov.	Nalepa & Quigley 1983
Tundra pond, USA	d	0.09[e]	0.03	mean for June–Aug.	Hobbie 1980

[a] biomass of meio- and microbenthos : biomass of macrobenthos

[b] dry weight

[c] ash-free dry weight

[d] meio- and microfauna defined to include flatworms, nematodes, rotifers, gastrotrichs, tardigrades, copepods, and ostracods

[e] original data as wet weight; converted to dry weight by multiplying by 0.15

[f] meiobenthos defined to include nematodes, copepods, cladocerans, ostracods, tardigrades, flatworms, rotifers, mites, and hydrids

benthic metazoans on the gyttja is 1,200,000 m^{-2}. Because of the methodological considerations to be discussed below (cf. Fig. 67), there are no comparable data from other lakes.

The meio- and microbenthic animals contribute 98% of the numerical density of the zoobenthos in Mirror Lake (Table 35). Nematodes are numerically dominant in Mirror Lake, constituting 59% of all metazoan individuals in the benthos. Similar figures have been reported from other lakes, where nematodes constitute from 40% to 80% of all meiobenthic animals (HOLOPAINEN & PAASIVIRTA 1977; ODEN 1979; NALEPA & QUIGLEY 1983).

I estimate a mean lakewide standing stock of benthic animals of 2.5 g DW m^{-2} in Mirror Lake, of which about 0.6 g DW m^{-2} belongs to the micro- and meiofauna. As WALTER (1985a) has already pointed out, the biomass of benthic macroinvertebrates in Mirror Lake is low, but comparable to values reported from other oligotrophic lakes. There are few estimates of biomass for freshwater micro- and meiobenthic communities (Table 37), and among-lake comparisons are hampered by methodological differences among studies. In particular, estimates of meiofaunal biomass given by NALEPA & QUIGLEY (1983) and by FENCHEL (1975) for Lake Michigan and a tundra pond, respectively, are probably too low. These authors defined the meiofauna by taxonomic rather than methodological considerations. In both of these studies, all oligochaetes and chironomids, regardless of size, were assigned to the macrofauna, even though many of these taxa pass coarse sieves (e.g., JONASSON 1958; STRAYER 1985a). As a result, their "macrofauna" includes some members of the "meiofauna" as defined by me, and their data on meiofauna are probably underestimates by my criteria. Apparently, the biomass of the meiofauna is usually about 10% to 100% of macrofaunal biomass in lakes, a value somewhat higher than the 1% to 10% thought to be typical of marine sediments (GERLACH 1971; FENCHEL 1978). Little more can be said without further data.

Faunal variation with water depth

There are great changes in the structure of the zoobenthos between different water depths in Mirror Lake. Every species that I studied has a distribution that is related to water depth. In the most common pattern of distribution, a species is present throughout a region extending from the shoreline down to some depth contour, beyond which it is rare or absent. The location of the lower boundary varies depending on the species, and occurs in the littoral zone for some species (e.g., the chironomid *Heterotanytarsus* sp.; Fig. 55), and in the profundal zone for others (e.g., the flatworm *Rhynchoscolex simplex;* Fig. 11). Such a pattern probably occurs because the physical and chemical environments of the deepwater sediments are relatively harsh (compared to the littoral environment). I do not know what particular aspects of the deepwater environment are responsible for the distribution of each species, but some likely candidates include: dissolved oxygen, which is scarce or absent above the deepwater sediments (Fig. 2); H_2S, which is present at the deepest stations (Fig. 2); temperature, which decreases with increasing water depth (Fig. 2); the relatively homogeneous deepwater sediments, which may be unsuitable for some species; the absence of macrophytes beyond the 7.5-m station (Fig. 5); and the probable decrease in benthic algal densities with increasing water depth. I suspect that dissolved oxygen is of prime importance. Many groups of metazoans are obligate aerobes (e. g., von Brand 1946; Hochochka et al. 1973), and changes in the zoobenthic community are especially pronounced at the aerobic-anaerobic boundary in Mirror Lake (i.e., many species drop out between 7.5-m and 10.5-m; cf. Fig. 63). In Table 38, I have listed the zoobenthic species that I found under anoxic conditions in Mirror Lake. The list is similar to those compiled by Moore (1939) for Douglas Lake, Michigan, and by Cole (1955) for Crystal Lake, Minnesota.

Table 38. Benthic species found under anoxic conditions in Mirror Lake.

Nematoda
Ethmolaimus sp.
Monhystera sp.
Tylenchidae indet.

Gastrotricha
Chaetonotus spp.
Lepidodermella trilobum
Gastrotricha sp. 1

Rotatoria
Rotaria tridens

Copepoda
Diacyclops nanus
Mesocyclops edax

Ostracoda
Cypria turneri

Acari
Piona sp. (larvae only)

Diptera
Chironomus anthracinus
Chaoborus spp.
Procladius sp.
Zalutschia zalutschicola

Of course, it is possible that some species are restricted from the deepwater sediments because of biological interactions, rather than by physical or chemical conditions. The tubificid oligochaetes offer a possible example. These worms are known to tolerate extended anoxia, and are commonly found in soft organic sediments, but are absent entirely from the 10.5-m station in Mirror Lake (Figs. 33–34). A plausible explanation for their absence is that the dipteran *Chaoborus* spp., which feeds preferentially on oligochaetes (Swuste et al. 1973), is very abundant at 10.5-m in Mirror Lake (Figs. 60, 61) and may crop the tubificid population severely (cf. Howmiller 1977). Other analogous examples may exist.

A less common kind of depth distribution is shown by 15–20 species like the oligochaete *Nais communis* (Fig. 31), the ostracod *Cypria turneri* (Fig. 49), and *Chaoborus* spp. (Figs. 60, 61). These species are rare or absent in the littoral zone, but are abundant on the deepwater sediments. Again, there are several possible explanations for such distributions: these species may prefer the soft sediments or cold temperatures of the profundal zone. In fact, many of the species in this group are known to prefer soft, organic sediments (e. g., gastrotrichs, the cladoceran *Ilyocryptus sordidus, Chaoborus* spp.). More puzzling are the species that have a deepwater distribution in Mirror Lake, but are known to be ecologicaly tolerant and widely distributed elsewhere. Three common species fall into this group: the bdelloid rotifer *Rotaria tridens,* the naidid oligochaete *Nais communis,* and the ostracod *Cypria turneri.* It is difficult to believe that environmental conditions keep these species out of the littoral zone in Mirror Lake, since all three are known from littoral habitats elsewhere. I am forced to conclude that biological interactions probably restrict these species to the deepwater sediments in Mirror Lake, although I have no idea what these biological interactions might be. A few simple experiments could go a long way toward understanding these puzzling depth distributions.

As a consequence of the depth distributions just described, species richness falls sharply with increasing water depth in Mirror Lake (Fig. 63). Other workers have found a similar pattern in many other lakes (e.g., BRINKHURST 1974; JONASSON 1978). Biomass and abundance vary relatively little with water depth in Mirror Lake, although there is a minimum in zoobenthic abundance at 7.5-m (Figs. 63, 64).

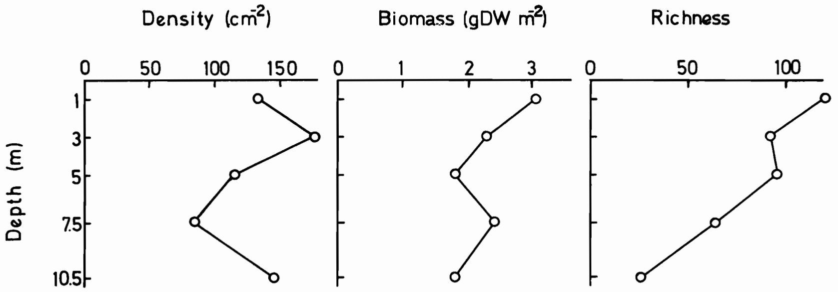


Fig. 63. Abundance, biomass, and species richness of benthic metazoans in Mirror Lake, from transect data.

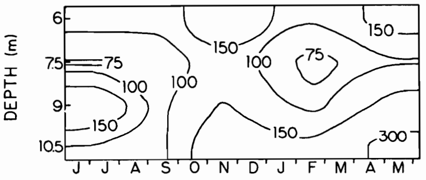


Fig. 64. Abundance (cm^{-2}) of benthic metazoans on the gyttja sediments of Mirror Lake.

This minimum is due to low nematode densities at this depth (Figs. 15, 16). A mid-depth minimum in zoobenthic abundance has been observed frequently in lakes, although its position (with respect to the thermocline) is not consistent among lakes (e. g., BRINKHURST 1974).

Vertical distribution

About half of the benthic animals in Mirror Lake live in the top 1 cm of sediment (Fig. 65). Relatively few species regularly penetrate more than 2 cm into the sediments; the flatworm *Rhynchoscolex simplex,* the nematodes, the bdelloid rotifer *Rotaria tridens,* the oligochaetes *Nais communis* and the tubificids, the ostracod *Cypria turneri,* and *Chaoborus* spp. are some examples. Many other workers have found peak densities of the zoobenthos to be at the sediment surface, although the proportion of animals that penetrates deeply and the maximum depth of penetration vary among lakes (e. g., BERG 1938; MOORE 1939; COLE 1953; NALEPA & ROBERTSON 1981a). In some lakes, a few taxa may penetrate 15–40 cm into the sediments (e.g., BERG 1938; MOORE 1939; FRANK 1982).

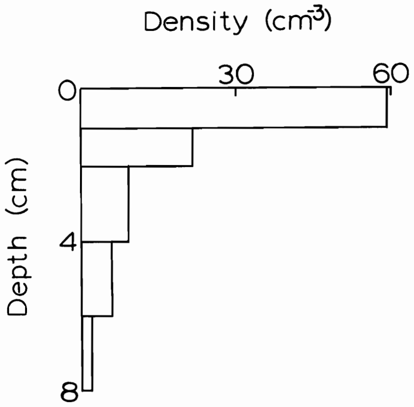


Fig. 65. Vertical distribution of benthic metazoans within the sediments of Mirror Lake, as a function of depth from the sediment surface. Data are lakewide means from the transect.

Seasonality

There are seasonal fluctuations in the population densities of many benthic animals in Mirror Lake. The chydorid cladocerans are rare or absent during winter, while another cladoceran, *Ilyocryptus sordidus,* is most abundant during autumn (Fig. 41). Most of the naidid oligochaetes also are most abundant during the autumn (Figs. 31–32). In addition, animals like copepods, ostracods, and chironomids all have seasonal life histories in Mirror Lake, even though they are present throughout the year. However, many members of the zoobenthos show relatively little seasonal fluctuation in density. Furthermore, populations of benthic animals that do show seasonality are usually much less variable than the highly seasonal zooplankton (cf. MAKAREWICZ & LIKENS 1975). MOELLER et al. (1985) suggested that "probably this relative stability of numbers (of the zoobenthos) reflects a continued supply of food, even in winter, via bacteria and fungi of the detrital food chain".

Energy flow in the zoobenthos

Based on my tentative estimates of zoobenthic metabolism, secondary production and respiration of the zoobenthos in Mirror Lake are about 14 g DW m^{-2} yr^{-1} and 8 g C m^{-2} yr^{-1}, respectively. Approximately half of this metabolic activity can be attributed to the meio- and microfauna (Table 35). HOLOPAINEN & PAASIVIRTA (1977) concluded that the meiofauna contributed about 80% of zoobenthic production in the oligotrophic lake Paajarvi in Finland, and NALEPA & QUIGLEY (1983) suggested that the meiofauna may be responsible for roughly a third of zoobenthic metabolism at near-shore sites in Lake Michigan. Thus, on the basis of some admittedly weak evidence, it appears that the micro- and meiofauna may be at least as important energetically as the macrofauna in lakes.

Major contributors to energy flow in Mirror Lake include the chironomids, oligochaetes (especially the Naididae), copepods, *Chaoborus,* and the nematodes. Together, these groups account for 80% of zoobenthic assimilation. It seems likely that these same groups dominate zoobenthic energy flow in other lakes, although supporting data are unavailable. Nematodes may play a larger role in energy flow in other lakes than they do in Mirror Lake, where they account for only 7% of zoobenthic assimilation, since nematode biomass is low in Mirror Lake (Table 6).

A detailed energy budget for the Mirror Lake zoobenthos has been presented elsewhere (STRAYER & LIKENS 1985). Briefly, it appears that detritus (including its attached bacteria) and benthic algae are about equally important in supporting zoobenthic production in Mirror Lake. As might be expected, the algae are relatively more important in the littoral sediments, while detritivory supports the bulk of zoobenthic production on the deepwater sediments. A budget of the fates of zoobenthic production shows that invertebrate predators take 70% of production, insect emergence 25%, and vertebrate predators 15%. Note that it is not necessary to assume any "natural mortality" (e.g., old age) to make that fates of production sum to 100%.

Size structure of the zoobenthos

I have discussed the size structure of the Mirror Lake zoobenthos elsewhere (STRAYER 1985b); here, I will make only a few points. Data presented by STRAYER (1985b) show no evidence of a distinct macrofauna and meiofauna in Mirror Lake. The community contains animals spanning the entire size range from 10^{-9} g DW to 10^{1} g DW (see also Fig. 66). In contrast, results emerging from recent marine studies show that the macrofauna and meiofauna are more or less distinct entities,

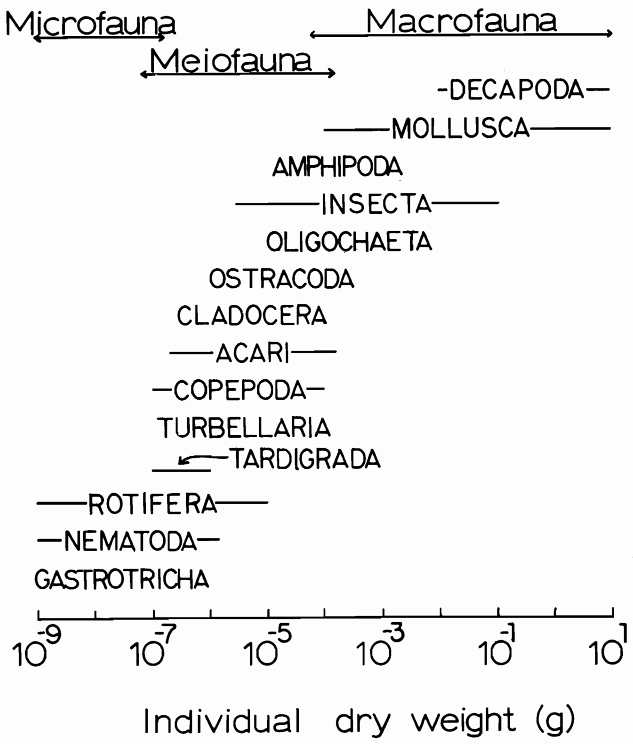


Fig. 66. Schematic diagram of the size structure and taxonomic composition of the lacustrine zoobenthos. The size ranges spanned by each taxon are taken from my study and various other sources, and are only approximate.

at least for shallow-water, temperate sites (SCHWINGHAMER 1981a, 1983; WARWICK 1984). At present, the significance and explanation of these results are not clear.

Also, I would like to make a plea for limnologists to chose their sieve mesh sizes more carefully. Historically, the mesh sizes used have been highly variable (e.g., DOWNING & RIGLER 1984: table 4.8), and have been chosen by individual investigators. The reason for this variability is that the "ideal" mesh size (i.e., one that retains the most animals and the least sediment) varies with the sediment type and the objectives of the study. While this approach has been useful for individual scientists, it has also left the field of limnology with a body of "quantitative" data that is very difficult to interpret. It is difficult to make rigorous comparisons among lakes, since many important parameters vary with mesh size (e.g., Fig. 67; see also HUMMON 1981; NALEPA & ROBERTSON 1981b). In spite of the extreme importance of mesh size, it is not rare to see papers published without any mention of the mesh size of the sieve used in the study. It is essential that the mesh size used be published, and it might be desirable for limnologists to settle on a standard

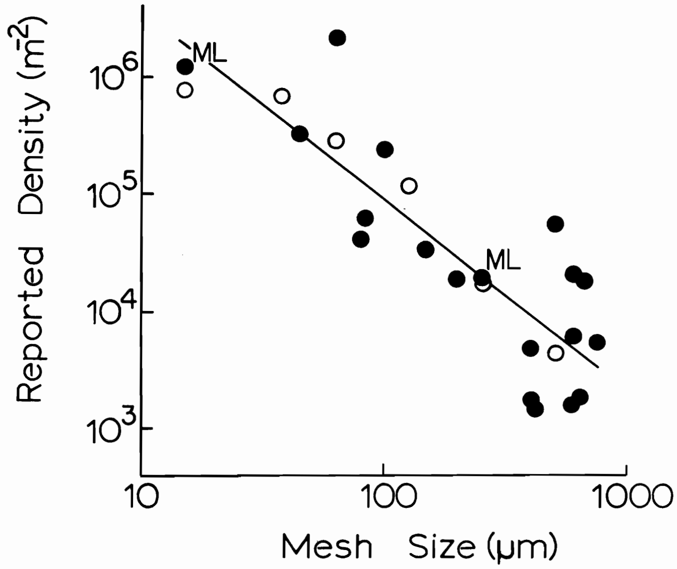


Fig. 67. The effect of mesh size on apparent density of the zoobenthos. Black dots are reported mean densities from various lakes, including Mirror Lake (ML). Open dots are HUMMON's (1981) data from the Mississippi River, and the line is a least-squares regression through the black dots. $r = -0.82$, $p < .01$.

series of mesh sizes to be used in routine studies. Adoption of a standard series of, say, five mesh sizes would facilitate comparisons among studies, while allowing for flexibility in individual studies.

Reproductive strategies in the zoobenthos

Many different kinds of life histories are represented in the Mirror Lake zoobenthos. Different kinds of life histories are thought to be favored in different environments (e.g., COLE 1954; STEARNS 1976). Because environmental conditions vary greatly with water depth in Mirror Lake, it seemed worthwhile to see how some patterns of reproduction in the zoobenthos vary with water depth in Mirror Lake. Based on my own observations and on various published sources, I classed each benthic species as either sexual and gonochoristic (having separate sexes), sexual and hermaphroditic, asexual and parthenogenetic, or asexual and reproducing by budding or fission. Species that are facultatively sexual but usually asexual (e.g., monogonont rotifers and naidid oligochaetes) were classed as asexual. The mode of reproduction of about 9% of the species in the Mirror Lake zoobenthos, mostly nematodes, is unknown to me.

The most remarkable result of this analysis is the lack of variation in reproductive mode with water depth (Fig. 68). Regardless of the water depth, the

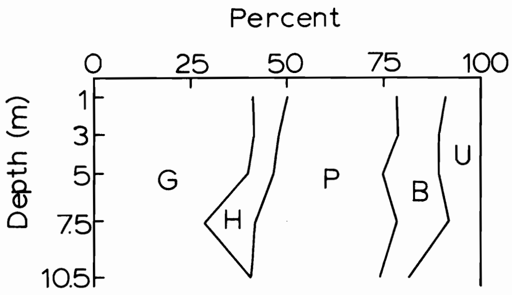


Fig. 68. Reproductive modes of the zoobenthos in Mirror Lake, as a function of water depth. Data are the percentages of species living at each depth that reproduce by a given mode G = gonochores, H = hermaphrodites, P = parthenogens, B = "budders", U = unknown mode of reproduction. From transect data. There are no significant differences among depths in the proportion of species reproducing by each mode ($X^2 = 9.8$, $p > 0.5$).

zoobenthic community consists of about 40% gonochores, 10% hermaphrodites, 35% parthenogens, and 15% species that reproduce by fission or budding. Roughly similar proportions occur in Lac de Neuchatel, Switzerland, and in the Bodensee in Germany (Table 39), although data from these two lakes are flawed by incomplete data about certain taxa (cf. Table 36). Thus, all four modes of reproduction are well represented in the zoobenthos, although gonochoristic sexual reproduction is especially common.

Table 39. Reproductive modes of the zoobenthic animals of lakes. Data are percentages of the species living in each lake that have each reproductive mode. Data from Neuchatel and the Bodensee are biased, because MONARD (1920) severely underestimated the number of insect species in Neuchatel, and because there are no data on the gastrotrich fauna of the Bodensee (cf. Table 36). About 10% of the species in each lake have reproductive modes that are unknown to me.

Reproductive mode	Mirror	Lake Neuchatel	Bodensee
gonochores	39	29	63
hermaphrodites	11	40	12
parthenogens	36	26	19
"budders"	14	6	6

A very different situation holds in the zooplankton. Most metazoans that live in the pelagic zone reproduce by parthenogenesis (rotifers and cladocerans), although some are gonochores (copepods). For example, in Mirror Lake, 79% of the metazoan species in the zooplankton are parthenogens and the remaining 21% are gonochores. Hermaphrodites and species that reproduce by budding or fission are almost unknown among the zooplankton (the only example that comes to mind is the hermaphroditic flatworm *Mesostoma* that is found occasionally as a member of the zooplankton – see HUTCHINSON 1967: 505–506).

What accounts for such a striking difference in the modes of reproduction between the zooplankton and the zoobenthos? Perhaps environmental conditions in the pelagic zone select strongly for parthenogenesis and against hermaphroditism and budding. However, it is not obvious to me why these last two modes of reproduction should be particularly maladaptive in the pelagic zone when they are successful in nearby benthic environments. There is another possibility. Suppose (as seems likely) that the zooplankton arose from the few groups of the zoobenthos that were able to cope with the pelagic environment. Even if reproductive modes have no adaptive significance in the pelagic zone, there then would be only a limited range of reproductive modes represented in the zooplankton. Perhaps it is only happenstance that two of the groups that were able to invade the pelagic zone are parthenogens and the third, gonochores.

Role of the meio- and microfauna in the lake ecosystem

From the meager evidence at hand, it appears that the meio- and microfauna is roughly as important as the macrofauna in terms of carbon or energy flow in lakes. It therefore seems likely that the meio- and microfauna are roughly as important as the macrofauna in nutrient regeneration and in grazing benthic algae and bacteria, since the rates of these processes must be roughly correlated with metabolic rate (PETERS 1983). Because we know so little about the quantitative significance of the macrofauna in regenerating nutrients and in grazing (or regulating) the benthic microbiota, it is difficult to speculate further on the importance of the smaller benthic animals in these processes.

The meio- and microfauna are likely to be somewhat less important than the macrofauna as a reservoir for nutrients, as food for fish, and as mixers of sediments. WALTER (1976) estimated that about 1/4 of the N and P held by the biota in Mirror Lake was contained in the benthic macrofauna. Because the meio- and microfauna have a lower biomass than the macrofauna, both in Mirror Lake and elsewhere (Table 37), they probably likewise hold smaller (but still substantial) standing stocks of nutrients than does the macrofauna.

Juvenile and adult fish feed primarily on large invertebrates in Mirror Lake (MASZA 1973; HELFMAN 1985), although it is possible that meio- and microfaunal organisms might not have been recognized in stomach contents. However, newts *(Notopthalmus viridescens)* feed heavily on meiofauna such as benthic cladocerans in Mirror Lake (BURTON 1977), and it is possible that very young fish may prey heavily on the meiofauna.

Bioturbation (sediment mixing) by the macrofauna has been shown to be important in altering sediment stratigraphy and nutrient exchange between the sediments and the overlying water (MCCALL & FISHER 1980; ROBBINS 1982). Although members of the meiofauna are known to cause bioturbation (CULLEN 1973), it is unlikely that they mix the sediments as vigorously as the tubificid oligochaetes. Many members of the meio- and microfauna presumably live in the sediment interstices, and none are known to transport sediments nearly as effectively as the tubificids.

In summary, meio- and microbenthic animals probably play qualitatively many of the same roles in lakes as does the macrofauna. The quantitative importance of the meio- and microfauna remains to be demonstrated, but it is probably similar to that of the macrofauna.

Prospects

Studies of the freshwater meio- and microfauna will be scarce until two conditions are satisfied: (i) better methods to extract small benthic animals from sediments are developed, and (ii) limnologists are convinced that these animals are important or interesting. It seems clear that neither sieving nor direct sorting (such as practiced in this study) is generally a practical way to extract the meio- and microfauna. In many lakes, any sieve that is fine enough to retain the small benthic animals also retains prohibitive amounts of sediment. Where sediments are sufficiently fine-grained, of course, simple sieving may be an acceptable way to extract micrometazoans quantitatively. Direct sorting is simply too tedious and time-consuming for routine or widespread use.

There are other extraction techniques, but they have not been used widely by limnologists. For example, the UHLIG (1964, 1968) ice-water technique has been used successfully by marine biologists to extract small motile animals from sediments. In situ trapping methods may be useful for some motile taxa (e. g., WHITESIDE & WILLIAMS 1975). If the sediments are primarily inorganic, the sample may be shaken with water, then the supernatant poured through fine screen to concentrate the animals (e.g., JENSEN 1983). However, density gradient centrifugation seems to me to be the most promising class of extraction methods. GOULDEN (1971), NICHOLS (1979), SCHWINGHAMER (1981b), and others have centrifuged benthic samples in various media and have achieved good extraction of the meiofauna from the sediment. Regardless of the method chosen, it will be necessary to test its extraction efficiency with the many kinds of animals and sediments encountered in freshwater habitats. I am confident that simple, inexpensive methods for the quantitative extraction of meio- and microfauna can be developed.

However, development of suitable techniques to study the benthic micrometazoans will not occur unless the limnological community is interested in knowing about the meio- and microfauna. Why should limnologists care about these animals? First, I have just argued that meio- and microbenthic animals are probably about as important in benthic processes as is the macrofauna. If this is true, ecologists who limit their studies to the macrobenthos will probably underestimate (sometimes severely) the importance of the benthic fauna in lake ecosystems.

More importantly, the meio- and microfauna contain most of the species of animals in lakes (Table 35). Most of the physiological, morphological, and behavioral adaptations, and most of the intra- and interspecies interactions in the zoobenthos occur in the meio- and microfauna. Ecologists who study only the macrofauna are simply missing the bulk of the diversity of freshwater animal life. The small benthic animals provide many subjects for ecological and evolutionary studies. Furthermore, without a knowledge of the meio- and microfauna, comprehensive analyses of the whole community (such as the admirable work of WIGGINS et al. 1980) will be incomplete or impossible. In short, as long as limnologists continue to ignore the benthic micrometazoans, we will be ignorant of a large, interesting, and potentially important part of the lacustrine biota.

Summary

There has never been a detailed and quantitative study of the small benthic animals of a lake. To fill this gap, I examined 95 core samples from Mirror Lake, a small oligotrophic lake in New Hampshire. Samples were sorted alive under a dissecting microscope, both before and after sieving them through a 105-µm mesh sieve, so that even the smallest metazoans were recovered quantitatively. I describe a modification of the "removal" method of population estimation that may be useful in estimating sorting efficiency for benthic samples. Animals were identified to species or genus.

At least 322 species, representing 12 phyla of metazoans, inhabit the sediments of Mirror Lake (Table 35). Species richness falls sharply with increasing water depth (Fig. 63). Total zoobenthic density is 1,200,000 m^{-2}, and shows relatively little variation with water depth or season (Figs. 63, 64). About half of the animals live in the top centimeter of sediment (Fig. 65). The biomass of benthic metazoans in Mirror Lake is 2.5 g DW m^{-2}, and zoobenthic production is estimated to be in the neighborhood of 14 g DW m^{-2} yr^{-1}. The micro- and meiofauna (i.e., animals that pass a 250-µm mesh screen) constitute 65% of the species, 98% of the individuals, 25% of the biomass, and about half of the assimilation of the zoobenthos in Mirror Lake (Table 35).

The most prominent groups in the Mirror Lake zoobenthos are the chironomids, oligochaetes, chaoborids, nematodes, and copepods. Detailed information is presented on the distribution of 81 abundant species or genera in the community, along with notes on the natural history of some species.

The flatworms are abundant (27,000 m^{-2} lakewide) on the oxygenated sediments of Mirror Lake. *Rhynchoscolex simplex* is the most abundant of the 23 species encountered (Fig. 9). Of special interest is the occurrence of an acoel flatworm, the first found in fresh water outside of Europe. I found nematodes in every sample that I took from the lake; 60% of the benthic metazoans in Mirror Lake are nematodes (Figs. 14–16). *Ethmolaimus* and *Monhystera* are especially abundant, although I found 20 genera in all. Gastrotrichs also are abundant (130,000 m^{-2}) and are widely distributed in Mirror Lake (Figs. 18, 20, 21). Apparently about 25 species are present, including an unidentified species that is a facultative hermaphrodite (Fig. 19). The rotifers are represented by at least 63 species, and have a mean lakewide density of 150,000 m^{-2} (Figs. 23–30). Most species are restricted to oxygenated sites, but one species, the bdelloid *Rotaria tridens*, is especially common under anaerobic conditions (Figs. 27, 28).

The Naididae dominate the oligochaete fauna, which contains 23 species. Oligochaetes are abundant (30,000 m^{-2}) (Figs. 31–38), and constitute about 15% of zoobenthic biomass in the lake. Microcrustaceans have a mean lakewide density of 60,000 m^{-2}. Cladocerans (Figs. 41–43), cyclopoids (Figs. 44–48), harpacticoids (Figs. 45, 47, 48), and ostracods all are well represented. Most microcrustaceans live in the littoral zone, but two species of cyclopoids are found under anoxic conditions in the profundal zone. Mites are not very abundant (3,300 m^{-2}). Of particular interest is the presence of four species of the Halacaridae (Table 27),

a largely marine group of mites. The Chironomidae dominate the biomass (50%) and probably the metabolism of the zoobenthos in Mirror Lake. At least 48 species of chironomids are present in the lake; the Chironomini and Tanytarsini are quantitatively dominant (Figs. 55–59). *Chaoborus* spp. are very abundant on the deepwater sediments (Figs. 60–61).

Other, less abundant, animals include poriferans, *Hydra* (Figs. 7, 8), nemerteans, tardigrades (Table 15), ectoprocts, amphipods (Fig. 54), decapods, non-dipteran insects, and mollusks (Fig. 62).

Zusammenfassung

Bisher hat es noch keine detaillierte quantitative Studie von benthischen Tieren im See gegeben. Um diese Lücke zu schließen, habe ich 95 Bohrproben aus dem Mirror Lake untersucht, einem kleinen oligotrophischen See im Staate New Hampshire. Die Proben sind lebend unter dem Stereomikroskop sortiert worden, und zwar nicht nur vor, sondern auch nach dem Durchsieben durch ein Sieb mit 105 µm Maschenweite, so daß auch die kleinsten Metazoen quantitativ mit berücksichtigt werden konnten. Ich beschreibe eine Modifikation der „removal"-Methode für die Populationsschätzung, die nützlich sein mag zur Feststellung der Sortiergenauigkeit von benthischen Proben. Die Tiere wurden identifiziert nach Gattung und Art.

Wenigstens 322 Arten, die 12 Phyla der Metazoen angehören, leben im Sediment des Mirror Lake (Table 35). Die Dichte der Arten fällt stark ab mit Zunahme der Wassertiefe (Fig. 63). Die Gesamtdichte der zoobenthischen Lebewesen ist 1 200 000 m^{-2} und zeigt eine nur geringe Abhängigkeit von Wassertiefe oder Jahreszeit (Fig. 63 und 64). Etwa die Hälfte der Tiere befindet sich im oberen Zentimeter des Sediments (Fig. 65). Die Biomasse der benthischen Metazoen im Mirror Lake ist 2,5 g Trockengewicht m^{-2}, und die zoobenthische Produktion wird angenommen mit ca. 14 g Trockengewicht $m^{-2}\,yr^{-1}$. Die Mikro- und Meiofauna (d. h. Lebewesen, die ein 250-µm-Sieb passieren können), machen 68% der einzelnen Arten, 98% der Individuen, 25% der Biomasse und ungefähr die Hälfte der Assimilation des Zoobenthos im Mirror Lake aus (Tab. 35).

Die prominenteste Zoobenthos-Gruppe im Mirror Lake sind die Chironomiden, Oligochaeten, Chaoboriden, Nematoden und Copepoden. Über die Verteilung von 81 Arten oder Gattungen innerhalb der Gesamtbevölkerung wird ausführlich berichtet, mit Bemerkungen über die Biologie einzelner Arten.

Turbellarien sind auf den oxidierten Sedimenten des Mirror Lake sehr häufig (27 000 m^{-2} im See-Durchschnitt). Am häufigsten unter den 23 vorgefundenen Arten ist *Rhynchoscolex simplex.* Ein acoeler Strudelwurm ist von besonderem Interesse, der erste, der im Süßwasser gefunden wurde außerhalb Europas. Nematoden sind in jeder Probe aus dem See gefunden worden. 60% der benthischen Metazoen im Mirror Lake sind Nematoden (Fig. 14–16). Besonders verbreitet sind *Ethmolaimus* und *Monhystera;* insgesamt fand ich 20 Genera. Gastrotricha sind ebenfalls häufig (130 000 m^{-2}) und weit verbreitet im Mirror Lake (Fig. 18, 20 und 21). Es ist anzunehmen, daß etwa 25 Arten vorhanden sind, einschließlich einer nicht identifizierbaren Art, die ein fakultativer Zwitter ist (Fig. 19). Von Rotiferen sind mindestens 64 Arten vertreten, die eine durchschnittliche Dichte von 150 000 m^{-2} besitzen (Fig. 23–30). Die meisten Arten befinden sich an O_2-reichen Stellen, eine Art jedoch, die Bdelloide *Rotaria tridens,* ist besonders häufig unter anaeroben Bedingungen (Fig. 27 und 28).

Naididae dominieren die Oligochaeten-Fauna, welche 23 Arten enthält. Oligochaeten sind häufig (30 000 m^{-2}) (Fig. 31–38) und konstituieren ungefähr 15% der zoobenthischen Biomasse im See. Microcrustacea haben eine seeweite Dichte von 60 000 m^{-2}. Cladoceren (Fig. 41–43), Cyclopiden (Fig. 44–48), Harpacticiden (Fig. 45, 47 und 48) und Ostracoden (Fig. 49–51) sind durchaus gut repräsentiert. Die meisten Microcrustaceen leben in der

litoralen Zone, allerdings zwei Arten von Cyclopiden wurden unter anoxischen Bedingungen in der profundalen Zone gefunden. Milben sind nicht stark vertreten (3300 m^{-2}). Das Vorhandensein von 4 Arten der Halacaridae (Table 27) ist besonders interessant, da diese Gruppe überwiegend marine Milben enthält. Die Chironomiden dominieren in der Biomasse (50%) und vielleicht auch den Metabolismus des Zoobenthos im Mirror Lake. Mindestens 48 Arten von Chironomiden wurden im See gefunden; quantitativ dominieren die Chironomini und Tanytarsini (Fig. 55–59). *Chaoborus* spp. kommen sehr häufig in den Profundal-Sedimenten vor (Fig. 60–61).

Andere, weniger häufige Arten schließen Porifera, *Hydra* (Fig. 7 und 8), Nemertea, Tardigrada (Table 15), Ectoprocta, Amphipoda (Fig.54), Decapoden, Insekten und Mollusken (Fig. 62) ein.

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