

Zoobenthos of Fifteen Lakes in the Experimental Lakes Area, Northwestern Ontario¹

ANDREW L. HAMILTON

Fisheries Research Board of Canada
Freshwater Institute, Winnipeg 19, Man.

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The composition of the profundal and sublittoral zoobenthos of 15 lakes in northwestern Ontario was closely related to morphometric features of the individual lakes. The amphipod *Pontoporeia affinis* Lind., and the sphaeriid *Pisidium conventus* Clessin, were the dominant species in the larger deeper lakes whereas species of Chironomidae and Chaoborinae were the dominant forms in all lakes with mean depths of less than 10 m. Dissolved oxygen concentration and temperature of the bottom water, two characteristics that are largely a function of lake morphometry, are probably the primary factors limiting the distribution of individual species.

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The objectives of this investigation were to define the main features of the benthic communities in lakes within the Experimental Lakes Area (ELA) and to correlate these features with environmental parameters. The study was restricted to the sublittoral and profundal zones of 15 lakes in ELA. These lakes represent a variety of morphometric types with maximum depths ranging from 2.5 to about 117 m and surface areas from about 1.3 to 1008 ha. A summary of the relevant physical and chemical characteristics of the lakes in the area is given by Armstrong and Schindler (1971), Brunskill et al. (1971), Brunskill and Schindler (1971), and Schindler (1971).

Previous information on the benthos of Precambrian Shield lakes in Canada is, for various reasons, not directly comparable with what is being attempted here. Most previous studies have been of much larger lakes, usually on the southern boundary of the Shield. Examples include Rawson (1953, 1960), Oliver (1960, 1964), and Slack (1967). Miller (1941) gives a detailed analysis of the chironomids of a small Precambrian Shield lake but other components of the fauna were not treated.

¹The eleventh in a series of 14 papers on the work of the Fisheries Research Board of Canada, describing background environmental data on the Experimental Lakes Area, northwestern Ontario. For location of numbered lakes see insert map at the back of this issue of the *Journal of the Fisheries Research Board of Canada*. A key to lake locations is given by Cleugh and Hauser (1971).

Methods

A total of 121 samples was collected with a 15 × 15 × 23-cm tall Ekman dredge equipped with a No. 30 brass wire mesh (apertures approximately 60 μ square) across the top. All samples were taken at least 10 m from shore and in most lakes a total of 10 samples from two or three transects were analyzed. Sampling was conducted during the period from May 1-14, 1969, i.e., within 3 weeks of the disappearance of ice cover. Only about three of the common species were beginning to emerge by this time; consequently the problem of interpreting species abundance was only moderately complicated by the emergence of insects. In this series of samples the screen-equipped dredge was always lowered slowly so as to minimize pressure buildup and the associated blowout of surface sediments. The accessory screen used with the Ekman dredge was a necessity because most of the lake sediments encountered are so soft that it is impossible for the dredge operator to detect when the dredge reaches the sediment surface. Test samples with an unmodified Ekman dredge often yielded no organisms because the sampler penetrated beneath the surface layer. A multiple core sampler has since been developed for use in these very soft sediments (Hamilton et al. 1970).

All the samples analyzed were sieved through nylon mesh nets (apertures 400 μ sq) except those from lakes 81, 303, and 304 where the sediments were extremely difficult to sieve and a larger mesh (apertures 600 μ sq) was required to reduce the sieve residue to about 200 cc. The residues were preserved in 10% formalin. Later the contents were emptied into a large half black and half white pan and forceps were used to separate the organisms from the residue. Samples containing large quantities of residue (more than about 100 cc) were first stained with rhodamine B and then examined with longwave ultraviolet light (Hamilton 1969). Organisms were preserved in 70-75% ethanol. Identification,

counting, and enumeration were done with the aid of a dissecting microscope. When necessary, specimens were mounted on slides as outlined by Sæther (1969) and identified using a compound microscope. All major components of the fauna except the Oligochaeta were identified at least to genus and usually to species. The major groups are classified according to Bousfield (1958), Herrington (1962), Hamilton et al. (MS 1969), and Sæther (1970).

Results and Discussion

The benthic faunas of lakes in ELA proved to be very diverse. Not surprisingly the major physical and chemical features that have given rise to this diversity appear to be depth, temperature, and the level of dissolved oxygen.

For the purposes of discussion two relatively stable physical parameters, mean depth and surface area, were used to divide the lakes into six general categories. This somewhat arbitrary classification is outlined graphically in Fig. 1. The diagnostic physical and biological features of the lakes in each of the categories may be summarized as follows:

(A) Rather small (9.93 ha) shallow ($z_m = 2.5$ m) lakes with a low relative depth² ($z_r = 0.70$). Stratification³ type III. Benthos primarily Diptera. Dominants⁴ all Chironomidae. One lake investigated. (B) Very small (1.3-1.67 ha) relatively deep ($z_m = 7.0-13.6$ m) lakes with high relative depths ($z_r = 5.44-9.33$). Stratification type I, including one meromictic lake. Benthos primarily Diptera. Dominants all Chaoborinae and Chironomidae. Three lakes investigated. (C) Small (3.62-7.17 ha) shallow ($z_m = 6.7-10.0$ m) lakes with typical relative depths ($z_r = 2.78-3.96$). Stratification type I, II, or III. Benthos primarily Diptera. Dominants all Chaoborinae and Chironomidae. Four lakes investigated. (D) Lakes of intermediate size (12.2-44.1 ha) and depth ($z_m = 12.8-13.8$ m) with typical relative depths ($z_r = 1.75-3.25$). Stratification type I or II. Benthos primarily Diptera. Dominants all Chaoborinae and Chironomidae. Three lakes investigated. (E) Rather large (52.0-181 ha) deep ($z_m = 30-32.7$ m) lakes with typical relative depths ($z_r = 1.98-4.02$). Stratification

²Following Hutchinson (1957), relative depth is defined as the maximum depth as a percentage of the mean diameter, which is equal to $50 z_m \sqrt{\pi}(\sqrt{A})^{-1}$.

³Following Hutchinson (1957). Bottom temperatures greater than 5 C are considered to represent significant warming.

⁴Dominants are defined as species constituting more than 10% by number of the estimated total May standing crop.

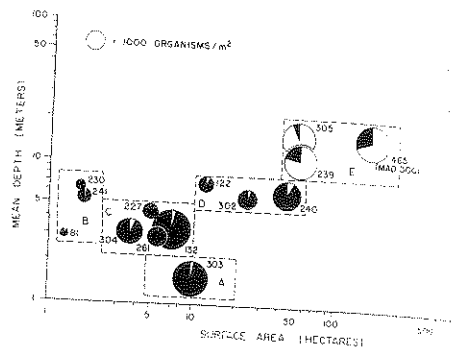


FIG. 1. Importance of mean depth and surface area to the distribution of invertebrates in ELA lakes. Rectangles indicate "approximate" boundaries of categories treated in text. The areas of the circles are proportional to the estimated standing crop of benthic macroinvertebrates and the darkened portions correspond to the percentage Diptera. Locations of lakes are indicated on ELA insert map.

type I or II. Benthos primarily Amphipoda and Sphaeriidae. Dominants all Amphipoda and Sphaeriidae. Three lakes investigated. (F) Large (4-1000 ha) very deep ($z_m = 117$ m) lakes with a typical relative depth ($z_r = 3.27$). Stratification type I. Benthos primarily Amphipoda and Sphaeriidae. Dominants all Amphipoda and Sphaeriidae. One lake investigated.

A more detailed list of the physical and chemical features of these ELA lakes is presented in Table 1. Within categories, lakes with lower relative depths generally have higher bottom temperatures. The lakes in category B are exceptions probably because the relative depths of all of them are high. Partly as a consequence of this the thermal and chemical stratification is strong and little hypolimnetic warming occurs in any of them. Lake categories E and F include only those lakes that have strong thermal stratification, yet because of the large volume of the hypolimnion they do not suffer severe oxygen depletion.

Some of the influence of these physical and chemical features on the bottom fauna is summarized in Table 2. All of the smaller lakes, whether thermally stratified or not, had a benthic macroinvertebrate fauna consisting overwhelmingly of Diptera. Numerically they made up from 85.7 to 99.2% of the fauna in categories A-D. The larger, thermally stratified, and well-oxygenated lakes in categories E and F are in sharp contrast to this. In them, Diptera made up only 11.2-30.1% of the fauna compared with percentages of 31.4-68.5 and 15.7-27.1 for the Amphipoda and Sphaeriidae respectively. In addition the dominant

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TABLE 1. Some physical and chemical features of the 15 ELA lakes selected for zoobenthic studies. Arrangement of lakes within categories is in order of increasing relative depth. Temperature and oxygen readings are from July and August and, unless indicated otherwise, are from 0.5 to 1.5 m off the bottom. Data incorporated in this table are primarily from Brunskill and Schindler (1971) and Schindler (1971).

Lake category	Lake	Surface area (ha)	Maximum depth (z _m , m)	Mean depth (z̄, m)	Relative depth (z _r , %)	Summer bottom temp (C)	Summer bottom oxygen (mg/liter)	Stratification type
A	303	9.93	2.5	1.5	0.70	14.3	8.2	
B	81	1.3	~7	~3	5.44	4.3	0.1	III
	241	1.75	12.5	5.5	8.37	4.9	0.0	I
	230	1.67	13.6	6.2	9.33	4.0	0.1	Meromictic
C	132	7.17	8.4	3.3	2.78	10.5	5.3	I
	304	3.62	6.7	3.2	3.12	7.4	0.0	III
	261	5.57	9.6	2.9	3.60	5.7	0.1	II
	227	5.00	10.0	4.4	3.96	4.4	0.1	II
D	240	44.1	13.1	6.1	1.75	7.3	0.6	I
	302	23.7	13.8	5.4	2.51	5.3	0.1	II
	122	12.2	12.8	7.2	3.25	4.0	2.9 ^a	I
E	465 (Mad Dog)	~181	~30	~15	1.98	5.1	5.5	II
	239	56.1	30.4	10.5	3.60	4.8	4.1	I
	305	52.0	32.7	15.1	4.02	4.8	7.8	I
F	161 (Hillock)	~1008	~117	~40	3.27	4.1	8.8	I

^aSample from 2.8 m off the bottom.

of mean depth and surface area of invertebrates in ELA lakes. Reciprocal boundaries of categories as of the circles are proportional to the crop of benthic macroinvertebrates. The shaded portions correspond to the locations of lakes are indicated.

is primarily Amphipoda and is all Amphipoda and Sphaeriidae. (F) Large (~1008 m) lakes with a typical (3.27). Stratification type I, Amphipoda and Sphaeriidae, Amphipoda and Sphaeriidae. One

of the physical and chemical lakes is presented in Table 1. Lakes with lower relative depths and bottom temperatures. The exceptions probably because all of them are high. Partly is the thermal and chemical and little hypolimnetic of them. Lake categories those lakes that have strong yet because of the large opinion they do not suffer

of these physical and chemical bottom fauna is summarized in smaller lakes, whether thermal and a benthic macroinvertebrates, overwhelmingly of Diptera, up from 85.7 to 99.2%, as A-D. The larger, thermal, well-oxygenated lakes in sharp contrast to this, up only 11.2-30.1% of the percentages of 31.4% or the Amphipoda and in addition the dominant

organisms (those constituting more than 10% of the total) were always species of Diptera in the smaller lakes and always *Pontoporeia affinis* (an amphipod) and *Pisidium conventus* (a sphaeriid) in the larger deeper lakes. In categories C, D, and E, an increase in the relative depth invariably coincided with a reduction in the estimated standing crop. As outlined in Table 3 many of the nonchironomid species found in ELA lakes are, presumably because of their environmental requirements, present in only a small percentage of the lakes. Not surprisingly *P. affinis*, *Mysis relicta*, and *P. conventus* were essentially restricted to large lakes with cold well-oxygenated hypolimnetic waters. In contrast, two of the chaoborines, *Chaoborus brunskilli* and *C. americanus*, were restricted to the small, relatively deep (z_r = 5.44-9.33), and colored lakes that have cold deoxygenated water below the thermocline. Another species of *Chaoborus*, *C. albatus*, was found only in lake 303, a shallow unstratified lake, whereas *Chaoborus flavicans* and *C. punctipennis* were found primarily in the more intermediate lakes (categories B and D). The apparent habitat selection on the part of species of *Chaoborus* was somewhat unexpected. Cook (1956) and Stahl (1966) considered that the species in this genus were quite capable of living in a wide variety of lentic habitats.

Chironomidae were present in lakes of all categories (Table 4) and were particularly abundant in shallow well-oxygenated basins such as those found in lakes 132 and 303. Some taxa, including *Polypedilum* cf. *nubeculosum*, *Psectrocladius* spp., and *Pagastiella* sp., were not present in samples from any of the deeper lakes. *Pagastiella* is extremely abundant in Marion Lake, a shallow lake in British Columbia (Hamilton MS 1965), but has not previously been recorded from elsewhere in North America.⁵ The deepwater species *Heterotrissocladius subpilosus* was found only in lake 161 (Hillock), the most oligotrophic of the 15 lakes investigated (Brunskill and Schindler 1971; Schindler and Holmgren 1971). Brundin (1958) considers that this species is the best indicator of ultraoligotrophic conditions in northern European lakes.

A mathematical index, the percentage similarity of community (PS_c), was used to obtain a numerical measure of the similarities between the benthic communities in these lakes. This index is calculated as follows:

$$PS_c = 100 - 0.5 \sum |a-b| = \sum \min(a,b)$$

⁵*Paralauterborniella ostansus* Webb, recently described from Costello Lake, Ont., by Webb (1969), appears to be a typical *Pagastiella*.

TABLE 2. Selected aspects of the bottom fauna of some ELA lakes. Arrangement of lakes within categories is again in order of increasing relative depth.

Lake category	Lake	Relative depth (z _r , %)	Total no. per m ²	% Diptera	% Amphipoda	% Sphaeriidae	Dominant (D) and indicator (I) organisms ^a for lake category
A	303	0.70	2946	97.8	0	1.5	D: <i>Polypedilum</i> cf. <i>nubeculosum</i> D: <i>Procladius</i> spp. I: <i>Chaoborus albatus</i>
B	81	5.44	104	85.7	0	0	DI: <i>Chaoborus brunskilli</i>
	241	8.37	461	93.5	3.2	0	D: <i>Procladius</i> spp. D: <i>Phaenopsectra coracina</i>
	230	9.33	236	93.8	0	0	D: <i>Polypedilum</i> cf. <i>nubeculosum</i> I: <i>Chaoborus americanus</i>
C	132	2.78	3556	96.9	0.7	1.1	D: <i>Chaoborus flavicans</i>
	304	3.12	1734	93.3	0	5.8	D: <i>Microtendipes</i> sp.
	261	3.60	911	99.2	0	0	D: <i>Chaoborus punctipennis</i>
	227	3.96	672	96.1	0	2.6	D: <i>Chironomus</i> cf. <i>anthracinus</i>
D	240	1.75	1642	88.9	6.8	1.4	D: <i>Chaoborus flavicans</i> D: <i>Chaoborus punctipennis</i>
	302	2.51	768	93.6	0	0	D: <i>Phaenopsectra coracina</i>
	122	3.25	518	89.7	0	5.1	
E	465 (Mad Dog)	1.98	2921	30.1	31.4	21.7	DI: <i>Pontoporeia affinis</i>
	239	3.60	2654	19.1	45.3	24.6	DI: <i>Pisidium conventus</i>
	305	4.02	2454	11.2	68.5	15.7	I: <i>Mysis relicta</i>
F	161 (Hillock)	3.27	1699	15.2	54.4	27.1	DI: <i>Pontoporeia affinis</i> DI: <i>Pisidium conventus</i> I: <i>Heterotrissocladius subpilosis</i> I: <i>Mysis relicta</i>

^aDominants are arranged within categories in decreasing order of abundance and are considered as any taxa making up more than 10% by number of the estimated total May standing crop. Indicator organisms are taxa that consistently occur in lakes falling in one or more categories and for some reason or other appear to be absent from other categories. Indicator organisms may or may not be dominants.

where a and b are, for each taxon, the percentage of the total animals in samples from lakes A and B respectively. The taxonomic divisions used for calculating this index are those in Tables 3 and 4. High PS_c values are generally indicative of a high similarity between the samples being compared. As outlined in Table 5, PS_c values within categories ranged from 23 to 72 with a mean of 51 ($n = 15$). The comparable values for the between-category comparisons were 0-70 with a mean value of 18 ($n = 90$). Most between-category comparisons were consistently low, indicating that the zoobenthos in the lakes of different categories were generally

quite distinctive. Comparisons between adjacent categories did, however, tend to result in relatively high PS_c values. This was particularly true with comparisons between categories C and D and between categories E and F. These very high values (means of 41 and 66 respectively) are a reflection of the many taxa shared by these groups of lakes.

In general the results reported here are consistent with those reported elsewhere in the literature. The benthic fauna in ELA lakes, even at the species level, bears a resemblance to the fauna found in many Swedish shield lakes (Brundin 1949). The general shift, with increasing depth, from a

TABLE 3. Estimated early May densities (numbers/m²) of benthic macroinvertebrates (excluding Chironomidae) in some ELA lakes. Arrangement of lakes within categories is in order of increasing relative depth. Organisms arranged approximately in order of their abilities to live in deep water.

Lake category:	A	B				C			D			E		F	
Lake:	303	81	241	230	132	304	261	227	240	302	122	465	239	305	161
No. samples:	7	3	3	6	10	5	6	10	10	10	10	10	10	10	11
<i>Pedilum</i> cf. <i>beculosum</i>															
<i>Pisidium</i> spp.															
<i>Chaoborus albatrus</i> Johnson	25	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pisidium casertanum</i> (Poli)	13	-	-	-	27	27	-	-	-	-	-	-	-	-	-
<i>Limnias lacustris</i> Sars			15	-	27	-	-	-	-	-	-	9	-	-	-
<i>Chaoborus brunskilli</i> Saeth.		74	74	111	-	-	-	-	-	-	-	-	-	-	-
<i>Chaoborus americanus</i> (Joh.)		15	-	30	-	-	-	-	-	-	-	-	-	-	-
<i>Chaoborus flavicans</i> (Meig.)		-	-	44	2224	-	104	186	315	297	58	-	-	-	-
<i>Chaoborus punctipennis</i> (Say)		-	-	22	-	551	326	213	373	186	44	466	4	71	-
Juvenile <i>Pisidium</i>	32	-	-	-	13	53	-	13	22	-	9	93	617	315	32
<i>Oligochaeta</i>	6	-	-	-	13	18	7	-	49	40	22	431	151	93	44
<i>Pontoporeia affinis</i> Lind.									111	-	-	919	1203	1685	925
<i>Mysis relicta</i> Loven															
<i>Pisidium conventus</i> Clessin													13	18	9
													533	31	71
Others (excluding Chironomidae)	19	15	30	15	49	62	-	9	4	9	31	44	138	9	12
Total (excluding Chironomidae)	95	104	119	222	2353	711	437	421	874	532	164	2508	2162	2253	1445

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dominantly dipteran fauna to one consisting largely of the amphipod *P. affinis* coincides with findings reported from other lakes on the Canadian Shield (Oliver 1960; Slack 1967). The relations that, in ELA lakes, apparently exist between the benthic faunas and the physical and chemical conditions of the lakes they inhabit will probably have some application to other small Canadian Shield lakes.

Acknowledgments

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TABLE 4. Estimated early May densities (numbers/m³) of Chironomidae in some ELA lakes. Arrangement of lakes within categories is in order of increasing relative depth. Organisms arranged approximately in order of their abilities to live in deep water.

Lake category:	A		B			C				D			E			F
Lake:	303	81	241	230	132	304	261	227	240	302	122	465	239	305	161	
No. samples:	7	3	3	6	10	5	6	10	10	10	10	10	10	10	11	
<i>Polypedilum</i> cf.																
<i>nubeculosum</i> (Meigen)	2502	-	89	0	9	9	-	44	-	-	-	-	-	-	-	
<i>Psectrocladius</i> sp.	6	-	-	-	-	27	37	-	-	-	-	-	-	-	-	
<i>Pagastiella</i> sp.	-	-	-	-	-	9	22	-	-	-	-	-	-	-	-	
<i>Microtendipes</i> sp.	-	-	-	-	728	240	126	-	-	-	-	-	-	-	-	
<i>Chironomus</i> spp. ^a	-	-	30	7	102	267	252	155	27	89	-	-	-	31	-	
<i>Procladius</i> spp.	318	-	104	7	191	124	37	31	147	58	93	-	-	-	4	
<i>Heterotrissocladius</i> sp. A	-	-	-	-	-	-	-	-	4	-	18	-	-	22	-	
<i>Chironomus</i> cf. <i>atritibia</i>																
Malloch	-	-	-	-	84	-	-	-	62	80	75	138	164	84	69	
<i>Phaenopsectra coracina</i>	-	-	89	-	18	-	-	13	422	-	142	93	98	18	89	
(Zett.) ^b																
<i>Tanytarsini</i> spp.	-	-	-	-	27	196	-	4	102	9	13	169	155	89	48	
<i>Protanypus</i> sp. ^b	-	-	15	-	-	-	-	-	-	-	-	13	22	4	4	
<i>Heterotrissocladius</i>																
<i>subpilosus</i> (Kieff.) ^b	-	-	-	-	-	-	-	-	-	-	-	-	-	-	44	
Other Chironomidae	25	-	15	-	44	151	-	4	4	-	13	-	-	4	-	
Total Chironomidae	2851	-	342	14	1203	1023	474	251	768	236	354	413	492	203	254	

^aAt least two species, including *C. anthracinus* Zett. and *C. attenuatus* Walk., are included in this category.

^bThese species were already emerging at the time of sampling and consequently the density estimates are probably low.

TABLE 5. Percentage similarity of community (PS_c) for the zoobenthic populations of 15 lakes in ELA. The figures above the diagonal line are comparisons between individual lakes, those below the line are averages of values between and within lake categories.

Category	Lake	Category														
		A		B			C				D			E		
		303	81	241	230	132	304	261	227	240	302	122	465	239	305	161
A	303	-	1	32	4	8	11	5	13	11	9	14	2	2	2	2
B	81		-	23	66	1	-	-	1	-	1	6	2	5	-	1
	241	12	39	-	29	13	21	11	21	30	15	46	5	10	2	6
	230				-	26	19	33	35	39	35	29	11	5	4	1
C	132				-	27	33	39	31	52	24	6	7	5	5	
	304	9		15			68	57	40	46	27	27	15	11	6	
	261					49		70	43	52	28	17	2	4	1	
	227								52	70	30	22	6	7	5	
D	240									59	66	40	25	22	23	
	302	11		22		41			56		44	28	14	12	9	
	122											26	25	16	17	
E	465													58	53	65
	239	2		5		11				23		61		72	63	
	305														70	
F	161	2	3		4				16			66				

of 15 ELA lakes. Arrangement of lakes approximately in order of their ability...

D	E	F
302	122	465
10	10	10
89	93	31
58	18	22
80	75	138
9	13	169
236	354	413

are included in this category. The density estimates are probably...

of 15 lakes in ELA. The figures are averages of values between...

	E	F
122	465	239
14	2	2
6	2	5
46	5	10
29	11	5
24	6	7
27	27	15
28	17	2
30	22	6
66	40	25
44	28	14
	26	25
		58
	61	53
		72
		65
		63
		70
	66	

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