The Chironomidae (Diptera) of Shallow, Humic Lakes and Bog Pools, and Their Value as Palaeoenvironmental Indicators

by

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ABSTRACT

The ecology and distribution of chironomids, and their value as palaeoecological indicators for shallow, humic waters is assessed. A survey of the present benthos of humic lakes and peat pools is provided, as are more detailed studies of chironomid ecology in four of these habitats. A comparison of chironomid biocenoses with the thanatocenoses of surficial sediments is made.

The results indicate a sharp differentiation between the chironomid fauna of peat pools and most lakes. Peat pools are distinguished by the abundance of Psectrocladius, Monopsectrocladius, Chironomus, Ablabesmyia, and/or Zalutschia. In most lakes, Procladius and/or Tanytarsus dominate. The fauna of strongly acid lakes is distinguished from less acid lakes not by their chironomid fauna, but by the presence of Chaoborus, and absence of Ephemeroptera, Hirudinea, and Amphipoda. The natural succession of these lakes, as a result of gradual encroachment by Sphagnum bogs, is from a weakly-acid lake, through a strongly-acidic phase. Eventually, conditions approach those of a peat-pool environment. The value of the Chironomidae as palaeoecological indicators is limited by the poor preservation of Procladius, extensive mixing of sediments, and stability of the chironomid fauna over a broad environmental gradient.

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I. Introduction

In 1980 the author (Walker 1980) conducted a palaeolimnological investigation of Wood's Pond, a shallow, polyhumic lake in southeastern New Brunswick, Canada. Employing chironomids as palaeolimnological indicators, it was possible to discern, within the sediments, distinct faunal zones. Corresponding segments had been defined within a pollen diagram, and a tenative interpretation linked the lake's ontogeny to regional forest changes. Unfortunately basic ecological data for chironomids of shallow humic waters were lacking and little was known concerning the representation of chironomid communities as subfossil assemblages in lake sediments.

To facilitate interpretation of core data in further analyses, the present investigation was initiated. Three objectives were defined:

1) To assess the proposed benthic classifications of Brundin (1949, 1956), Saether (1975, 1979) and other authors, thereby establishing whether the cause-effect relationships alluded to in the author's earlier research (Walker 1980) were correct.

2) To document aspects of chironomid ecology in a series of shallow, acid lakes believed to represent stages in dystrophic lake succession.

3) To examine the representation of extant chironomid communties as subfossil assemblages in the sediments of shallow, humic waters.

Numerous investigators have sought to classify lakes on the basis of their benthic fauna. Thienemann (1918) had conceived his Baltic and sub-alpine types on distinctions in their chironomid fauna. These Thienemann (1921) later equated with Naumann's (1919) eutrophic and oligotrophic classes. Tanytarsus and Chironomus were respectively, associated with sub-alpine (oligotrophic) and Baltic (eutrophic) waters. Chironomus was also noted to dominate in humic (dystrophic) waters.

Numerous authors (Alm 1922; Brundin 1949; Miyadi 1933; Pesta 1929) proposed slight modifications to this scheme, or proposed entirely new classifications. Lundbeck (1926) introduced the first two-dimensional benthic classification. Each association was considered indicative of a region defined by axes of productivity and degree of dystrophy. Decksbach (1929) recognized Sergentia (now part of Phaenopsectra) and Stictochironomus as mesotrophic indicators. It was Brundin (1949, 1951, 1956) who first rejected the generalization that members of a chironomid genus could be considered ecological equivalents. Saether (1975), however, has since argued that where one expected species of chironomid is not present in a lake, it will usually be replaced by a closely related taxon. The Chironomus of European dystrophic waters Brundin (1949, 1956) discovered was not C. plumosus or C. anthracinus but a new species which he described as C. tenuistylus. C. tenuistylus (Saether 1979) is a palaearctic species.

In North America Deevey (1941) identified lakes in Connecticut which appeared to fit the Chironomus and Tanytarsus types of Europe. He, however, also included a Trissocladius (probaby now Zalutschia) type of uncertain trophic status.

Many investigators, including Brundin (1949, 1951) and Stahl

(1959) emphasized the importance of hypolimnetic oxygen regimes in determining chironomid associations. In his earliest classification, Brundin (1949) recognized a division between stratified polyhumic lakes, and mesohumic or polymictic-polyhumic lakes. Previously, benthic chironomid classifications had been limited to stratified waters. Brundin considered Chironomus tenuistylus, Trissocladius naumanni (now Zalutschia zalutschicola), and Sergentia longiventris indicative of stratified polyhumic waters. All other dystrophic waters had a Stictochironomus rosenscholdi - Tanytarsini association, from which the Tanytarsini disappeared at high humic concentrations.

Few contributions to benthic classifications have since been made. Saether (1979) reviewed the ecological distributions of various Chironomidae and defined a series of associations for harmonic waters. Saether demonstrated an excellent correlation between his associations and both chlorophyll and total phosphorous. He concluded that such a scheme could not yet be extended to mesohumic or polyhumic lakes. He, however, considered Zalutschia one of the best indicators of humic conditions. Studies of acidified lakes in Scandanavia (Mossberg and Nyberg 1979; Whiteside and Lindegaard 1982; Wiederholm and Eriksson 1977) have found the taxa Chironomus, Psectrocladius, and Zalutschia zalutschicola to be most abundant.

Recent studies of the benthos of humic waters (Clair pers. comm.; Kreamer 1980) have revealed associations which do not appear to conform to the classifications previously proposed. These studies, and those of Saether (1979) and Raddum and Saether (1981) emphasize our poor understanding of humic lake Chironomidae.

Although early limnologists speculated as to the ontogeny of lake ecosystems, the documentation of trophic histories was the realm of palaeoecologists. Andersen (1938) speculated that subfossil Chironomidae could potentially provide clues to lake conditions as valuable as pollen had to forest composition. This goal has not yet been realized. Chironomid analysis has lagged behind the use of diatoms.

Chironomid remains have long been known from the sediments of lakes (Andersen 1938; Deevey 1937; Ekman 1915; Gams 1927; Lundbeck 1926; Williams et al. 1981). The first serious attempt to employ chironomids as palaeoecological indicators was made by Stahl (1959). Later researchers (Alhonen et al. 1969; Bryce 1962; Carter 1977; Czeczuga et al. 1979; Goulden 1964; Wiederholm 1979; Wiederholm and Eriksson 1979) conducted similar studies documenting the evolution of lakes from oligotrophy toward eutrophy. Although this aging process is now generally perceived, it is contrary to Naumann's (1919) original speculation that lakes should become less productive as a result of leaching processes.

In relation to salinity, subfossil chironomids (Paterson and Walker 1974) have been studied in one Australian lake. Clair and Paterson (1976) noted the effects of a salt-water intrusion upon chironomids. The recent detailed chironomid analyses of Hofmann (1971) and Warwick (1980) provided a new standard against which future work may be judged. Warwick's (1980) palaeolimnological study of the Bay of Quinte appears to have influenced Saether's (1979) proposed associations of extant chironomids. A single study (Henrikson et al. 1982) has examined chironomid succession in response to recent acidification of an oligotrophic lake.

Prior to Iovino (1975) the problem of representation of extant communities as subfossils was ignored. Although early instars were greatly under-represented, Iovino concluded that chironomid remains generally were accurate representations of the extant communities. Redistribution of head capsules in shallow-water systems appeared as a potential flaw. This is certainly true where seasonal flooding of impoundments (Hicks 1977; Ward 1980) results in extensive sediment disturbance. For most natural situations, it might however be argued that redeposition of subfossil Chironomidae in adjacent regions serves to integrate the thanatocenoses. Thus, particularly for shallow lakes, redistribution might prove advantageous.

As previously stated, the present investigation poses two principal questions. Are the proposed benthic classifications valid for shallow, humic lakes? How are the extant communities represented as subfossils in the sediments? The results of this investigation assess the value of chironomids as palaeoecological indicators for shallow, humic waters.

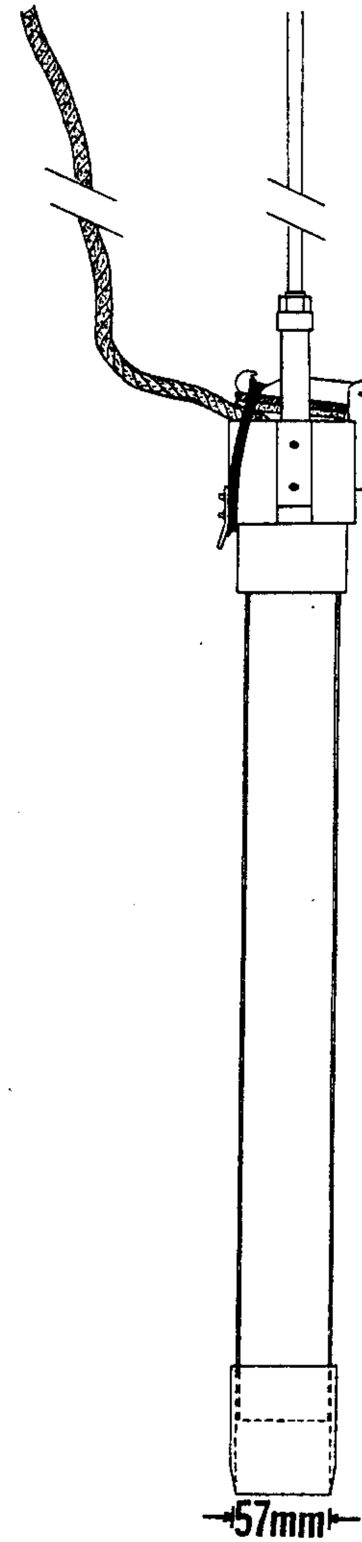
II. Methods

2.1 Assessment of Benthic Classifications

To assess the value of the proposed classifications, a survey of the benthos of 29 lakes and ponds in eastern New Brunswick and adjacent Nova Scotia was conducted during the ice free period of 1980, 1981, and 1982. Samples were collected from a canoe using a corer developed for sampling the soft sediments of humic lakes (Fig. 1). The original design was modified slightly over the period of sampling. The addition of a sharpened steel collar surrounding the mouth of the corer in June 1981, slightly increased the area (10%) sampled, but protected the plexiglas cylinder of the corer and improved its penetration of hard substrates. The corer was manipulated from attached rods in shallow waters. In deeper waters (>2 to 2.5 m) the corer, with rods attached, was lowered by rope and would penetrate the sediments with its own weight. Coarse sand and wood particles were sampled with difficulty. Providing a larger opening at the upper end of the cylinder might have improved its sampling performance on most substrates. This would have eliminated pressure waves (Brinkhurst 1967, 1974) which might be created at the mouth of the corer if allowed to drop too quickly.

Normally, 15 benthic samples were collected from each lake per visit. Usually only a single visit was made. The sampling sites were distributed throughout the lakes surveyed, and not normally randomly assigned. To reduce sorting time only the upper 10 to 15 cm

Figure 1. Core sampler used for collecting benthic samples. (Lid, with foam rubber seal, is closed by elastic following pull on "trigger" rope.)


57mm

of sediment were retained. Few invertebrates would penetrate to greater depths (Berg 1938; Cole 1953; Kajak and Dusoje 1971). Observations of characteristics of these lakes are summarized in Table 1.

Temperature and percent oxygen saturation were often determined, but inevitable problems, including broken thermometers and malfunctions of the oxygen meter (E.I.L. model 1520), frustrated attempts to collect such data. The value of such data is limited due to the variability of weather conditions, season, and the time of day during sampling. Most trips were limited to warm, sunny days with little wind. Obviously, conditions observed during visits to many of the lakes might be very different at night or on cold, wet, overcast days with strong winds.

Benthic samples were sorted as soon as possible after collection, usually the same day. Excess water was removed from the samples by allowing the samples to sit in a 355 μm sieve. Active sieving proved too time consuming and was only employed for inorganic sediments. The benthic invertebrates were floated in white enamelled pans with a nearly saturated $MgSO_4$ solution. Aggregates of organic debris, including tubes, sediment bound by roots, wood, etc. were broken. The surface of the $MgSO_4$ solution was carefully examined for invertebrates. Initial clouding of the surface by flocculent organic material usually dissipated within minutes as this material sank. $MgSO_4$ solutions float invertebrates for more than 30 minutes (Flannagan 1973). Samples were examined several times and were not discarded until no further invertebrates were found. Any tubes remaining intact were examined for larval chironomids. Floatation techniques such as this provide the only practical method of sorting such substrates (Anderson 1959) and recover most (80%) of the chironomids present (Kreamer 1980; McLachlan and McLachlan 1975).

Chironomids were mounted on slides in ACS medium (Searle Diagnostic, High Wycombe, Bucks, England) and identified to genus. The taxonomy follows Hamilton et al. (1969). Notes were kept on the occurrence of other invertebrates. These were then preserved in 10% formalin for future identification.

Two water samples were collected from each lake's surface. Water samples were used for determinations of pH, colour, and conductivity. Colour was determined using a Hach (model CO-1) visual colourimeter, a Fisher Accumet Model 220 pH meter was employed for pH determinations. Conductivity was determined at 23 degrees C using a Radiometer type CDM 2c conductivity meter. At low pH a conductivity correction (Sjors 1950) was calculated to assess hydrogen ion activity.

Principal component ordination offers methods of constructing classifications of benthic communities. These methods have frequently been employed, yet the selection of suitable measures of distance remains a subjective problem. For the present investigation, a distance matrix for the relative abundances (as a %) was calculated, following transformation (In X%+1) using the BASIC program EUCD of

Orloci (1975). Euclidean distances were calculated between the lake vectors. This matrix provided measures of distance necessary for Orloci's program PCAD, which performs D algorithm of principal component ordination.

2.2 Detailed Studies of Benthic Ecology

Of the lentic habitats surveyed, four were selected for a detailed investigation of their present chironomid larval populations. A comparison of these extant communities was also made with subfossil remains present in their surficial sediments. The four waters selected were Wood's Pond, Portey Pond, Folly (Smith) Lake, and Fox Creek (Melanson Settlement) Lake. The three latter lakes were selected not only for their proximity to Mount Allison University in Sackville, N.B., but also because their current state may well reflect different stages in the development of Wood's Pond. These lakes represent a gradient in terms of pH, colour, conductivity, oxygen availability, macrophyte development, area, and depth (Table 1).

Each of these four lakes were visited twice each month through the period June 1, 1980 to August 30, 1980. Sampling was continued at monthly intervals for the period April 15, 1981 to December 5, 1981. During the 1981-82 winter, sampling was restricted to one visit in mid-March. On each sampling date 15 samples were taken from the same, randomly assigned sites. Methods for sampling, sorting, identification, and chemistry followed those outlined for the lake survey. In May of 1981 water samples were collected for determinations of phosphorous, nitrogen, and carbon. Analyses of these water samples were performed by the Water Quality Branch, Inland Waters Directorate, Environment Canada, Moncton, N.B.

2.3 Thanatocenoses - Biocenoses Comparison

For comparison of extant and subfossil associations, the data on the relative abundance of chironomid species obtained above were compared with the subfossils recovered from the surficial sediments at five of the fifteen sampling sites. Sand and silt sites were avoided. The surficial sediments were collected in the core sampler described previously. As the corer and sample were about to be lifted from the water, the mouth of the corer was blocked, and the seal at the upper end of the corer was opened. A flexible plastic tube was inserted through this opening to the sediment surface. A rubber bulb at the opposite end of the tube provided suction, drawing a sample of sediment into the tubing. For Wood's Pond and Portey Pond extant associations were also compared with subfossils in the upper 40 cm of a core previously examined from each lake (Walker 1980, unpublished data). The untreated wet sediment was examined (Walker 1980) as small aliquots in a plankton counting chamber under 40X magnification. Head capsules were mounted in ACS for identification. Identification was conducted as for live material. Because the antennae, an important taxonomic character, were rarely intact in the subfossils, the author did not distinguish Paratanytarsus, Cladotanytarsus, or Micropsectra from Tanytarsus. All these taxa were lumped as Tanytarsus. A minimum of 30 head capsules was removed from each sample.

Fragments containing only part of the hypostomial plate (mentum), where identifiable, were counted as one half.

III. Results and Discussion

3.1 Assessment of Benthic Classifications

3.1.1 Results

The locations of the lakes and ponds surveyed are indicated in Figure 2 and 3. Most lie in the lowlands of eastern New Brunswick. The podzolic soils of this region support mixed conifer-hardwood forests and in some areas have been succeeded by extensive Sphagnum peatlands. Carboniferous sandstones are the prevalent bedrock throughout most of this region, but are usually overlain by a thick layer of till. The region has a moderate to high susceptibility to acidification (Shilts 1981).

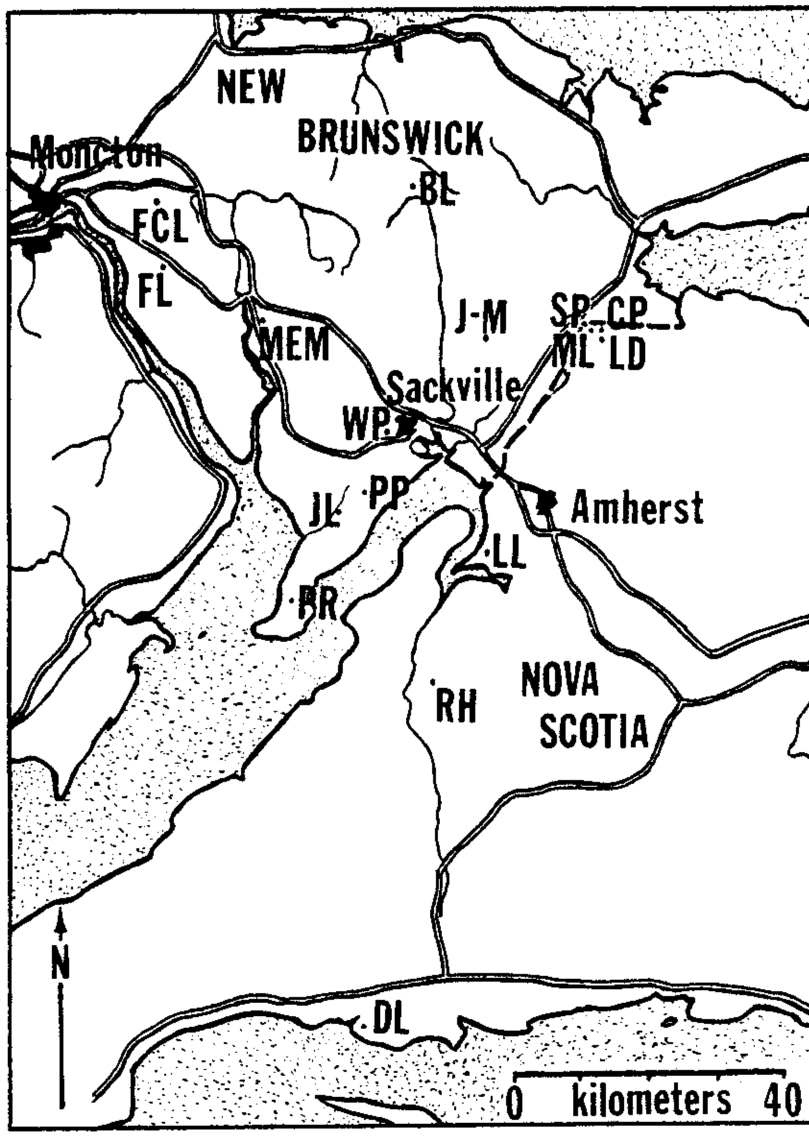
Thirty-five chironomid genera were recorded from the lakes and ponds surveyed. Representatives of sixteen additional groups of invertebrates were found, some occasionally constituting important components of the benthic fauna. Densities of chironomids varied from 660 to 7800 individuals/m^2. The lowest densities were recorded from Despres Lake, the highest from Smart's Pond. The results are presented in Tables 2 and 3.

The lakes and species are arranged in Tables 2 and 3 so as to emphasize apparent ecological relationships. These approximate a pH gradient. A range of lake surface area, colour, conductivity and macrophyte development is apparent in the lakes as presently arranged (Table 1).

The first four "lakes" are peat pools within a coastal bog at

Figure 2. Distribution of habitats sampled near the New Brunswick - Nova Scotia border.

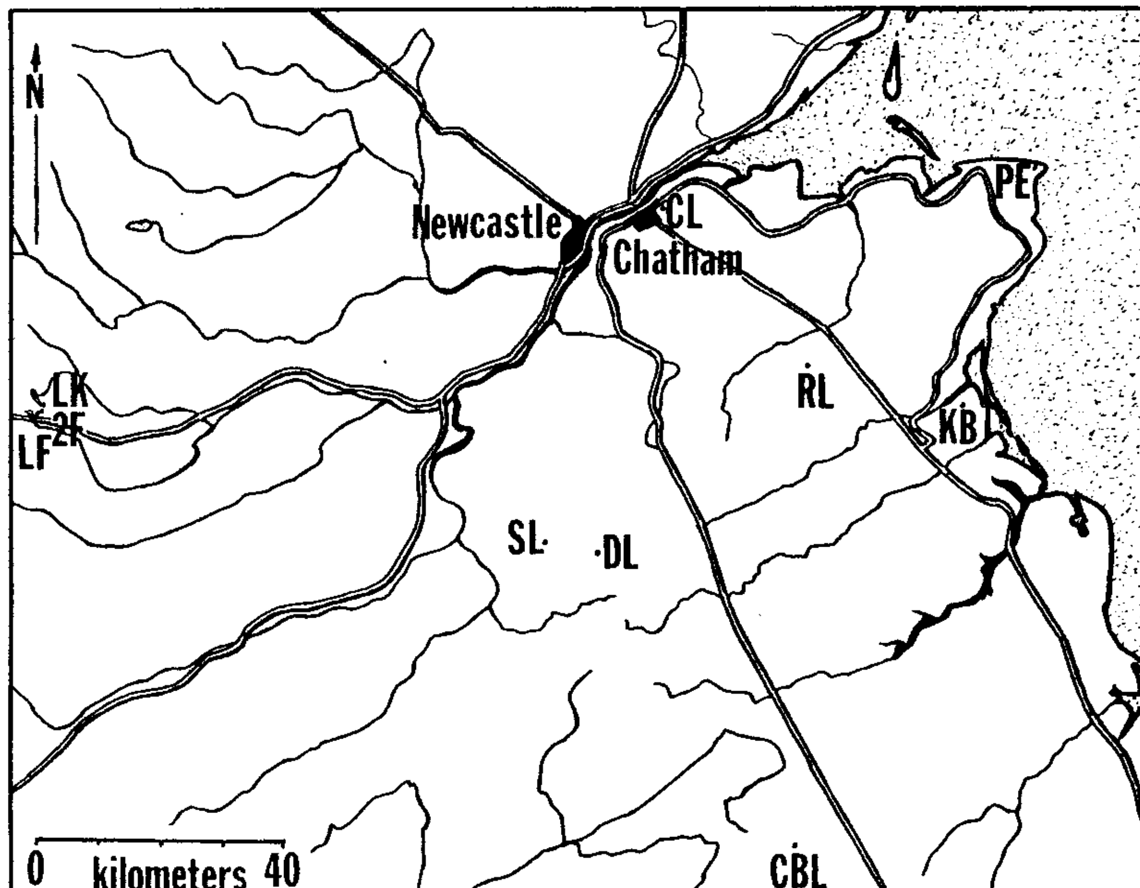
Habitats: River Hebert Bog = RH; Jolicure-Midgic Bog = J-M; Wood's Pond = WP; Diligent River Lake = DR; Folly Lake = FL; Fox Creek Lake = FCL; Johnson's Lake = JL; Black Lake = BL; Portey Pond = PP; Smart's Pond = SP; Missiguash Lake = ML; Memramcook Lake = MEM; Layton's Lake = LL; Copp's Pond = CP; Little Duck = LD; Pink Rock = PR.



NEW
BRUNSWICK
Moncton
BL
FCL
FL
J-M
SP
CP
ML
LD
MEM
Sackville
WP
JL
PP
Amherst
LL
PR
RH
NOVA
SCOTIA
N
DL
0 kilometers 40

Figure 3. Distribution of habitats sampled near Newcastle and Chatham in north-eastern New Brunswick.

Habitats: Point Escuminac = PE; Kelly's Bog = KB; Little Kennedy = LK; Chatham Lake = CH; Despres Lake = DE; Round Lake = RL; South Lake = SL; Coal Branch Lake = CBL; Little Fowler = LF; Second Fowler = 2F.



N
Newcastle
CL
Chatham
PE
RL
KB
LK
2F
LF
SL
DL
CBL
0 kilometers 40

TABLE 1

Selected Physical and Chemical Parameters (Summer Values) of the Habitats Surveyed

Units:
- Conductivity — umhos/cm @ 23 C (pH corrected)
- Colour — Pt - Co Units
- Macrophytes — proportion of habitat area colonized
- Depth — meters
- Area — hectares
- Sediment — P = peat, D = dark brown dy, G = grey-brown dy; GS = dy with H_2S, S = sapropel

Habitats: Point Escuminac = PE1, PE2, PE3, & PE 4; Kelly's Bog = KB; River Hebert Bog = RH; Jolicure-Midgic Bog = J-M; Wood's Pond = WP; Little Kennedy = LK; Diligent River Lake = DR; Chatham Lake = CH; Folly Lake = FL; Despres Lake = DE; Round Lake = RL; Fox Creek Lake = FCL; South Lake = SL; Coal Branch Lake = CBL; Johnson's Lake = JL; Black Lake = BL; Portey Pond = PP; Little Fowler = LF; Second Fowler = 2F; Smart's Pond = SP; Missiguash Lake = ML; Memramcook Lake = MEM; Layton's Lake = LL; Copp's Pond = CP; Little Duck = LD; Pink Rock = PR.

	PE1	PE2	PE3	PE4	KB	RH	J-M	WP	LK	DR	CH	FL	DE	RL	FCL
Conductivity (Corrected)	40	40	40	60	0	0	0	0	13	20	0	42	15	16	30
Colour	100	100	100	100	100	100	100	150	40	10	150	90	40	50	80
pH	3.8	3.8	3.8	3.7	4.2	4.0	4.0	4.0	4.8	4.5	4.1	4.9	4.4	4.8	5.6
Macrophytes	.7	.2	.2	.3	.8	.2	.4	.7	.1	.1	.2	.2	.1	.2	.3
Max. Depth	.7	1.5	2.0	1.5	2.0	2.5	1.5	2.0	2.0	10.	1.5	3.0	2.0	2.0	1.7
Area	.1	.5	.5	.5	.5	3.0	.5	1.0	2.0	.5	7.	19.	15.	26.	10.
Sediment	P	D,P	D,P	D,P	P	P	D,P	D,P	D,P	D,P	D	D	D	D	D

	SL	CBL	JL	BL	PP	LF	2F	SP	ML	MEM	LL	CP	LD	PR
Conductivity (Corrected)	16	15	80	18	70	18	25	41	128	150	410	40	41	43
Colour	110	40	80	0	85	100	60	200	53	40	50	22	20	90
pH	6.2	5.1	6.4	6.4	6.1	6.8	6.5	6.2	6.5	7.0	7.3	6.5	6.7	4.6
Macrophytes	.2	.3	.1	.1	.1	.2	.2	.3	.3	.1	.1	.1	.1	.1
Max. Depth	1.0	3.0	2.0	6.0	1.5	1.0	2.0	1.5	1.2	1.2	8.0	20.	9.0	20.0
Area	14.	41.	15.	17.	4.	3.	24.	2.	3.	30.	12.	4.	4.	2.
Sediment	D	GS	G	G	GS	D,G	GS	D	D	S	S	D	D	D

TABLE 2

Expected abundance of benthos, other than the Chironomidae, in fifteen* sampling units for each habitat. Abbreviations for habitats follow those given for Table 1.

*Where more or less than 15 sampling units were collected the abundances have been corrected. To convert the values to densities/m^2 multiply by 26.1.

	PE1	PE2	PE3	PE4	KB	RH	J-M	WP	LK	DR	CH	FL	DE	RL	FCL	SL	CBL	JL	BL	PP	LF	2F	SP	ML	MEM	LL	CP	LD	PR
Trichoptera	27	3	3	9	5	6.5	3.3	2.7			1.2	.3			.6	1	1.2	3	1	.5		4		1			1	1	
Cladocera	3		3	3		3.5	15	9.7		1	1				1.3	4			7	5.0								2	
Anisoptera	3			6	8	.5	5			1			1		.2	4				.2									
Zygoptera					2	3	1.7	.3			.2				1.2														
Chaoborus								7.7		6	3.2	4.6	4	3			2.5										.5	2	6
Oligochaeta			3				1.5	3.7			2.5	2.7	3		4.8	15	5	9	6	1.5	6	4		4		4	12	3	3
Copepoda	3					.5		.5							3.3		1.2		2									1	
Hydracarina	3				2	1.5					.2	.4								1.2	4	4		6		1	.5		
Bezzia					1	1.5	3.3	.5			.7	.7			5.2	4			4	.5	4			1				3	
Amphipoda								.2							.2			6	13	8.1		2		7		2	7	9	5
Hirudinea												.3	1		2.3	66		1.5		.2				1					
Ephemeroptera												.1			.6	19	1.2	10.		19.		20		11		1			
Corixidae								1.8				.2				1								1					
Lepidoptera											.2						1.2												
Coleoptera												.4															1	2	
Ostracoda																								1				1	
Other					3	1.5									.3														

TABLE 3

Expected abundance of the Chironomidae in 15 sampling* units. Habitat abbreviations follow those given for Table 1.

*Where more or less than 15 sampling units were collected the abundances have been corrected. To convert values to densities/m^2 multiply by 26.1.

	PE1	PE2	PE3	PE4	KB	RH	J-M	WP	LK	DR	CH	FL	DE	RL	FCL	SL	CBL	JL	BL	PP	LF	2F	SP	ML	MEM	LL	CP	LD	PR
Zalutschia	12	18	57	330		1		7.4		1		.7			.6														
Ablabesmyia	6	9	3	24	37	14	46.	2.1			8.2	.2	1	3	.2	7			5	2.7	2	6					4.5	3	
Psectrocladius	24	6	24	63	8	11.	18.	1.6	3	4		.2		1	.3	1				1.8			1					2	
Monopsectrocladius	15				3	5.5	8.3	43.	7	11	.3			1	1.3		5		1			2						1	
Chironomus				3	5	16.	73.	75.	27	8	6.7	.9	1		16		1.2			.1		2		10	2	14	6	4	3
Procladius			9			8.5	53.	43.	17	10	24.	5.8	9	47	13.	108	19.	18	47	38.	38	46	54	27	56	3	8.5		5
Tanytarsus					2	4.5		1.7		3	27.	6.0	1	3	18.	17		10.	8	4.1	4	2	140	43	3	1	6		
Paratanytarsus	3	3						.2			.3	.8		1	1.9	4	3.8	4.5	13	16.	4	2	1				4.5		
Polypedilum					3	1		2.7			3.1	.3	1	1	5.0	2	1.2	19.	5	1.9		2	25	7	2	2	.5	6	1
Cladopelma								1.7		1		1.3	7	8	9.2	1		1.5	1	1.9			39	12	5	3	.5	3	
Dicrotendipes					4	5		.1		2		.2			6.0					2.1			24	19					3
Cryptochironomus								.3				.3	1		.4	1		4.5	1	3.2			5		2	1			1
Glyptotendipes												3.6		1	2.9	48	3.8			.3		2	4	1					20
Pagastiella				3		1.5				1					.3	1	1.2			.3	6	2	1					3	
Phaenopsectra					1					4		1.4							1	.2							2		6
Stictochironomus						.5			1			1.3					6.2	1.5	2	.1			2						
Microtendipes								.4							16.	9				.6			1				6		
Heterotrissocladius												.3						1.5	23				1						
Others					3			0.6				2.0			1.8		1.2		2	4.1			5	5	4		4.7	2	9

Point Escuminac. Lying close to the sea, these pools probably receive substantial inputs of sea salts via the atmosphere, thus their high conductivity. The principal chironomid genera recovered include Zalutschia, Ablabesmyia, and Psectrocladius. Trichoptera,Anisoptera, and Cladocera include most of the remaining benthos. These pools were both strongly acid (pH = 3.8) and coloured (100 Pt-Co units). Macrophytes were generally well developed.

Ponds from three other Sphagnum peatlands were also included. Lying several kilometres from the coast, neither the River Hebert bog, Kelly's bog, nor the bog at Midgic are substantially influenced by the sea. Although these pools are almost as acid, and as strongly coloured as the pools of Point Escuminac, their conductivity is considerably less. Corrections for the contribution of H+ reduce the conductivity of these waters essentially to zero. Ablabesmyia, Psectrocladius, Monopsectrocladius, and Chironomus were recovered from the benthos of all three waters. Trichoptera, Zygoptera, Bezzia, and Cladocera were also common to the pools of both peatlands.

Wood's Pond, Little Kennedy Lake, and Diligent Lake are all small waters completely enclosed by thick Sphagnum mats; thus, conditions in these lakes approach those of the peat pools. All of these waters appear to stratify to some extent. Diligent Lake occupies a kettle. It is 10 metres deep despite its small surface. Unusually cold bottom waters were noted in the 2 metre deep Little Kennedy Lake, perhaps indicating the presence of a spring. Oxygen readings approached saturation for Little Kennedy and Diligent Lakes. Despite its shallow basin, oxygen concentrations remain low at Wood's Pond's maximum depth throughout the ice-free period. Densities of benthos in Wood's Pond (4900/m^2) are several times greater than the other two lakes. Perhaps this indicates the important contribution of macrophytes to the pond's productivity. Few macrophytes inhabit Diligent Lake or Little Kennedy Lake. Values for pH (4.0 - 4.8), colour (10 - 150 Pt-Co units), and conductivity (13 - 32 µmhos) vary within this group. Conditions in Wood's Pond most resemble those of the peat pools. Like most peat pools conductivity values for Wood's Pond reduce to zero upon correction for H+ activity. Psectrocladius, Monopsectrocladius, Chironomus, and Procladius are common to these three lakes. Other invertebrates were scarce except in Wood's Pond. Important constituents of Wood's Pond's benthos included Trichoptera, Chaoborus, Cladocera, and oligochaetes.

Folly, Chatham, Despres, Round, and Coal Branch Lakes have pH and conductivity values ranging from 4.0 to 5.2 and 15-60 µmhos respectively. All are shallow (<3 m), polymictic lakes with comparatively large surfaces. They also lie adjacent to extensive peatlands. Most chironomids belong to the genera Procladius, Tanytarsus, Polypedilum, and Cladopelma. The most acid of these lakes, Chatham Lake yielded the most Chironomus and Ablabesmyia larvae. Other invertebrates were scarce, although Chaoborus and oligochaetes were regularly collected.

Johnston's Lake, Black Lake, Portey Pond, Little Fowler, Second Fowler, South, and Fox Creek Lakes are less acid, (pH = 6.0 to 6.8) generally without extensive adjacent peatlands; conductivity (16-80 µmhos) varies. Procladius, Tanytarsus, Paratanytarsus, Ablabesmyia, and

Polypedilum include the more abundant genera. Other invertebrates include Trichoptera, Amphipoda, and oligochaetes. Hirudinea, Amphipoda, and Ephemeroptera were rare or absent in more acid waters.

Most frequently recorded from the lakes of reclaimed salt marshes were *Procladius*, *Tanytarsus*, *Polypedilum*, *Cladopelma*, and *Chironomus*. These lakes include Smart's Pond, Missaguash Lake, Memramcook Lake, and Layton's Lake. They are circum-neutral waters (pH = 6.0 to 7.2) with conductivity varying from 36 to 395 μmhos. The incomplete data concerning other invertebrates permits no generalizations as to their contribution. Macrophytes were abundant both in Smart's Pond and Missaguash Lake, but rare in both Layton's and Memramcook Lakes. These lakes are generally very shallow. Layton's Lake however includes a small, but deep (10 m) meromictic region.

The benthos of three deep stratified lakes were sampled. Copp's Pond and Little Duck Lake are circum-neutral, oligohumic lakes. Pink Rock Lake is acid (pH = 4.6) with strongly coloured waters (90 Pt-Co units). Few Chironomidae were shared by these lakes. In all cases, the benthos were much more abundant in the littoral regions. *Chaoborus*, oligochaetes, and Amphipoda were recorded from the three lakes.

Principal component analysis provides methods of constructing faunal classifications. The results of principal component ordination (Fig. 4) provide effective visual representations of the data. Three distinct clusters are evident on the basis of the chironomid fauna. The pools of Point Escuminac compose one cluster. In a second cluster are four lakes, and the pools of three *Sphagnum* bogs. The remaining habitats, all of which are lakes, are included in a third, larger cluster.

The results of a second ordination (Fig. 5), based on the other components of the benthos, provide somewhat different results. Three clusters are again evident. One cluster includes all the peat pools. The two remaining clusters separate weakly acidic lakes (pH = 5.5 to 7.5) from those more strongly acidic (pH = 3.5 to 5.5).

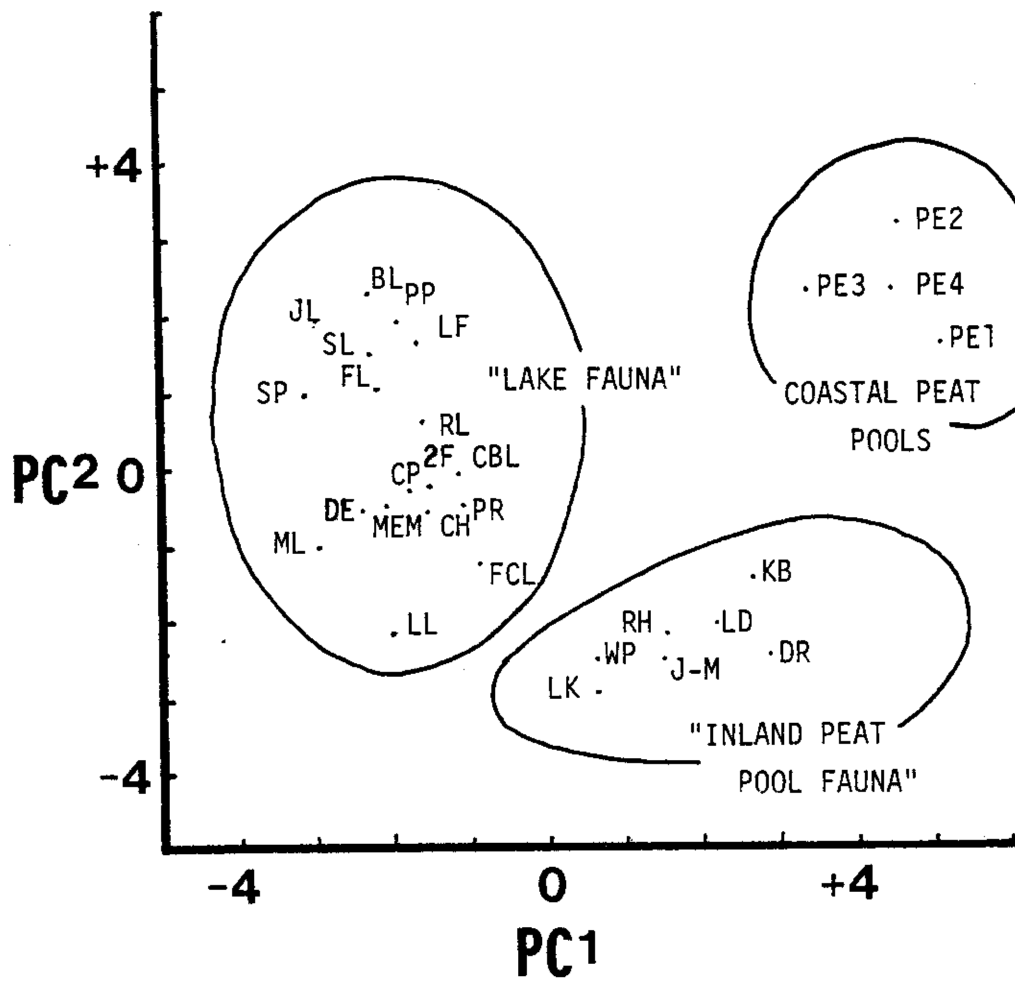
3.1.2 Discussion

The relative abundance data, as presented in Figure 6, facilitates a more detailed description of the three major faunal units.

1) Inland Peat Pool Fauna

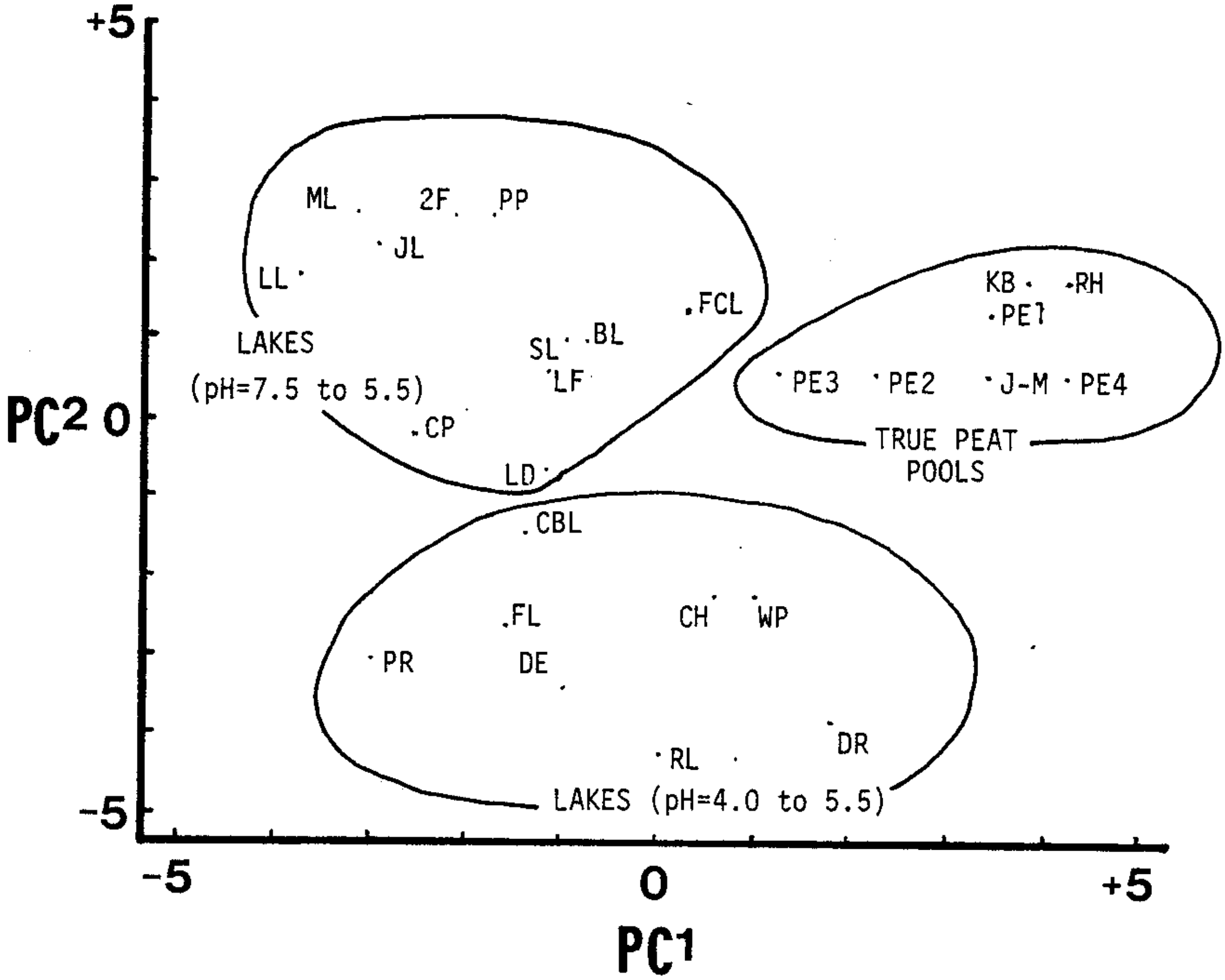
All peat pools lying beyond the immediate influence of the sea have a fauna in which *Chironomus*, *Ablabesmyia*, *Monopsectrocladius*, and/or *Psectrocladius* are most abundant. Within this group are four lakes. Little Duck Lake is a deep, circum-neutral oligohumic lake. Three of these lakes, however, are small, lentic habitats at the latter stages of bog lake evolution. Conditions within these habitats approach those of the peat pools. Worthy of note is the importance of *Procladius* to the lakes, and the comparatively low densities of *Ablabesmyia*. *Chaoborus* was collected from three of the lakes, but was absent from true peat pools.

Figure 4. Principal component ordination of habitats from relative abundances of chironomid taxa. Abbreviations for habitats follow those listed for table 1.



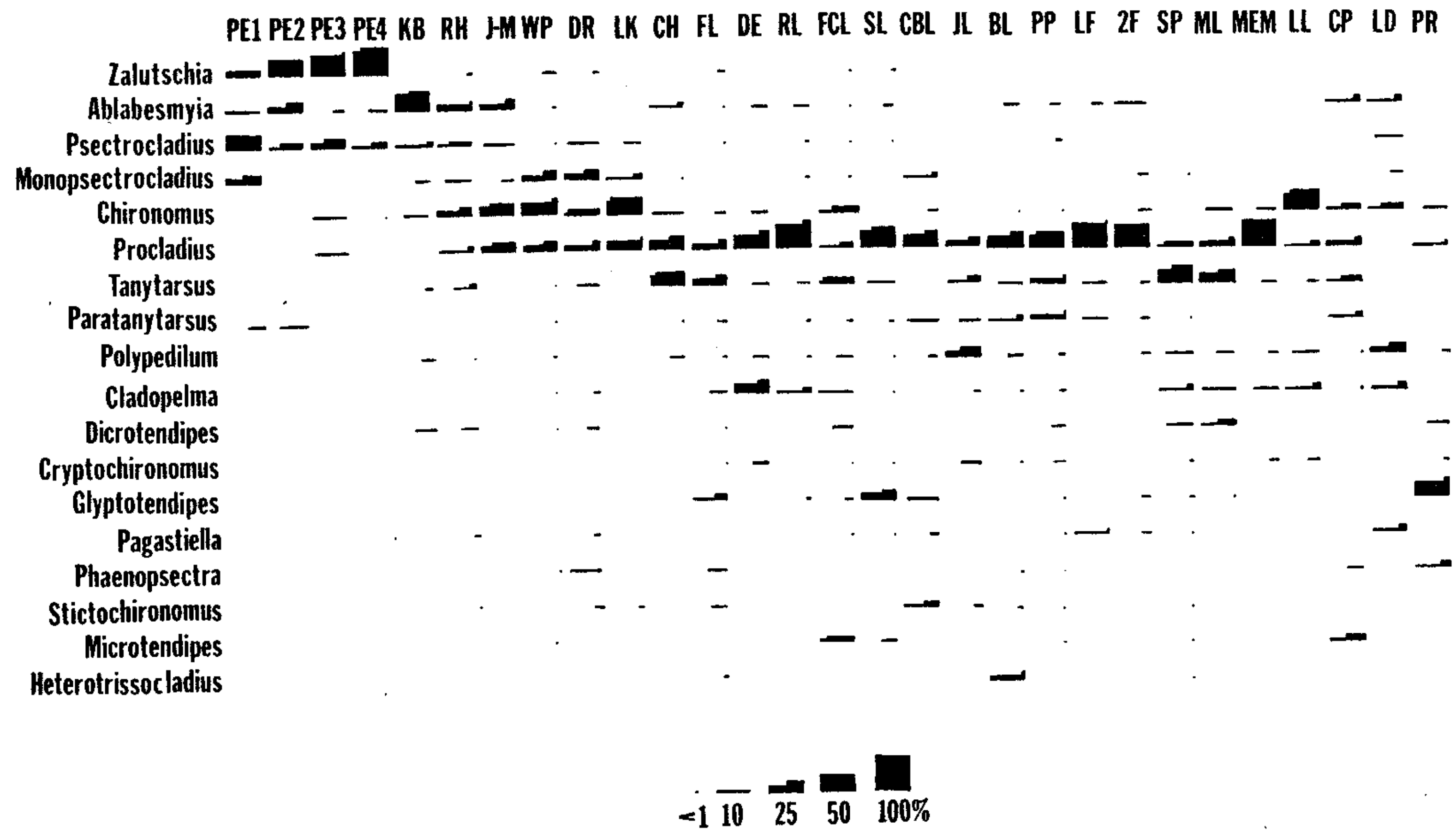
+4
PC2 0
-4
-4
0
+4
PC1
BL
PP
JL
SL
LF
FL
SP
"LAKE FAUNA"
RL
2F
CBL
CP
DE
MEM
CH
PR
ML
FCL
LL
PE2
PE3
PE4
PE1
COASTAL PEAT
POOLS
KB
RH
LD
WP
J-M
DR
LK
"INLAND PEAT
POOL FAUNA"

Figure 5. Principal component ordination of habitats from relative abundances of benthic invertebrates, exclusive of the Chironomidae. Abbreviations for habitats follow those listed for table 1.



+5
-5
PC2 0
-5
0
+5
PC1
ML
2F
PP
JL
LL
LAKES
(pH=7.5 to 5.5)
FCL
SL
BL
LF
CP
LD
KB
RH
PE1
PE3
PE2
J-M
PE4
TRUE PEAT
POOLS
CBL
FL
CH
WP
PR
DE
DR
RL
LAKES (pH=4.0 to 5.5)

Figure 6. Relative abundances of the common chironomid taxa in the habitats surveyed. Abbreviations for habitats follow those listed with table 1.


PE1 PE2 PE3 PE4 KB RH J-M WP DR LK CH FL DE RL FCL SL CBL JL BL PP LF 2F SP ML MEM LL CP LD PR
Zalutschia
Ablabesmyia
Psectrocladius
Monopsectrocladius
Chironomus
Procladius
Tanytarsus
Paratanytarsus
Polypedilum
Cladopelma
Dicrotendipes
Cryptochironomus
Glyptotendipes
Pagastiella
Phaenopsectra
Stictochironomus
Microtendipes
Heterotrissocladius
<1 10 25 50 100%

2) Coastal Peat Pools

The coastal peat pools of Point Escuminac appear as a distinct group. These are distinguished principally by the importance of *Zalutschia*. The high conductivity of these pools reflects their proximity to the sea.

3) Lake Fauna

Most of the remaining habitats, all lakes, are shallow, polymictic habitats in which *Procladius* and/or the Tanytarsini (combined *Tanytarsus* and *Paratanytarsus*) are numerically most abundant. Many other genera, notably *Polypedilum*, *Dicrotendipes*, *Cladopelma*, and *Glyptotendipes*, are common associates. The chironomids fail to provide an effective subdivision of the lakes despite the broad range of pH (4.0 to 7.2), colour (0 to 150 Pt-Co units), and conductivity (0 to 395 µmhos) apparent in these lakes. Of the other invertebrates, *Chaoborus* is distributed in the more acid (pH = 4.0 to 5.0) lakes. Amphipoda, Ephemeroptera, and Hirudinea are distributed in waters with higher pH (6.0 to 7.0).

The waters of the more eutrophic marsh habitats, Layton's Lake and Memramcook Lake, may be distinguished by the importance of *Chironomus*. The data for deep, stratified lakes, Copp's Pond, and Pink Rock Lake, are too scant to permit generalizations.

Apparent in the results is a sharp distinction between the fauna of most lakes and the peat pools. The peat pools are distinguished by a Chironomus-Monopsectrocladius-Psectrocladius association. Wood's Pond, Little Kennedy Lake, and Diligent Lake share this type. Most lakes have a Procladius-Tanytarsini fauna.

The division of the habitats into "peat pools" and "lakes" does not compare favourably with existing classifications. Brundin (1949) appears to have recognized that the fauna of polymictic, humic lakes differs from that of stratified lakes. He, however, described a "Stictochironomus-Tanytarsini" type for these lakes. Bryce (1965) investigated the Chironomidae of some British peat pools. He described distinct Chironomus and Tanytarsus pools, but failed to account for the differences in their distribution. It may be found that considerable regional variation exists in the fauna of bog lakes and peat pools.

The results of the faunal survey document trends which parallel those of an earlier palaeolimnological (Walker 1980) investigation. In that research, the most striking change in the chironomid fauna was a recent Tanytarsus to Chironomus shift at the latter stages of bog lake succession. In the latter stages, conditions in bog lakes approach those of small, ombrotrophic pools in Sphagnum peatlands. These waters have become completely enclosed by Sphagnum and possess a small surface area. The depth of such pools is large in relation to their surface. This limits the extent of mixing and subsequent sediment disturbance. Reduced disturbance may yield favourable habitat for certain benthic invertebrates and also conditions for macrophyte colonization.

Sphagnum is capable of greatly influencing water chemistry, by both organic acid secretion, and removal of cations (Sjors 1950). The exchange of H+ for other cations further increases acidity. At low pH many metals are mobilized. These so-called heavy metals may be toxic to organisms (Havas 1981) and are believed to eliminate fishes, the principal predators in aquatic ecosystems. This may benefit certain invertebrates.

The organic acids and humics of peat pools stain the waters, and sequester both plant nutrients, and metals. Complexing of metals may permit organisms to exist beyond their normal pH limit (Kerekes pers. comm.). Stained waters limit light penetration thus limiting phytoplankton production. Paradoxically, phytoplankton productivity within the photic zone may be greater in such waters, yet the smaller photic zone detracts from overall production (Beauchamp 1982). Reduced light penetration favors growth of floating-leaved macrophytes, and associated epiphytes. Nutrients trapped in the sediments may be accessible to macrophytes (Carignan and Kalff 1979, 1982) and not phytoplankton.

Recent studies of invertebrates in acid lakes (Mossberg and Nyberg 1979) suggest that *Chironomus*, *Psectrocladius*, *Zalutschia*, and Odonata may be favoured by low pH. Some authors have suggested that elimination of predators or competing species at low pH, may produce these faunal changes. Havas (1980) notes that low pH may interfere with osmoregulation, acid-base balance, and respiration. Larger species (Wiederholm and Eriksson, 1977) of the Chironomidae appear to be favoured by low pH; the smaller surface area-volume ratio of these species may be advantageous where osmoregulation and acid-base balance are disturbed. Where respiration is impaired, blood-gills and haemoglobin may be beneficial. Both Chironomus and Psectrocladius are often associated with more productive, eutrophic waters.

Examining the survey data neither pH nor the production enhancement by macrophytes appears capable of completely accounting for the observed distribution patterns. Wood's Pond and Chatham Lake appear to have similar chemical characteristics, yet differ in morphometry, macrophyte development, and chironomid association. Macrophytes may favour the "Chironomus - Psectrocladius" association in Wood's Pond. The division between Chironomus and Tanytarsus lakes does not appear clearly defined by oxygen concentrations. Oxygen varied greatly within the "Chironomus" lakes sampled. In winter, all shallow humic lakes are likely to experience oxygen deficiencies, and perhaps anoxia (Nagell and Brittain 1977).

The combined influence of metals, organic acids, sediments and production may provide a plausible separation between the two faunal types presently described. It is likely that the chironomids of peat pools are adapted to the range of conditions which normally occur there. No single factor adequately describes their distribution. As conditions in a bog lake approach those of a peat pool, the members of the Chironomus-Monopsectrocladius-Psectrocladius fauna appear to be favoured.

Zalutschia zalutschicola was recorded only from Little Duck Lake, which is deep and stratified. It was known formerly to have been abundant in Wood's Pond (Walker 1980). Saether (1975) suggests that the value of Zalutschia zalutschicola as a typological indicator may be limited by its present distribution.

As reported by Mossberg and Nyberg (1979), Odonata, and Trichoptera appear favored by low pH. Cladocera also appeared to be favoured. Ephemeroptera, Amphipoda, and Hirudinea were absent at low pH. No molluscs were collected, although both Gastropoda and Pelecypoda are presently known to occur in the benthos of Portey Pond.

3.2 Detailed Studies of Benthic Ecology

3.2.1 Results

Detailed investigations of the ecology of benthic invertebrates revealed aspects of their distributions spatially and temporally, their production, and relative abundance. Results from the four lakes are presented separately.

Wood's Pond

Wood's Pond (Fig. 7a) is a small, strongly acid (pH = 4.0 to 4.8), polyhumic (150 Pt-Co units) pond, completely enclosed by Sphagnum. The pH rises through the winter, peaking at ice-melt. In the spring of 1982 a pH of 4.8 was recorded. The waters of the lake at this time were clear (30 pt-Co units) with a higher conductivity (12 μmhos after pH correction) than is usual. It is believed that the dilution of the pond-water by run-off produces this phenomenon. In the other three lakes, the lowest pH values had been recorded in spring, as expected (Jeffries et al. 1979). The pond is shallow, having a mean depth and maximum depth

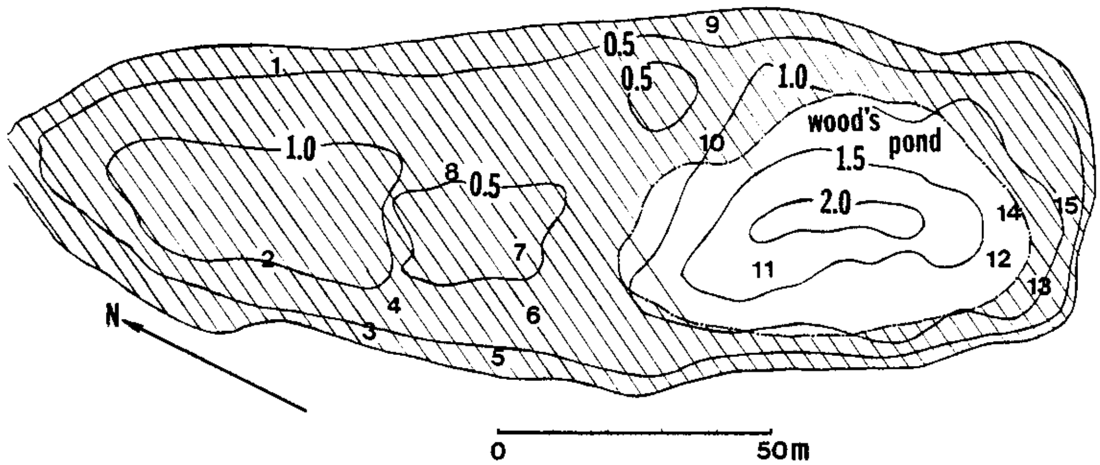
Figure 7. Maps of depth (contour depths given in metres), floating-leaved macrophytes, substrate, and sampling stations.

a) Wood's Pond

b) Portey Lake

floating-leaved macrophytes

sand


wood's pond
1.0
1.5
2.0
0.5
N
0 50m

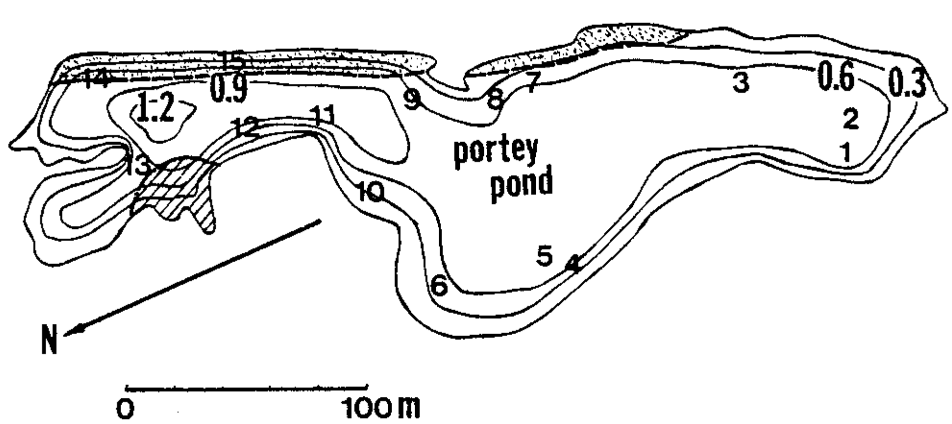
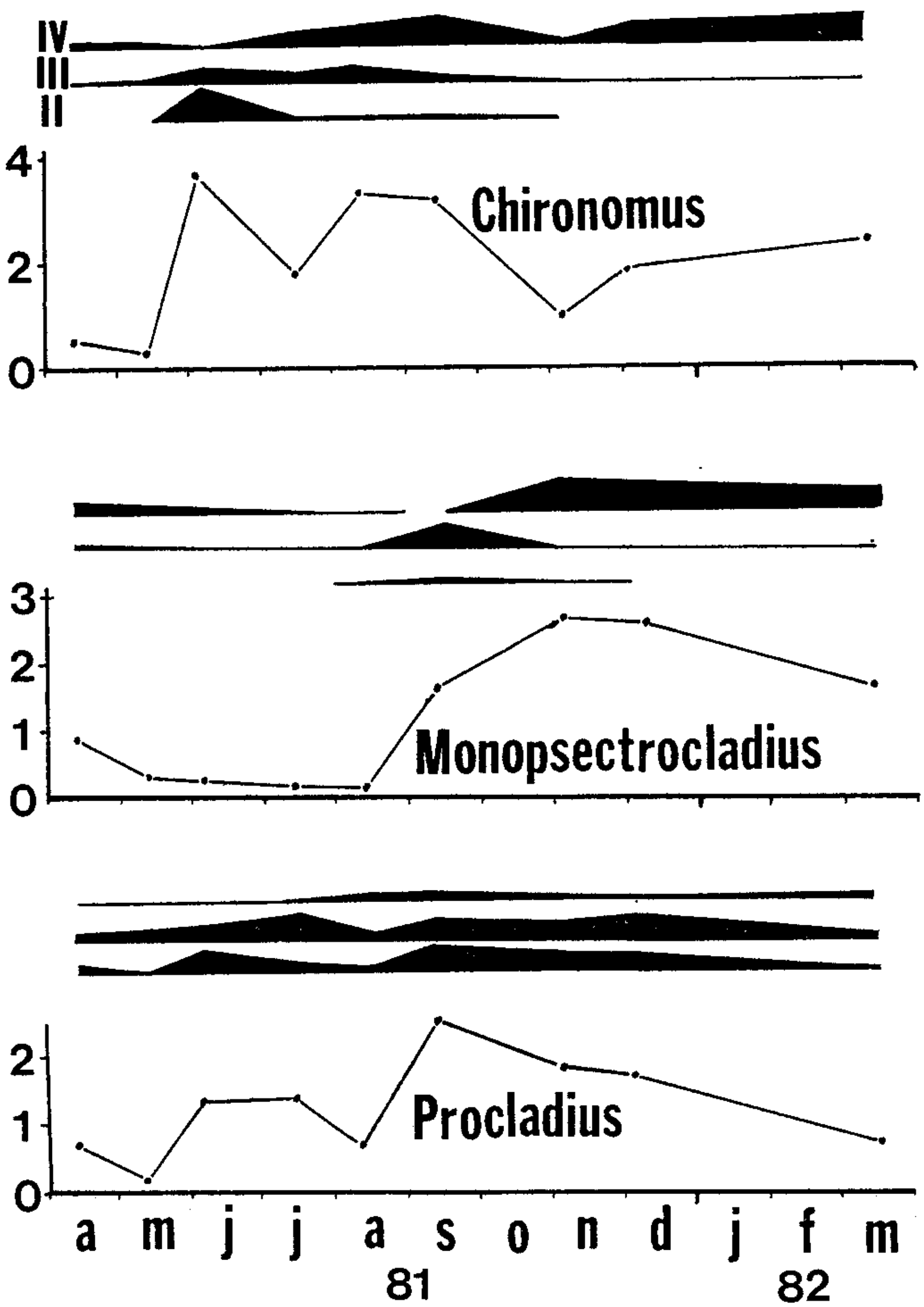

portey pond
1.2
0.9
0.6
0.3
N
0 100m

TABLE 4

Wood's Pond: Cumulative Abundance (= Total Number of Chironomids Collected from April, 1981 to March, 1982) of Each Chironomid Taxon at Each Sampling Station in Wood's Pond.

	Site														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Chironomus	8	16	117	54	25	71	72	9	10	30	21	53	46	35	105
Monopsectrocladius	59	31	17	36	51	68	7	21	47	5	4	1	0	7	29
Procladius	63	26	32	33	32	49	24	23	45	6	2	16	10	16	27
Zalutschia	4			1	2		12	45		3					
Cladopelma		3	3	1		2		1		1	2				2
Ablabesmyia	6	1			2	4	3	1		1			1		
Polypedilum	18				1	2		2	1						
Dicrotendipes										1					
Psectrocladius	1	1						6		2	2				2
Tanytarsus	1	2	2	1			1	2		3		2	1		
Parachironomus			1												
Paratanytarsus					1			1							
Microtendipes				1			1		2						
Diplocladius							1								
Phaenopsectra					1		1								1
Lauterborniella	1														
1st Instar Tanypodinae		1													
1st Instar Chironominae				1						1					1

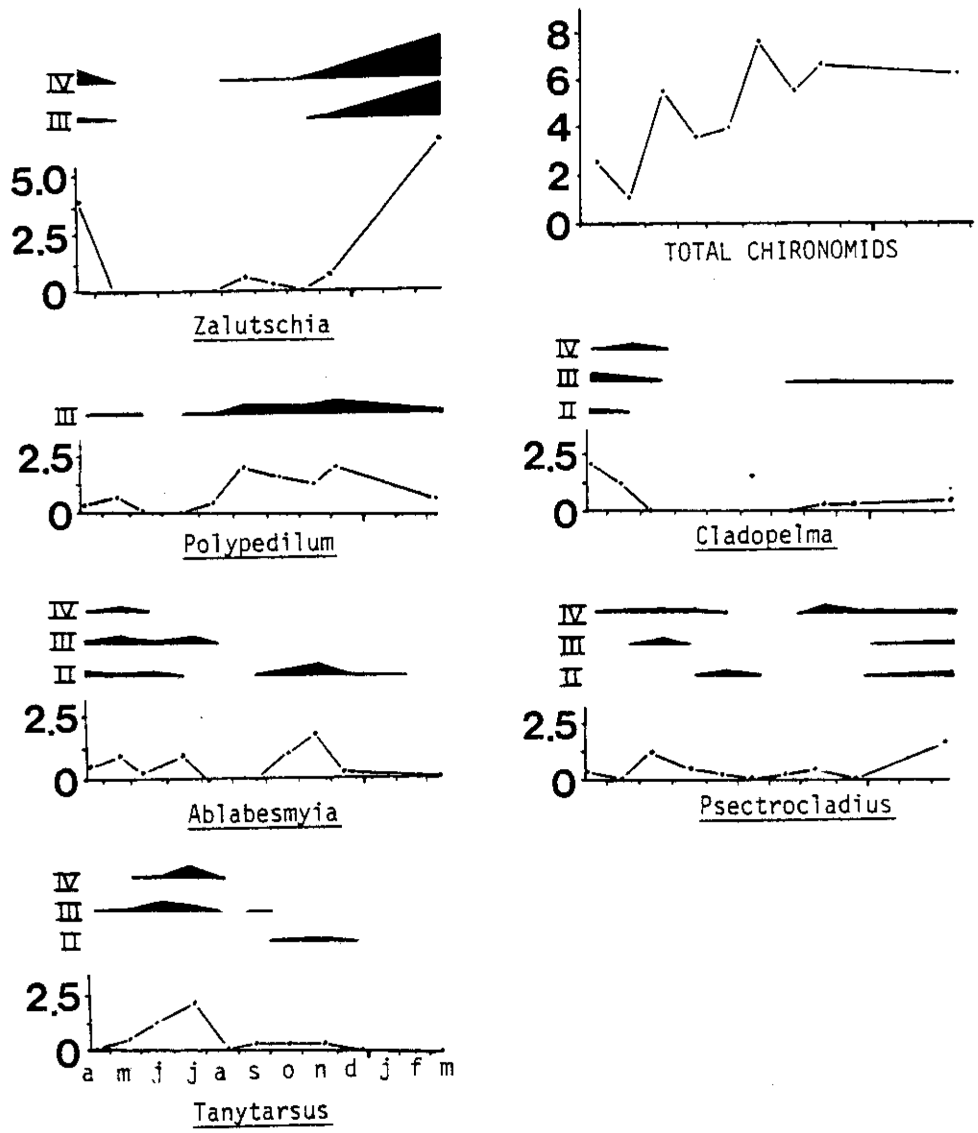
Figure 8. Seasonal distribution of *Chironomus*, *Monopsectrocladius*, and *Procladius* and instars II to IV for these species in Wood's Pond. (Densities expressed as thousands/m^2.)



IV
III
II
4
2
0
Chironomus
3
2
1
0
Monopsectrocladius
2
1
0
Procladius
a m j j a s o n d j f m
81
82

Figure 9. Seasonal distribution of the remaining* chironomid taxa and the seasonal distribution of the total Chironomidae in Wood's Pond. (Total Chironomids expressed as thousands/m^2, all others expressed as hundreds/m^2.)

*Several of the rarest taxa have been excluded.


IV
III
5.0
2.5
0
Zalutschia
8
6
4
2
0
TOTAL CHIRONOMIDS
III
2.5
0
Polypedilum
IV
III
II
2.5
0
Cladopelma
IV
III
II
2.5
0
Ablabesmyia
IV
III
II
2.5
0
Psectrocladius
IV
III
II
2.5
0
a m j j a s o n d j f m
Tanytarsus

of 1.0 and 2.0 metres respectively. Nuphar variegatum is the principal macrophyte. N. variegatum inhabits 75% of the pond's area, only being absent where the water depth exceeds 1.3 metres. Scirpus subterminalis also inhabits the shallow waters. Chamaedaphne calyculata, Calla palustris, and the alga Batrachospermum are important components of the pond's marginal zone flora. The proximity of the surrounding forests, and the dense macrophytes restrict mixing. In the vicinity of the pond's maximum depth conditions approach anoxia below 1 metre throughout the year.

Chironomus, Monopsectrocladius, and Procladius are the principal benthic invertebrates, accounting for 42%, 24%, and 24% respectively of the total chironomid fauna. Results for 1980 are comparable. Polypedilum, Ablabesmyia, Zalutschia, Tanytarsus, Psectrocladius, and 6 rarer genera account for only 11% of the chironomid fauna. Trichoptera, Chaobrous, Zygoptera, Oligochaeta, Bezzia, Copepoda, and Cladocera were also recorded. Total densities of chironomids averaged 4,900 individuals/ m^2.

Densities of benthos are higher in the northern end of the pond (Table 4) where macrophyte development is greatest. Seventy-six percent of the Monopsectrocladius larvae were collected from stations 1 to 8 inclusive. Similarly, 70% of the larval Procladius were collected from this region. While this pattern would appear to hold for the rarer Chironomidae (83% from stations 1 to 8), Chironomus shows no apparent preference for either region (55.4% from stations 1 to 8). Chironomid densities were lowest at one station (#11) located near the maximum depth. At this station 28% of all Chaoborus larvae were collected.

Densities of benthos (Fig. 8, 9) are lowest in spring, coinciding with the emergence of Chironomus. Densities of benthos increase throughout the summer with the recruitment of new generations. Most species appear to be univoltine. Two species of both Chironomus and Procladius (Ramcharan and Paterson 1978) are present. Most Chironomus emerge in early spring. Within days of ice-melt, mid-April, 1981, Chironomus was observed emerging. By early June the beginning of a new generation was evident. The emergence of Monopsectrocladius occurs somewhat later. By mid-August a few 1st instars were collected. By November these had entered their 4th instar. The two species of Procladius provide a complex seasonal population curve. The emergence of one species appears to occur in early spring; the emergence of the other probably coincides approximately with that of Monopsectrocladius. More difficult to interpret are the emergence patterns of rarer species. Some of these may be phytophilous. As the floating leaves of N. variegatum die in September phytophilous species must migrate to the benthos or other microhabitat.

Portey Pond

Portey Pond (Fig. 7b) is a very shallow, weakly acid pond (pH = 5.2 to 6.8). Lowest pH (5.2) and conductivity were recorded with ice-melt. As the season progressed, pH (6.8) and conductivity (130 μmhos/cm @ 23°C) increase, peaking in August or September. Colour ranges from 60 to 120 Pt-Co units. The pond is very shallow with a maximum depth of 1.3 m. and mean depth of 0.6 m. Water levels may drop as much as .3 m. towards late summer.

Few macrophytes inhabit the lake itself although rushes are abundant along the margins. Floating leaved macrophytes, N. variegatum and Nymphaea odorata are limited to the northern end of the pond. The sand and gravel along the eastern shore support Eriocaulon septangulare. A Utricularia species is visible in shallow water, most densely at the southern end. Benthic algae collect at the southern end as a result of sorting by wind and water.

The great exposure of the pond, low macrophyte development, and shallow waters permit continuous mixing. Disturbance of the sediments releases the distinct odour of hydrogen sulfide. In winter, much of the pond bottom may freeze.

In 1981 Procladius and Paratanytarsus accounted for 48% and 21% of the chironomid fauna respectively. The remaining 31% is divided among Tanytarsus, Cryptochironomus, Ablabesmyia, Dicrotendipes, Cladopelma, Psectrocladius, Stempellinella, Polypedilum, Lauterborniella, and ten other genera. Paratanytarsus was much more abundant during the summer of 1981 than 1980 (Table 8). None of these genera account for more than 6% of the total. Densities of chironomids averaged 2400 individuals/m^2.

Densities of benthos (Table 5) are highest at the southern end of the pond where benthic algae collect. Amphipoda and Ephemeroptera contribute a significant proportion of the benthos.

TABLE 5

Portey Pond: Cumulative Abundance (= Total Number of Chironomids Collected from April, 1981 to March, 1982) of Each Chironomid Taxon at Each Sampling Station in Portey Pond.

	Site														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Procladius	16	16	25	41	27	24	18	20	12	20	50	55	14	26	16
Paratanytarsus	28	30	17	3	3		14	6	1	5	1	5		30	22
Tanytarsus	8	5	2	2	2	1	3	4	1	1	4		3	4	1
Dicrotendipes	10	1	1		2	2				2	1				2
Polypedilum	8	2	2				2			1	1	1	1	1	
Cladopelma	2	9	4	2						2					
Cryptochironomus	1	5	1		2	5	1	9	1		1	4		1	2
Lauterborniella	2	10						1							
Psectrocladius	7	3	3	1		1	1				1				1
Cricotopus	1	2	1												2
Ablabesmyia	5	3	1	1		1	4		2		4	1	1	1	3
Pseudochironomus						2	1								4
Glyptotendipes								1				1			1
Pagastiella				1								1			1
Paratendipes															1
Chironomus	1														
Microtendipes						1	1	1		1		1			1
Phaenopsectra															2
Stictochironomus															1
Stempellina		3		2				1				1			
Stempellinella	4	7	2	1	1		1		1				1	1	
Corynoneura			1												

Figure 10. Seasonal distribution of _Procladius_, and _Paratanytarsus_ and instars II to IV for these species in Portey Pond. (Densities expressed as thousands/m^2.)

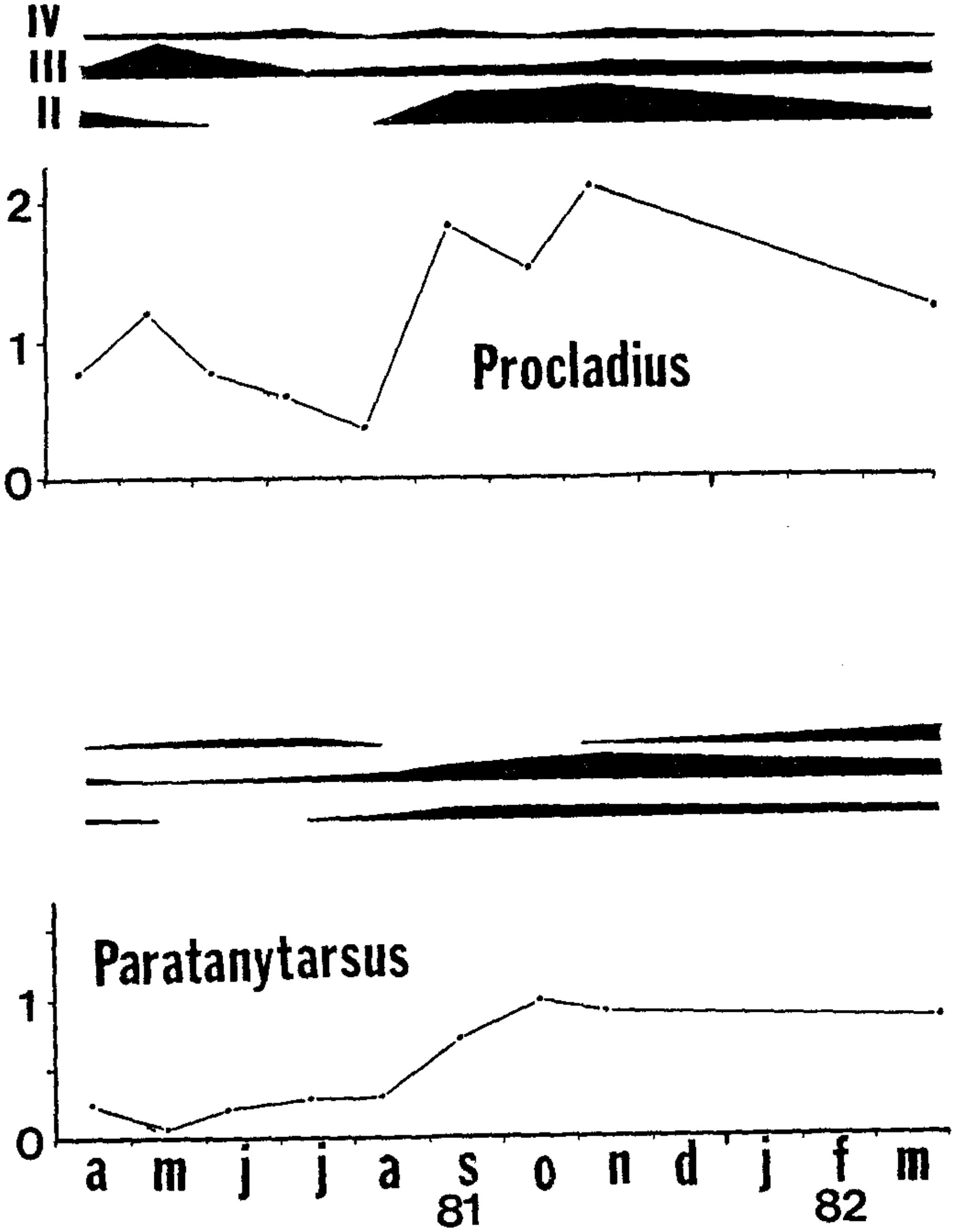
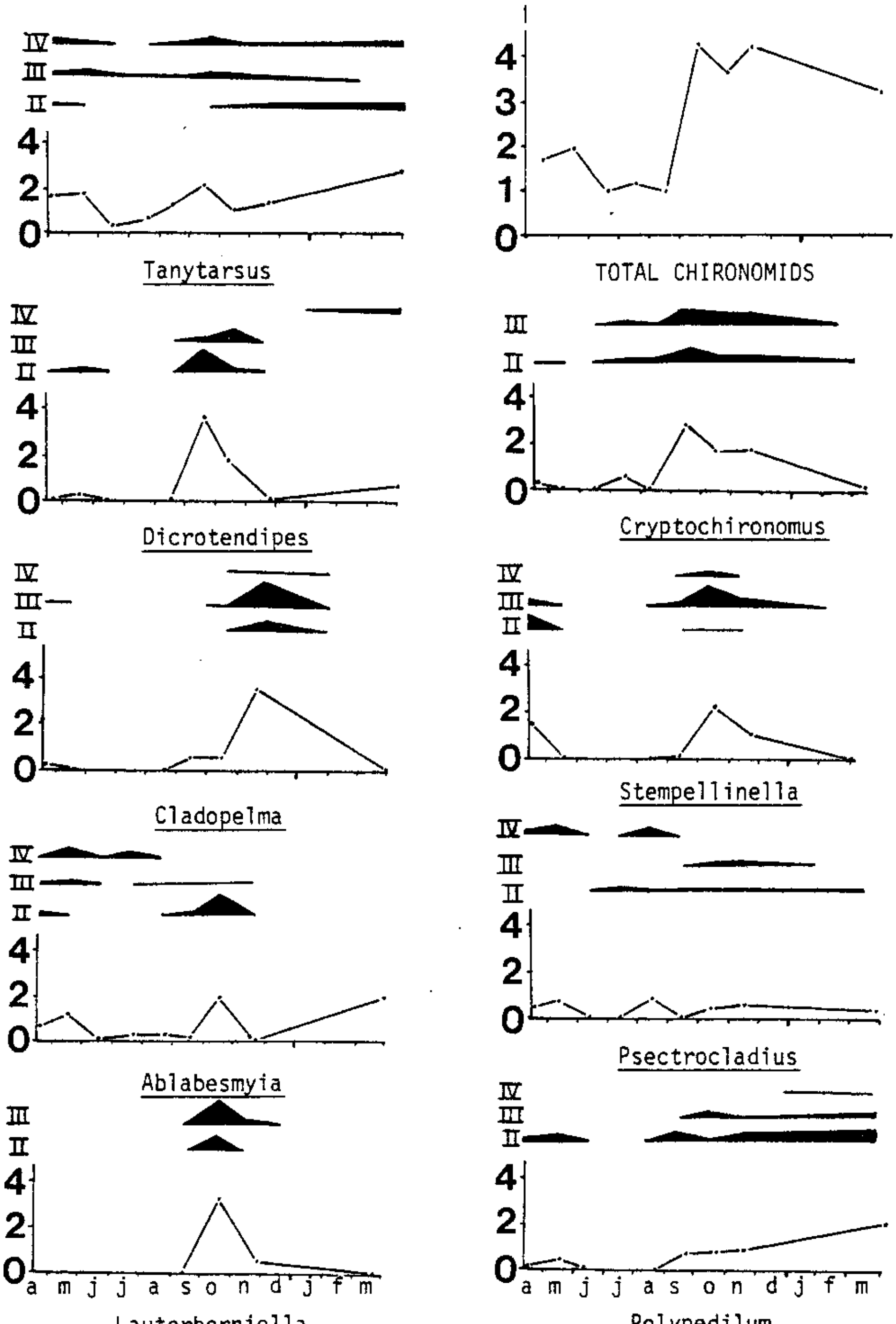

IV
III
II
2
1
0
Procladius
Paratanytarsus
1
0
a m j j a s o n d j f m
81
82

Figure 11. Seasonal distribution of the remaining* chironomid taxa and the seasonal distribution of the total Chironomidae in Portey Pond. (Total Chironomids expressed as thousands/m^2, all others expressed as hundreds/m^2.)

*Several of the rarest taxa have been excluded.


Tanytarsus
TOTAL CHIRONOMIDS
Dicrotendipes
Cryptochironomus
Cladopelma
Stempellinella
Ablabesmyia
Psectrocladius
Lauterborniella
Polypedilum
IV
III
II
0
1
2
3
4
a m j j a s o n d j f m

Densities of chironomids are lowest during mid-summer (Fig. 10,11). Procladius and Paratanytarsus, the two principal genera emerge during this period. This would appear to hold for many of the remaining genera. The simultaneous recruitment of individuals from many genera is apparent in September. Low water levels in September 1981 exposed marginal zone sediments and associated habitats. Species inhabiting the marginal zone may have been forced to retreat towards the pond's centre.

Folly Lake

Folly Lake (Fig. 12a) is a comparatively large lake, approximately 2 km long, with a 3.3 m maximum depth. The waters are moderately acidic (pH = 4.4 to 5.3) and coloured (60 to 125 Pt-Co units). Erosion at the eastern end, a consequence of the large fetch, has exposed a sand substrate. The region colonized by macrophytes is small relative to the lake's area. *Nuphar variegatum*, *Nymphaea odorata*, *Brasenia schreberi*, *Typha latifolia*, *Juncus* sp., *Potamageton*, *Sparganium fluitans* and *Utricularia* sp. are present. *Brasenia schreberi* is most abundant. *Nymphaea* persists in the lake, yet most plants fail to produce flowers. This may indicate recent acidification of this lake, followed by the vegetative persistence of these plants.

The two principal chironomid taxa, *Tanytarsus* and *Procladius* account respectively for 24% and 23% of the total number of chironomids sampled. Rarer taxa included *Glyptotendipes*, *Harnischia* cf. *curtilamellata*, *Stictochironomus*, *Phaenopsectra*, *Cladopelma*, and twelve others. Comparable results (Table 8) were obtained during the

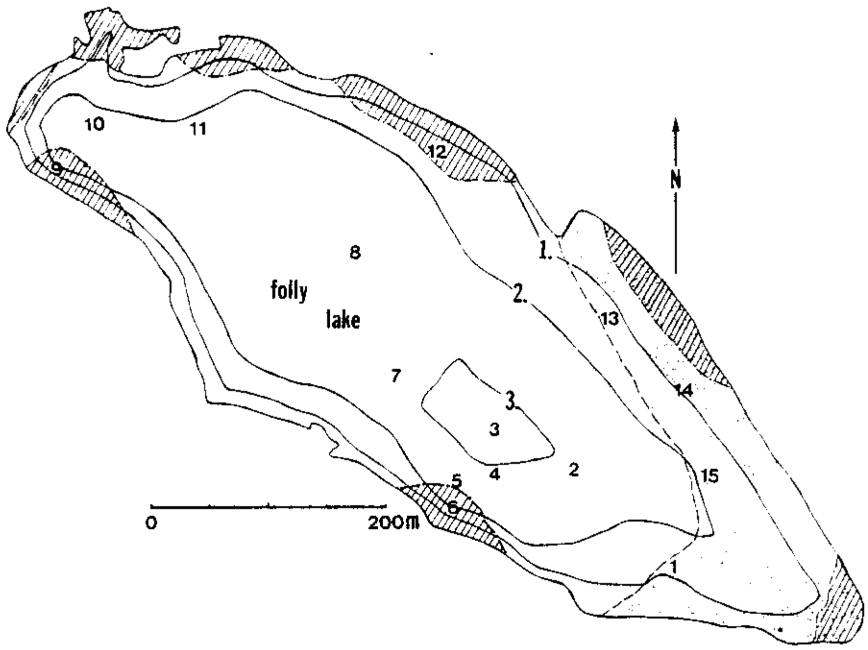
Figure 12. Maps of depth (contour depths given in metres), macrophytes, substrate, and sampling stations.

a) Folly Lake

b) Fox Creek Lake

macrophytes

sand


folly
lake
N
10
11
12
9
8
1.
2.
13
7
3.
3
14
2
4
5
15
6
1
0
200m

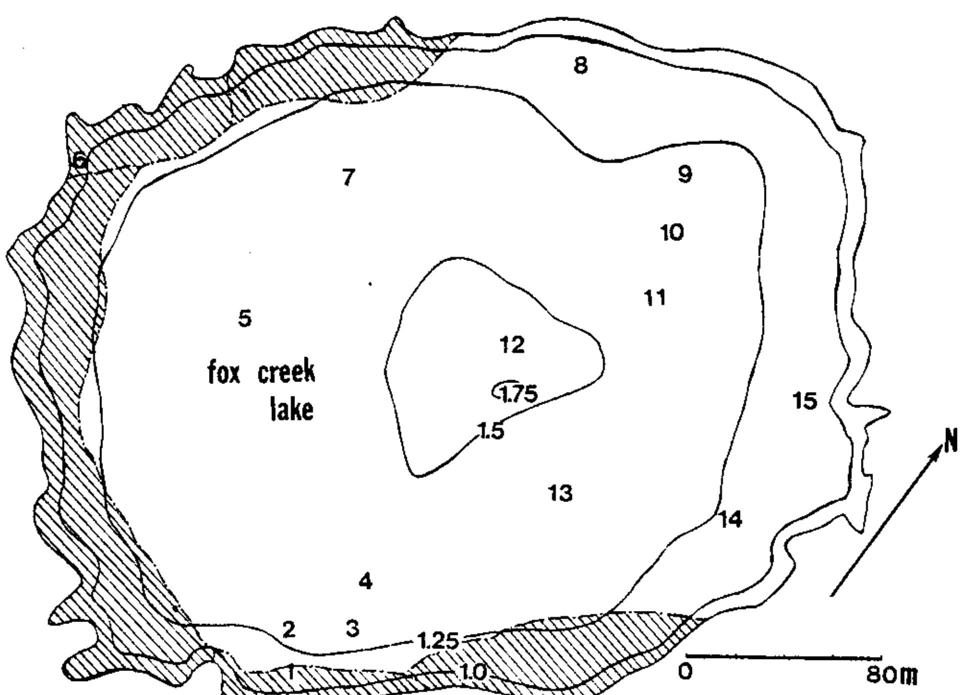

fox creek
lake
8
7
6
9
10
11
5
12
1.75
1.5
15
13
14
4
2
3
1.25
1
1.0
0
80m
N

TABLE 6

Folly Lake: Cumulative Abundance (= Total Number of Chironomids Collected from April, 1981 to March, 1982) of Each Chironomid Taxon at Each Sampling Station in Folly Lake.

	Site														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Tanytarsus	5		1	1	6	1	1	3	1	5	6	14	5	4	1
Procladius		2	5	5	6	5	6	6	6	5	2	6			
Glyptotendipes	2				1	1						21	1	2	
Harnischia cf. Curtilamellata	4	1	1					1				2			6
Stictochironomus	7												3	1	1
Phaenopsectra					4	4			3			1	1		
Cladopelma		1	1	1	2	5		1				1			
Ablabesymia					1							1			
Polypedilum												3			
Endochironomus	1														
Zalutschia												6			
Heterotanytarsus													1		
Heterotrissocladius	1										1	1			
Psectrocladius	1											1			
Dicrotendipes				1								1			
Diplocladius									1						
Chironomus			2	1				1				1	1	1	
Cryptochironomus									1	1		1			
Paratanytarsus	6												1		
1st Instar Chironominae					1										

Figure 13. Seasonal distribution of Procladius, and Tanytarsus and instars II to IV for these species in Folly Lake. (Densities expressed as hundreds/m^2.)

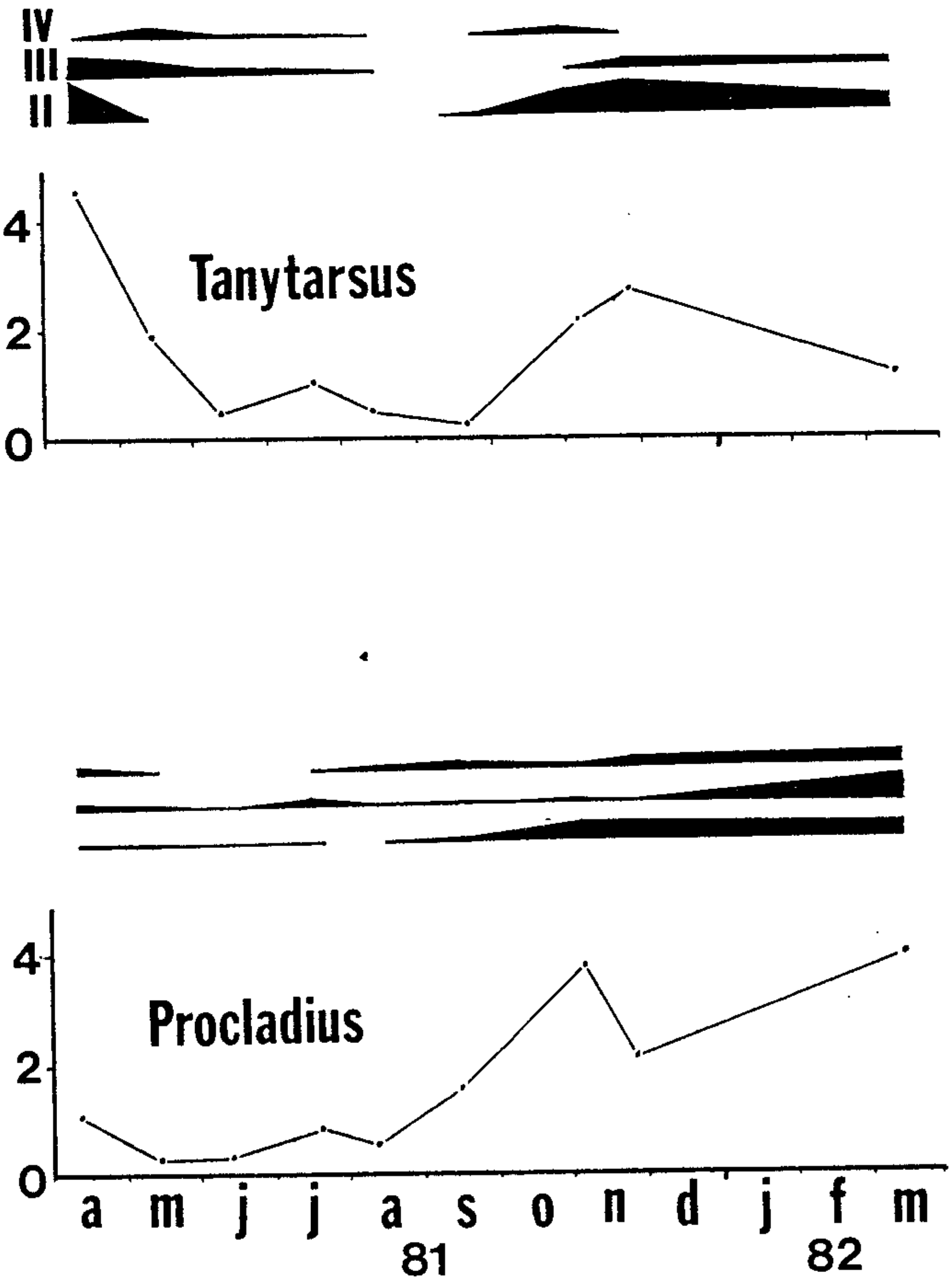
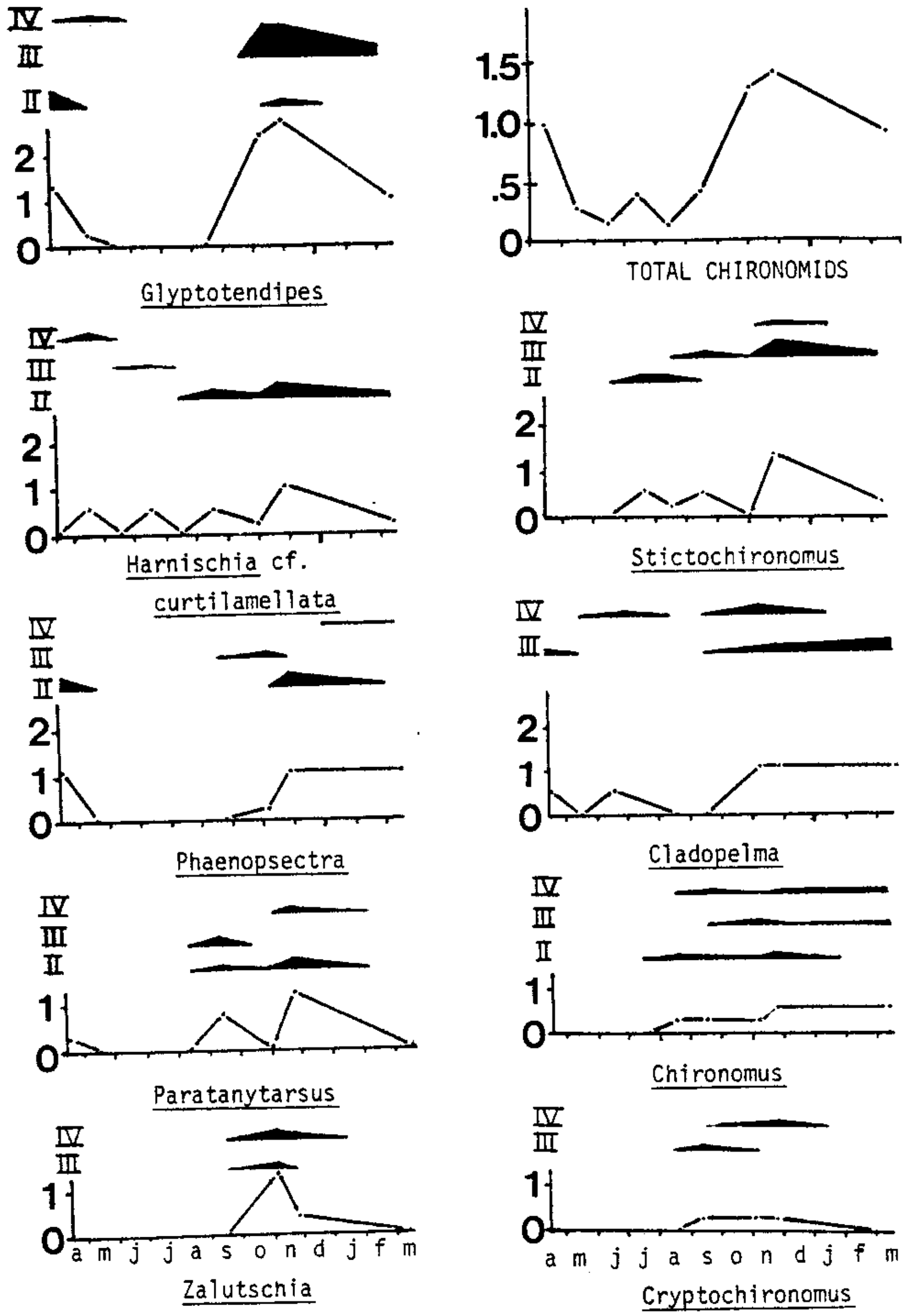

IV
III
II
4
2
0
Tanytarsus
4
2
0
Procladius
a m j j a s o n d j f m
81
82

Figure 14. Seasonal distribution of the remaining* chironomid taxa and the seasonal distribution of the total Chironomidae in Folly Lake. (Total Chironomids expressed as thousands/m^2, all others expressed as hundreds/m^2.)

*Several of the rarest taxa have been excluded.


IV
III
II
2
1
0
Glyptotendipes
1.5
1.0
.5
0
TOTAL CHIRONOMIDS
Harnischia cf. curtilamellata
Stictochironomus
Phaenopsectra
Cladopelma
Paratanytarsus
Chironomus
Zalutschia
Cryptochironomus
a m j j a s o n d j f m

1980 season. The total number of Glyptotendipes collected (14%) may not be representative as 66% of those specimens were collected (Table 6) from a single site (#12). Twenty-six percent of all chironomids were collected at site #12. Polypedilum and Zalutschia were only recorded from this site. Some taxa showed affinities for sand substrates. These included Harnischia cf. curtilamellata, and Stictochironomus. Procladius and Cladopelma were absent from sand.

Densities of chironomids were extremely low in Folly Lake, averaging $660/m^2$. A mid-summer minimum density (Fig. 13, 14) of benthos was observed. As in Portey Pond, recruitment of the two principal genera, Tanytarsus and Procladius, is not apparent until autumn. Many rarer taxa show synchronous life histories.

Fox Creek (Melanson Settlement) Lake

Fox Creek Lake (Fig. 12b) is a weakly acidic (pH = 4.8 to 6.1), peat-enclosed lake. In size this lake is intermediate between Folly Lake and the two ponds. Macrophytes are well-developed near shore, but appear to be limited by depths exceeding 1.3 metres. The maximum depth is 1.7 m. Macrophytes recorded from this lake include Nuphar variegatum, Sparganium fluitans, Utricularia sp., Potamageton, and Typha latifolia. A single remnant plant of Eriocaulon septangulare was observed on the peat at the waters edge.

Four chironomid taxa accounted for 67% of the fauna in 1981. The respective contributions of Microtendipes, Chironomus, Procladius and Tanytarsus were 18%, 17%, 14%, and 19%. Other genera recorded included

TABLE 7

Fox Creek Lake: Cumulative Abundance (= Total Number of Chironomids Collected from April, 1981 to March, 1982) of Each Chironomid Taxon at Each Sampling Station in Fox Creek Lake.

	Site														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Chironomus	5	11	1	2	9	90	5	3	2	2	1	8	3	0	0
Procladius	14	17	4	4	8	17	6	8	10	11	4	2	8	2	3
Microtendipes	14	24	6	5	20	8	1	2	6	15	18	5	2	4	20
Tanytarsus	14	21	9	9	6	0	12	4	13	12	15	10	8	13	15
Paratanytarsus	2	2			1		1	2	1	1	1	3	1	2	
Cladopelma	19	11	2	5	6	5	19		3	1	2	2	1	4	3
Glyptotendipes	3	3		2	3	2	2		2	2	3	2		2	
Dicrotendipes	3	11	5		3	2		1	7	5	5	3	3	3	3
Ablabesmyia							1	1							
Cryptochironomus				1								1		2	
Zalutschia	1					1		1		1					
Monopsectrocladius	2	1					4				3		1	1	
Polypedilum	10	14	6			2		1	3	2	1			6	
Psectrocladius		1				1	1								
Pagastiella				1										2	
Parachironomus					1	15									
Tribelos						5									
1st Instar Chironominae														1	

TABLE 8

Comparison of the Summer Abundance of Some Chironomidae (as % Total Chironomidae) for the Four Lakes in Two Consecutive Years.

Wood's Pond

	1980	1981
Chironomus	50.6	56.9%
Procladius	18.1	28.2
Monopsectrocladius	20.7	10.0
Other Orthocladiinae	2.1	1.2
Tanytarsus	5.8	1.5
Polypedilum	0.6	1.0
Others	-	1.2

Portey Pond

	1980	1981
Procladius	67.4	55.1
Tanytarsus	7.4	6.8
Paratanytarsus	2.9	26.3
Orthocladiinae	1.7	3.4
Ablabesmyia	6.9	1.7
Stempellinella	6.3	-
Others	7.5	6.7

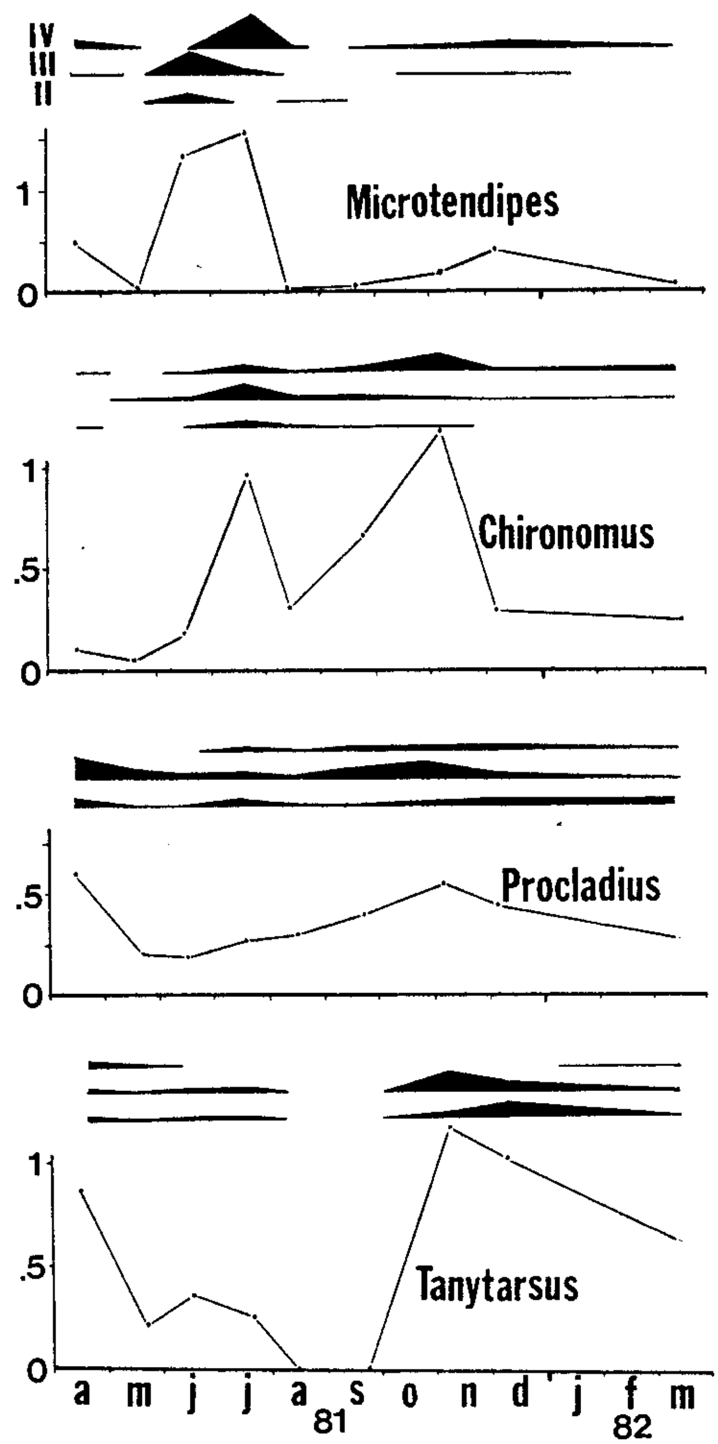
Folly Lake

	1980	1981
Procladius	35.2	24.1
Tanytarsus	34.1	29.6
Paratanytarsus	1.1	5.6
Stictochironomus	5.7	9.3
Harnischia	3.4	11.1
Glyptotendipes	3.4	1.9
Cladopelma	1.1	5.6
Others	15.9	13.0

Fox Creek Lake
(Melanson Settlement Lake)

	1980	1981
Microtendipes	3.3	45.6
Chironomus	9.2	22.4
Dicrotendipes	24.4	0.4
Tanytarsus	22.1	10.0
Paratanytarsus	7.0	1.7
Cladopelma	11.1	-
Procladius	8.5	11.6
Others	14.3	8.2

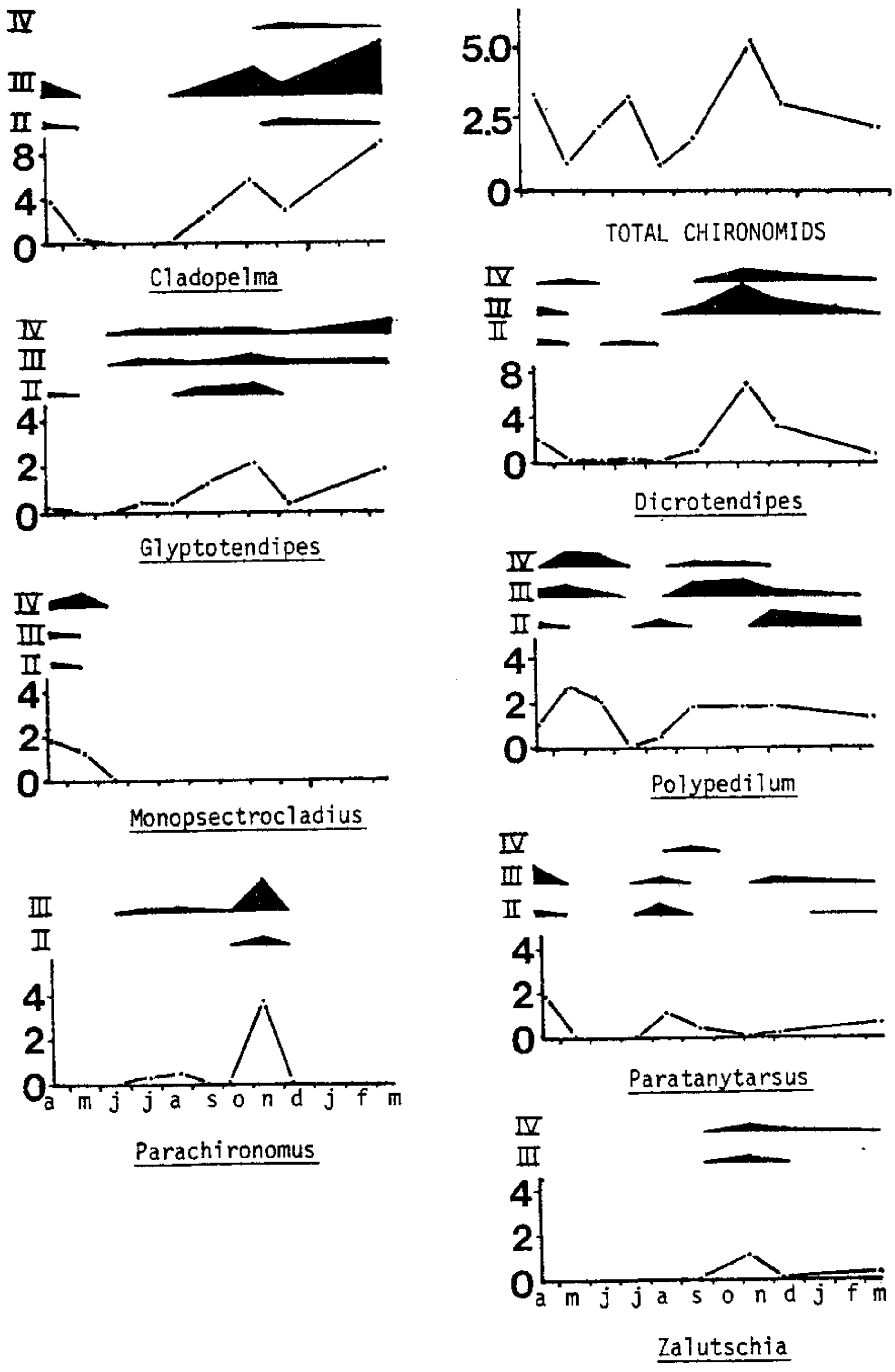
Figure 15. Seasonal distribution of _Chironomus_, _Microtendipes_, _Tanytarsus_ and _Procladius_ and instars II to IV for these species in Fox Creek Lake. (Densities expressed as thousands/m^2.)



IV
III
II
1
0
Microtendipes
1
.5
0
Chironomus
.5
0
Procladius
1
.5
0
Tanytarsus
a m j j a s o n d j f m
81
82

Figure 16. Seasonal distribution of the remaining* chironomid taxa and the seasonal distribution of the total Chironomidae in Fox Creek Lake. (Total Chironomids expressed as thousands/m^2, all others expressed as hundreds/m^2.)

*Several of the rarest taxa have been excluded.



TOTAL CHIRONOMIDS
Cladopelma
Dicrotendipes
Glyptotendipes
Polypedilum
Monopsectrocladius
Paratanytarsus
Parachironomus
Zalutschia
a m j j a s o n d j f m

Cladopelma, Dicrotendipes, Polypedilum, Glyptotendipes, Parachironomus, Paratanytarsus, and eight others. A striking change in the fauna had occurred over one year. Table 8 compares the data for the 1980 and 1981 summer period. The preceding summer, Dicrotendipes, Tanytarsus, and Cladopelma had been most abundant. Densities of chironomids averaged $2500/m^2$.

Two-thirds of all Chironomus larvae (Table 7) were collected from site #6 beneath a very dense patch of Nuphar variegatum. Tribelos and Parachironomus were also strongly aggregated in this region.

Life history patterns for 1981-82 are not as easily interpretable as in other lakes. Total numbers of chironomids were lowest in May (Fig. 15, 16) and August. Microtendipes is bivoltine, accounting for the mid-summer peak in chironomid densities. A similar mid-summer maximum for Chironomus is probably an error. This artifact may result from a strongly aggregated Chironomus distribution. Recruitment of Tanytarsus as in Folly Lake is apparent in autumn. This taxon appears to be univoltine. Two species may account for the population curve prepared for Procladius.

Of the remaining taxa, Polypedilum and Paratanytarsus appear bivoltine. Univoltinism is consistent with the temporal distribution of most other genera.

3.2.2 Discussion

The results of the above investigation document aspects of both the production and the spatial and temporal distributions of benthos in the four lakes studied. Great variations in the density of benthos were apparent. The author believes benthic production is related intimately with primary productivity in these lakes; thus, benthic densities reflect primary production. Although the nutrient data (Table 9) would appear to conflict with this statement, much of the production may be contributed by macrophytes and associated epiphytes, not phytoplankton. Macrophytes may incorporate most of the available nutrients. Carignan and Kalff (1982) demonstrated that nutrients incorporated into macrophyte tissue are not readily available to phytoplankton or epiphytic algae.

Densities of benthos were usually higher among the floating-leaved macrophytes. Interestingly, Monopsectrocladius is associated with regions where macrophyte cover is highest, yet recruitment occurs with the senescence of Nuphar in late summer. Most growth in Monopsectrocladius is completed in autumn with no macrophytes present. The author speculates that the decaying macrophyte leaves and associated microflora may provide important forage for this species. Senescing macrophytes may also release nutrients stimulating phytoplankton in autumn (Landers 1982). It has been noted in streams that many shredders have life histories synchronized with the input of leaf litter (Waters 1979; Anderson and Cummins 1979).

Although life history data may well reflect life strategies, the significance of the temporal distribution of Chironomidae, and their timing of growth and reproduction has largely been ignored (Butler 1982). Recruitment by taxa in autumn, may indicate the importance of senescent

TABLE 9

Analyses of Nutrient Concentrations in the Waters of the Four Lakes

in May 1981.

	Nutrient Data (mg/1)			
	Wood's Pond	Portey Pond	Folly Lake	Fox Creek Lake
Total Phosphorous	.025	.043	.030	.065
Total Organic Carbon	26	15	11	16
$NO_3 + NO_2$	$<.01$	$<.01$	$<.01$	$<.01$
N in NH_4	0.15	0.13	0.15	0.15
Total N	0.58	0.51	0.46	0.88
C/N	45	30	24	18

macrophytes and leaf litter as a food resource. Algal production and bacterial decomposition should be greatest in summer, assuming constant supplies of nutrients. Recruitment in spring and early summer may reflect the importance of this potential food to genera like Chironomus.

Many of the large Chironomini, including Chironomus, Microtendipes, Phaenopsectra, Dicrotendipes, and Glyptotendipes are filter-feeders. The Tanytarsini, small Chironomini, and Orthocladiinae are usually collector-gatherers (Merritt and Cummins 1978; Mozley 1982).

In light of the above speculation, the seasonal distribution of the total chironomid densities in each lake, may reflect available food. Whereas, Portey Pond and Folly Lake are distinguished by having the most abundant chironomids (collector-gatherers) recruiting in autumn, the Chironomidae in Wood's Pond and Fox Creek Lake are more evenly distributed over the season. Here, epiphytes may contribute more to production than phytoplankton. Densities of benthos were usually higher among the floating-leaved macrophytes than elsewhere. Certain Chironomidae show affinities to macrophyte cover. Other taxa were limited to sand substrates.

3.3. Biocenoses-Thanatocenoses Comparison

If subfossil chironomids are to accurately reflect the fauna of a lake at any given time during its history, a number of conditions should be met. These are listed below.

1) Head capsules of all species must be equally resistant to degradation.

2) All species must complete their life cycles over a period of approximately the same duration.

3) All species should have similar mortality rates (since early instars are poorly preserved).

4) Head capsules of each species must not be sorted by currents in the lake.

5) Old and new sediments should not be mixed.

The degree to which the above conditions are satisfied will determine the strength of the thanatocenosis-biocenosis relation. The results of the comparisons are summarized in Tables 10-13. For each lake, the results are discussed separately.

3.3.1 Results

Wood's Pond

Table 10 summarizes the relation among the fauna of the 1981-82 season, the subfossils of the surficial sediments, and the upper 40 cm of a core (Walker 1980) previously examined. The core was taken from the maximum depth (2 m) of the present lake. Surficial sediments had been collected from shallower sites (1.3 m) distributed throughout the remainder of Wood's Pond (Figure 11). The results demonstrate that a rough relation exists between subfossil chironomids of the surficial sediment, and the present fauna. *Chironomus* and *Monopsectrocladius* are two of the most abundant genera in both the sediments and the present fauna. *Procladius* is substantially under-represented in the sediments. Most other genera are recorded in the sediments in approximately the

TABLE 10

Wood's Pond:

Comparison of the Relative Abundances of Chironomidae as Subfossils in Surficial Sediments, and as Components of the Present Fauna.

	LIVE (%)	SUBFOSSIL CORE (%)	SUBFOSSIL SURFACE (%)
Monopsectrocladius	23.8	11	16.6
Zalutschia	4.2	4	7.0
Psectrocladius	0.9	3	7.0
Diplocladius	0.1		
Heterotanytarsus			0.7
Corynoneura			1.3
1st Instar Orthocladiinae			1.3
Chironomus	41.7	41	20.9
Cladopelma	0.9	12	2.0
Polypedilum	1.5	5	4.7
Dicrotendipes	0.1	3	1.0
Parachironomus	0.1		
Microtendipes	0.2		0.7
Phaenopsectra	0.2		
Lauterborniella	0.1		
Paratendipes			0.7
Tanytarsus s.lat.	1.1	12	20.9
1st Instar Chironominae	0.2		6.0
Procladius	23.9	6	6.0
Ablabesmyia	1.2	3	3.3

same abundance as they presently occur. One important exception is Tanytarsus. Although present as only a trace in the present fauna, it is second only to Chironomus in the sediments. A radio-carbon date determined for the upper 10 cm of sediment in the vicinity of the maximum depth produced an anamolously old date (540+/-80 yrs). Pollen and charcoal evidence (Walker 1980) indicate however that the upper 40 cm of sediment had been deposited since settlement (beginning ≈1700). Chironomus dominated throughout the settlement period while Tanytarsus was dominant prior to settlement. In situ mixing of pre-settlement and settlement sediments should have eliminated a sharp boundary such as this. It is suggested that old sediments are being eroded in shallow water, mixed with recent sediment, and redeposited in the deep-water zone. The ratio of Tanytarsus to Chironomus in the shallows and core indicate that between 25% and 50% of the sediment is derived from the pre-settlement period. The head capsules of Procladius are thin, very different in structure to most other Chironomidae, and appear to be easily degraded. Goulden (1964) also noted this phenomenon.

Portey Pond

The results for Portey Pond are presented (Table 11) in a manner similar to that for Wood's Pond. Procladius was noted to be drastically under-represented in the sediments and was excluded from the thanatocenosis-biocenosis comparison. It is assumed that the head capsules of Procladius are poorly preserved. Exclusion of Procladius

TABLE 11

Portey Pond:

Comparison of the Relative Abundances of Chironomidae as Subfossils in Surficial Sediments, and as Components of the Present Fauna.

		SUBFOSSIL	
	LIVE (%)	CORE (%)	SURFACE (%)
Procladius	48.2	6.7	7.3
excluding Procladius:			
Ablabesmyia	6.6	6.7	10.7
Labrundinia			0.7
1st Instar Tanypodinae			0.7
Paratanytarsus	39.9	55.3	38.7
Tanytarsus	10.0		
Stempellinella	4.6	3.4	2.6
Stempellina	1.7		
Lauterborniella	3.2	1.1	3.0
Dicrotendipes	5.1	5.6	7.5
Cladopelma	4.6	2.2	0.7
Stictochironomus	0.2	4.5	2.2
Phaenopsectra	0.5		
Polypedilum	4.6	5.6	7.4
Cryptochironomus	7.8	2.2	2.2
Glyptotendipes	0.7	1.1	0.7
Pseudochironomus	1.7		4.8
Pagastiella	0.7		0.7
Paratendipes	0.2		
Chironomus	0.2		
Microtendipes	1.5		5.5
1st Instar Chironominae			2.2

TABLE 11

Portey Pond:

Cont'd.

		SUBFOSSIL	
	LIVE (%)	CORE (%)	SURFACE (%)
Cricotopus	1.2	1.1	3.3
Psectrocladius	4.4	7.8	1.8
Monopsectrocladius			0.7
Corynoneura	0.2		0.7
Zalutschia		1.1	2.6
Other Orthocladiinae	0.2		1.5

from the comparison produces a satisfactory biocenosis-thanatocenosis relation.

The shallow waters of Portey Pond must permit sediment disturbance in excess of that in Wood's Pond. This is supported by erratic pollen data in the sediment core (Walker unpublished data). The apparently good correlation between the thanatocenoses and biocenoses may result from long term stability in the chironomid fauna. The core data (Walker unpublished data), although of limited value in this discussion, gives no evidence of any major faunal shifts since the early post-glacial period.

Folly Lake

Table 12 includes percentages for Folly Lake. As noted in both Portey and Wood's Ponds, Procladius is under-represented. Exclusion of Procladius from the comparison yields comparable figures for Tanytarsus biocenoses and thanatocenoses. Glyptotendipes, Harnischia cf. curtilamellata, and Stictochironomus were much more common in the 1981-82 collections than in the sediments. Harnischia and Stictochironomus occur only on the sand substrates. No surficial sediments were examined from these sites. These chironomids probably burrow into the sand. Their head capsules may not be transported to other zones in the lake. If they were transported, abrasion by sand could destroy these head capsules. As noted in the preceding section, 66% of the Glyptotendipes larvae collected were recovered from a single site. This site appears not to be representative of the lake. Psectrocladius, Polypedilum, and

TABLE 12

Folly Lake:

Comparison of the Relative Abundances of Chironomidae as Subfossils in Surficial Sediments, and as Components of the Present Fauna.

	LIVE (%)	SURFACE (%)
Procladius	22.6	10.8
excluding Procladius:		
Ablabesymia	1.1	3.0
Labrundinia		0.4
Tanytarsus	29.5	32.6
Paratanytarsus	3.9	
Stempellinella		0.8
Glyptotendipes	18.0	3.8
Harnischia cf. curtilamellata	8.4	
Stictochironomus	6.7	0.8
Phaenopsectra	7.3	2.3
Cladopelma	6.7	3.8
Polypedilum	1.7	6.1
Endochironomus	0.6	1.5
Dicrotendipes	1.1	9.1
Chironomus	4.5	3.8
Cryptochironomus	1.7	
Parachironomus		0.8
Pseudochironomus		2.3
Microtendipes		1.5
1st Chironominae	0.6	2.3
Zalutschia	3.4	5.3
Heterotanytarsus	0.6	3.4
Heterotrissocladius	1.7	2.3

TABLE 12

Folly Lake:

Cont'd.

	LIVE (%)	SURFACE (%)
Psectrocladius	1.1	11.8
Monopsectrocladius		2.3
Diplocladius	0.6	

Dicrotendipes are over-represented in the sediment. These are genera often reported in close association with macrophytes. The sampling methods employed may not have been adequate for these phytophilous species.

Fox Creek Lake

As noted previously, striking changes were observed in the fauna of Fox Creek Lake over a single year. Sediment analyses cannot hope to resolve such sudden change. A comparison (Table 13) of the 1981-82 fauna, with the sediments illustrates this problem. Chironomus, Procladius, and Microtendipes are poorly represented in the sediments. The proportion of Tanytarsus in the sediments exceeds their present abundance in the benthos. It is suggested that recent eutrophication has produced rapid successional changes in the lake. Wastes from a nearby pig farm contaminate an intermittant stream which leads to the adjacent bog mat. This stream does not feed directly into the lake during summer, autumn, or winter. Spring floods may flush waters across the bog into Fox Creek Lake, however.

3.3.2 Discussion

Iovino (1975) concluded that generally a good relation existed between biocenoses and thanatocenoses. Sediment mixing posed special problems for shallow lakes. If subfossils of surficial sediment are to accurately represent extant chironomid communities in shallow lakes, either little mixing of sediment should occur, or stability must have

TABLE 13

Fox Creek Lake:

Comparison of the Relative Abundances of Chironomidae as Subfossils in Surficial Sediments, and as Components of the Present Fauna.

	LIVE (%)	SURFACE (%)
Procladius	13.9	7.8
Ablabesmyia	0.2	4.2
Chironomus	16.7	5.7
Microtendipes	17.7	8.6
Cladopelma	9.8	3.0
Dicrotendipes	6.4	6.8
Polypedilum	5.3	8.0
Glyptotendipes	3.1	1.5
Cryptochironomus	0.2	1.2
Parachironomus	1.9	0.9
Pagastiella	0.4	
Tribelos	0.5	
Stictochironomus		0.9
Phaenopsectra		2.3
Lauterborniella		1.1
Pseudochironomus		1.5
Paratendipes		1.2
Tanytarsus	19.0	34.2
Paratanytarsus	2.0	
Stempellinella		2.0
1st Instar Chironominae	0.1	2.8
Zalutschia	0.6	
Monopsectrocladius	1.4	0.9
Psectrocladius	0.4	3.5
Heterotrissocladius		1.1
Cricotopus		1.1

existed in the chironomid fauna over an extended period. The first condition, little mixing of sediment is clearly violated in shallow lakes such as those investigated. Sediment has been deposited in these lakes at an average rate in the order of only 1 mm/year. As a result of mixing of sediments, the surficial samples collected must represent an "average" chironomid fauna deposited over an extended period. The results from Wood's Pond suggest that this period may be measured in the order of hundreds of years. In Wood's Pond, sediment mixing has produced a "hybrid" thanatocenosis of the present "*Chironomus-Monopsectrocladius*" fauna, and the pre-settlement *Tanytarsus* association.

The head capsules of *Procladius* appear to be poorly preserved in all the lakes. This had also been noted by Goulden (1964). In Portey Pond, the stability of the chironomid fauna over an extended period produces a good biocenosis-thanatocenosis relation despite extensive sediment mixing.

The depauperate benthos of Folly Lake contributes large errors to estimates of the present faunal composition. The phytophilous chironomid fauna, which was not sampled, appears to have contributed significantly to the Chironomidae present in the sediments.

Studies of sediment in shallow lakes cannot hope to resolve sudden faunal changes as are apparent in Fox Creek Lake.

Palaeoecological studies have limited application for shallow lakes due to the problems outlined above. Short term changes cannot be resolved. The resolution is sufficient only for long-term changes, spanning a period of hundreds of years or more. Even in these studies caution must be exercised in the interpretation.

An interesting feature is the recovery of 1st instar chironomids as subfossils from the sediments of all four lakes. These have not previously been reported. Iovino (1975) was able to partially account for their absence due to resorption of the 1st instar head capsules during ecdysis. The head capsules of 1st instars dying prior to ecdysis would still be expected in the sediments however.

IV. Summary

The present investigation has assessed the value of the Chironomidae as palaeoecological indicators for shallow, dystrophic waters. It is apparent that the chironomid fauna of lakes is eurytopic, existing over a broad pH range. Many other invertebrates appear more responsive to pH changes. Striking changes in the fauna are apparent only in the latter stages of bog lake evolution. At this point, conditions approach those existing in the pools of Sphagnum peatlands. A "Chironomus-Monopsectrocladius-Psectrocladius" association typical of peat-pools eventually replaces the "Tanytarsini-Procladius" fauna characteristic of shallow, humic lakes. The physical, chemical, and biotic factors accompanying this succession are complex. Psectrocladius, Monopsectrocladius, and other genera displayed affinities to macrophyte cover. The author has speculated as to the significance of the temporal distribution of chironomids in humic waters.

Mixing of sediments imposes difficulties in the interpretation of subfossil assemblages. The resolution is sufficient only for investigations of long-term successional changes spanning hundreds or thousands of years. The thin head capsules of Procladius were consistently under-represented in the sediments. It is suggested that Procladius head capsules are not as resistant to decomposition or mechanical damage. For other genera, a good relation probably exists between biocenoses and thanatocenoses. Mixing of sediment obscures this relation. Where benthic chironomid production is low, the phytophilous fauna may contribute significantly to the thanatocenoses.

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