PAST AND PRESENT BENTHIC FAUNA OF LAKE MARATOTO WITH SPECIAL REFERENCE TO THE CHIRONOMIDAE

A thesis

presented to the

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for the Degree

of

Doctor of Philosophy

by

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Frontispiece - *Chironomus zealandicus*, SEM photo of larval head.

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Page	
19	In caption to Figure 1.6 add: 'Darkened areas indicate periods of low oxygen tension.'
55,61,127	In captions to Figures 2.3, 2.5 and 3.6 add: 'Mean = mean total larval density as defined on page 43. For each station n = 5.'
60,140	In captions to Figures 2.4 and 3.8 add: 'Each point is the "grand mean" of five replicate samples taken fortnightly from 5/3/79 to 12/3/80.'
98,100	In captions to Figures 3.1 and 3.2 add: 'Descriptive statistics for these data are listed in Table 3.1.'
124	In caption to Figure 3.3 add: 'n = 5 for all stations on each sampling date.'
125	In caption to Figure 3.4 add: 'Curve drawn using mean total numbers as defined on page 43.'
126	In caption to Figure 3.5 add: 'Values given are the percentage composition of the estimated total lake population shown in Figure 3.4.'
133	In caption to Figure 3.7 add: 'Values given are the mean total numbers for each larval instar as defined on page 43.'
150	In Table 3.4 column 4, 26/3/80 should be read as 2, 21, 65.
166	Line 4 should read: 'Microfossil remains were determined using a modification of the methods of Deevey (1942, 1955). A 1 ml ...'
187	In caption to Table 4.9 add: 'Rank values determined from limnological characteristics given in Table 4.1, visual inspection and aerial photographs and maps of the lakes.'

ABSTRACT

The benthic fauna of Lake Maratoto, a eutrophic dy (dystrophic) lake in the Waikato basin, was investigated from 19/9/78 to 13/3/80. Core samples were taken at approximately fortnightly intervals from six stations of varying depths. Fifty taxa were recognised and the distribution and seasonal abundance of the 20 major ones is given together with notes on their biology. A major emphasis was placed on Chironomidae which, after oligochaetes, were the most numerous benthic macroinvertebrates encountered.

The fauna had a clumped distribution and was concentrated on the edge of the lake. This was due to higher food supplies and more diverse sediment types on the edges and anoxic conditions in the centre. Some re-distribution of the fauna occurred during periods of wind turbulence but planktonic activity in the Chironomidae was of short duration.

The annual mean standing crop of chironomid larvae was 2970 per sq. m. This was made up of 40% Calopsectra funebris, 37% Chironomus zealandicus, 5% Kiefferulus opalensis, 5% Tanypodinae, and 1% Podonominae and Orthocladiinae. Photographs of some of the distinguishing features of the chironomid taxa identified are given as well as measurements for separating larval instars.

Recruitment in the chironomids was continuous but with periods of increased rates. Species with dissolved haemoglobin in the blood (e.g. Chironomus zealandicus and Cladopelma curtivalva) increased in numbers during the summer, while in winter, species which lacked this trait e.g. Calopsectra funebris were more abundant. Lowest numbers were recorded in the spring. It is hypothesised that increases in larval numbers are

linked to algal production and eventual sedimentation of autochthonous organic matter.

Principal component analyses were used to predict the limnological characteristics of a lake from knowledge of its surficial sediment chironomid remains. Dystrophic lakes were characterised by high numbers of most species, particularly Kiefferulus opalensis, Tanypodinae, Calopsectra spp. and Paucispinigera spp. but low numbers of Paratanytarsus agameta. Clear lakes had proportionally more Corynocera sp. and Cladopelma curtivalva while lakes which were dominated by Paratanytarsus agameta, Orthocladiinae and Polypedilum spp. were productive and/or turbid.

The developmental history of Lake Maratoto since its formation 17,000 years ago was studied by analysis of chironomid remains from a 4 m sediment core. Numbers of fossils were low initially but climatic improvement about 14,000 yr B.P. led to an increase which culminated at 5,000 yr B.P.. Peat, which began to develop close to the lake about 12,000 yr B.P. had significant effects in the top section of the core, with maximum influence on the fauna about 7,000 years ago. Other changes in the core were largely expressions of climatically controlled fluctuations of water level which altered the area of the littoral zone.

Twelve stratigraphic zones of chironomid microfossils were derived from cluster and multiple discriminant analyses. These are discussed in relation to zones derived from pollen, stratigraphy and chemical analyses of the sediments.

Key words: Benthos, Chironomidae, Lake Maratoto, palaeolimnology, surficial sediments, Waikato lakes.

ACKNOWLEDGEMENTS

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CONTENTS

Page

CHAPTER THREE: CHIRONOMIDAE FROM LAKE MARATOTO AND OTHER WAIKATO LAKES

CHAPTER FOUR: LIVING AND FOSSIL LARVAL CHIRONOMID LARVAE AND THEIR REPRESENTATIVENESS IN SURFICIAL SEDIMENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF PLATES

CHAPTER 1

INTRODUCTION

1.1 RATIONALE AND OBJECTIVES

In 1977, a survey of the small lakes in the Waipa County was undertaken by the University of Waikato for the Waipa County Council (Chapman and Boubée 1977). Of the 22 lakes examined, Lake Maratoto was found to be the least modified by agricultural practices. This lake, bordered to the west by the Rukuhia peat swamp, was dystrophic and had remained in this state, largely because of the difficulties and economics of developing the deep peat that surrounded it. There was also a strong willingness by the owners to retain it in a near natural state.

Although lakes of the same type as Lake Maratoto were once prevalent in the Waikato Basin, clearing of the native vegetation, drainage of the swamps and increased nutrient inflow have greatly altered most of them so that many are now either dried up or reduced to swampy hollows. Among the lakes remaining, Lake Marototo is unique in having a large buffer of scrub and native vegetation along its shore and in being flanked by about 25 hectares of untouched peat swamp. On the shore of the lake there are still the remains of an artificial island pa (1) with some well preserved pallisade posts. Scattered throughout the lake are many wooden artifacts, including a number of canoes which have been preserved by the acidity and low oxygen content of the water.

Increases in agricultural development of the lake catchment, including the continuing drainage and clearing of the Rukuhia peat swamp, are unfortunately starting to irrevocably alter the lake. It was important therefore that baseline information be obtained for future

(1) Fortified Maori village built on man-made mound and surrounded by swampy grounds.

assessment of the lake's rate of eutrophication, the knowledge gained being applicable to many other lakes in the Waikato region.

Humic lakes, such as Lake Maratoto, are particularly amenable to comprehensive ecological studies as they contain only a limited number of recognisable habitats. They have also a low trophic diversity but are not necessarily unproductive, enabling patterns to be easily discernible. This study, which deals mainly with the benthic fauna of the lake, is part of an extensive and ongoing research programme on the Waikato lakes undertaken at the University of Waikato which includes: zooplankton (M. A. Chapman and J. D. Green), phytoplankton (M. K. Etheredge), basin morphology and stratigraphy (J. D. Green and D. J. Lowe), vegetation (A. S. Edmonds), palaeolimnology (J. D. Green).

The benthic fauna of lakes is an important link in the food chain. It has received considerable attention overseas, but as yet is a poorly known aspect of New Zealand's limnology. In Lake Maratoto, the chironomids form a numerically important component of this benthic fauna, and are probably the most important single group in terms of biomass. Most chironomid larvae are microphagous in their feeding habits and in their turn are widely eaten by many aquatic carnivores, including eels, which form the basis of an important fishing industry in the Waikato. Adult midges are also widely eaten by a variety of birds.

Chironomids have been shown to be good indicators of environmental conditions and are therefore useful for studies on the classification of present day lakes. Yet, in New Zealand, primarily because of incomplete taxonomy, the distribution, seasonal abundance and adult emergence patterns of the various species of chironomid are little known.

Chironomids are also useful for palaeolimnological studies as they leave recognisable remains in the sediments. However, this study is the first attempt to use them to trace lake history in New Zealand.

The objectives of this thesis were accordingly formulated as follows:

1) To determine the limnological characteristics of Lake Maratoto (Chapter 1).

2) To document the taxonomic composition of the fauna (Chapter 2).

3) To supplement present information on aquatic invertebrate life histories and ecological requirements (Chapters 2 and 3).

4) To analyse seasonal and depth changes in the abundance of the benthic fauna, notably of the chironomids (Chapter 3).

5) To determine the usefulness of chironomid larvae and of their remains in the assessment and classification of lakes (Chapter 4).

6) To analyse the chironomid fossils in Lake Maratoto sediments and make inferences on the climatic and other changes during the lake's history (Chapter 5).

1.2 DESCRIPTION OF LAKE MARATOTO

Lake Maratoto (37' 53.2"S, 175' 18.2"E) is a small acid, humic stained lake on the edge of the Rukuhia swamp, in the Waikato basin (Figure 1.1). It is one of a series of small lakes formed by the aggradation of sediments from the old Waikato River system (McCraw 1967). Its development has been greatly affected by the growth and spread of the surrounding Rukuhia peat swamp (Green 1979; Lowe et al. 1980). Recently the drainage and cultivation of the swamp has had some marked effects on the lake, notably on the water table level and by increasing nutrient inputs.

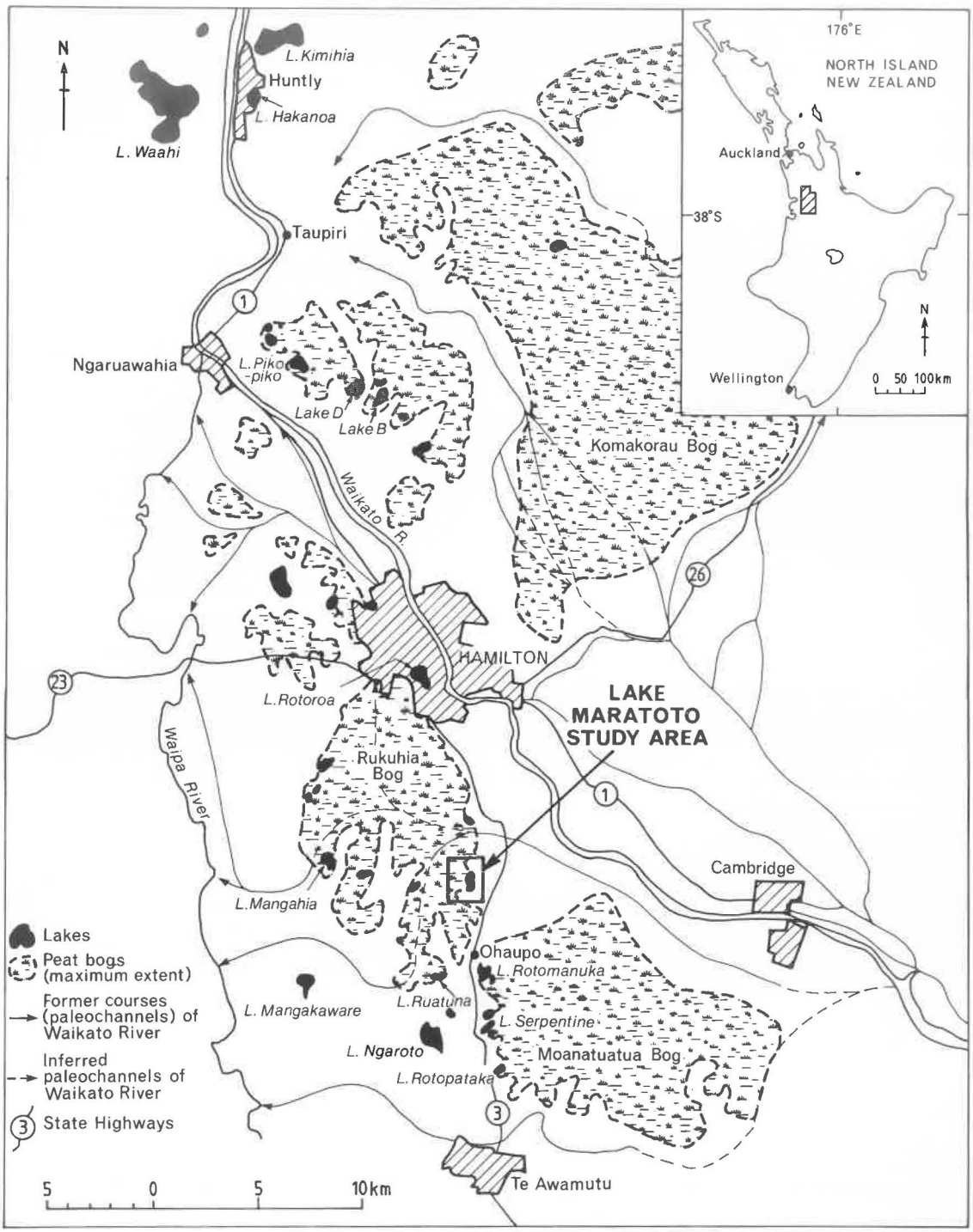
1.2.1 Geological History

Lake Maratoto was formed about 17,000 years ago at the end of the last ice age, when sand and gravel (Hinuera formation) deposited by the Waikato River blocked a valley that drained to the south west of the lake. Initially, the lake would have been shallow but of similar extent to the present one. About 13,000 years ago, peat began to develop locally. This became more extensive 10,000 years ago and caused the water to rise substantially (Green and Lowe in prep.).

1.2.2 Soils

The low hills to the east and south of the lake are predominantly Hamilton clay loam and Ohaupo silt loam (Grange et al. 1939). Between these hills and the lake there is a narrow band of peat intermixed with significant quantities of tree trunks, branches and roots, the remains of a lowland forest dominated by large kahikatea (Podocarpus dacrydioides) and Dacrydium spp. The western side of the lake is flanked by the Rukuhia peat swamp. Here, peat depths of up to six

Figure 1.1. Location of Lake Maratoto and of some of the other lakes sampled in this study.


N
L. Kimihia
Huntly
L. Hakanoa
L. Waahi
Taupiri
1
Ngaruawahia
L. Piko-piko
Lake D
Lake B
Waikato R.
Komakorau Bog
26
HAMILTON
23
L. Rotoroa
Waipa River
Rukuhia Bog
LAKE MARATOTO STUDY AREA
1
Cambridge
L. Mangahia
Ohaupo
L. Rotomanuka
L. Mangakaware
L. Ruatuna
L. Serpentine
L. Ngaroto
Moanatuatua Bog
L. Rotopataka
3
Te Awamutu
Lakes
Peat bogs (maximum extent)
Former courses (paleochannels) of Waikato River
Inferred paleochannels of Waikato River
3 State Highways
5 0 5 10km
176°E
NORTH ISLAND NEW ZEALAND
Auckland
38°S
N
Wellington
0 50 100km

metres have been recorded (Green and Lowe in prep.). Increased drainage in recent years is causing major peat shrinkage and many of the once buried hill tops have now resurfaced.

1.2.3 Physiography and Morphometry

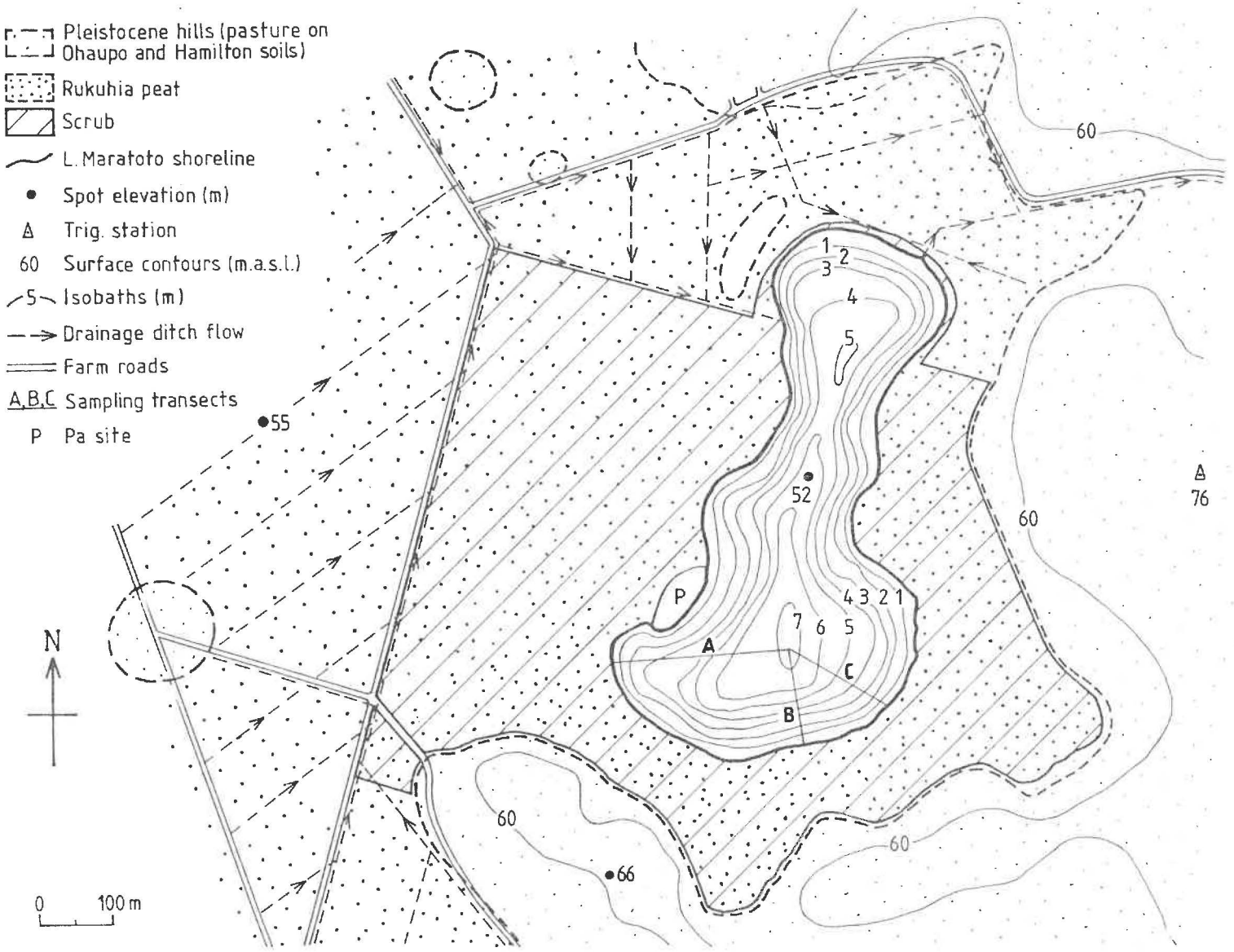
A bathymetrical map of Lake Maratoto compiled in 1979 from echo sounding traverses (Irwin 1982) is shown in Figure 1.2 . Areas enclosed by isobaths have been calculated from the original chart with a compensating polar planimeter (Welch 1948) and these and other morphometrical parameters are given in Table 1.1 .

1.2.4 Sediment Distribution and Description

1.2.4.1 Methods -

Sediment samples for particle size and organic matter analyses were collected from six stations along transect A (Figure 1.2) in December 1979. This transect was chosen as it typified most of the lake. Five cores of 6 cm internal diameter were taken at each station and the top few centimetres of each combined to reduce variability. For carbon analysis, a portion of the samples was dried at 80 'C, ground to a powder in a mechanical steel mortar and replicate subsamples ignited at 550 'C for half an hour. Particle size analysis was made by wet sieving 500 ml of the remaining sediment and measuring the volume of the fractions retained by each sieve. To give further indications of the sediment make-up and variability, core samples were collected from the same stations bi-weekly from April 1979 to March 1980. On 25/10/79 samples were also taken along transects B and C (Figure 1.2). All of these samples were sieved through a 225 µm sieve and visually classified according to the categories given in Table 1.2. The presence of pumice

Figure 1.2. Lake Maratoto catchment. Bathymetry of the lake and sampling transects.


Pleistocene hills (pasture on Ohaupo and Hamilton soils)
Rukuhia peat
Scrub
L. Maratoto shoreline
Spot elevation (m)
Trig. station
60 Surface contours (m.a.s.l.)
5 Isobaths (m)
Drainage ditch flow
Farm roads
A,B,C Sampling transects
P Pa site
N
0 100 m
55
52
66
76
60
P
A
B
C
1 2 3 4 5
4 3 2 1
7 6 5

Stratum (m)	Area (sq. m)
0.0-0.3	4000
0.0-1.5	33680
0.3-0.8	7120
0.8-1.5	22560
1.5-3.5	50060
3.5-5.5	51640
5.5-7.5	24500

Maximum length	710 m
Maximum breadth	420 m
Maximum depth	7.5 m
Mean depth	3.35 m
Direction of main axis	NNE,SWW
Area	159880 m^2
Elevation (NZMS 270 S15B)	52 m
Length of shore line	2060 m
Shoreline development	0.0129
Volume	535100 m^3

Table 1.1. Some morphometrical and physiographical parameters of Lake Maratoto.

		% by volume of sediment retained by 225 μm sieve			
		< 15	15 - 45	45 - 60	> 60
Dominant size of particles retained (μm)	225 to 500	1	5	9	13
	500 to 1000	2	6	10	14
	1000 to 2000	3	7	11	15
	> 2000	4	8	12	16

Table 1.2.

Codes used in particle size classification of L. Maratoto sediments.

and sand, wood remains, rootlets and rush stems was also noted.

To determine the sediment stratigraphy, a two metre long core was taken with a hand operated piston corer. This is discussed in Chapter 5.

1.2.4.2 Results and Discussion -

Results of the sediment analyses are summarised in Table 1.3 and Figure 1.3 .

In the deeper parts of the lake, the sediment is best described as fine gelatinous mud made up of flocculated humic material, intermixed with animal remains and excreta. Only the occasional plant fragment is present here, but increasing amounts are found as one nears the shoreline. Below the mud surface the organic sediment is intercalated with several distinct volcanic ash layers of known origin and age (Lowe et al. 1980). The youngest of these airfall tephras, the Taupo ash of 1,800 yr B.P., is composed predominantly of pumice particles up to 2 cm in diameter.

Deposition rates throughout the lake's history have remained relatively constant and towards the mud surface have been calculated to be 0.075 mm/year (Green et al. in prep.). This means that the Taupo ash should be some 10 to 15 cm below the sediment surface, but in places it is within the top 5 cm. At the 0.5 m station particularly, wave action has eroded most of the overlying organic matter and the sediment surface is often left covered by a thin layer of pumice and sand. This is the cause of the low carbon content recorded here (Figure 1.3). On the more exposed southern edge of the lake (transects B and C), more intense wave action has removed or prevented organic material from being deposited above the Mamaku ash (7,000 yr B.P.) and large areas of this 2

	water Depth (m)	n	Sediment size code FINE 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	COARSE 16	W	P	R
Transect A	0.2	83		1				7	2	1	1	66	13			7			22	17	79
	0.5	93	1	12	4			25	48	2		1	7	1					13	80	1
	1	91	1	9	17			33	30	4		3	5	1		1			37	28	2
	2	86		9	13		1	38	38	2									13	2	2
	5	90	71	19	3		1	3	1											9	2
	7	95	76	19	3		1	1												10	2
Transect B	0.5	5		80	20															40	60
	1	5		80				20											20	60	
	2	5		20					40	40									60	80	
Transect C	0.5	5		20				60	20										60		60
	1	5		60	20				20											80	
	2	4						25	50				25						75	75	

Table 1.3.

Percentage frequency of sediment types in sample cores from each station in L. Maratoto between 2.4.79 and 26.3.80. Codes as in Table 1.2. Transects are those shown in Figure 1.2. W = wood fragments, P = sand/pumice, R = Rootlets and reeds stems.

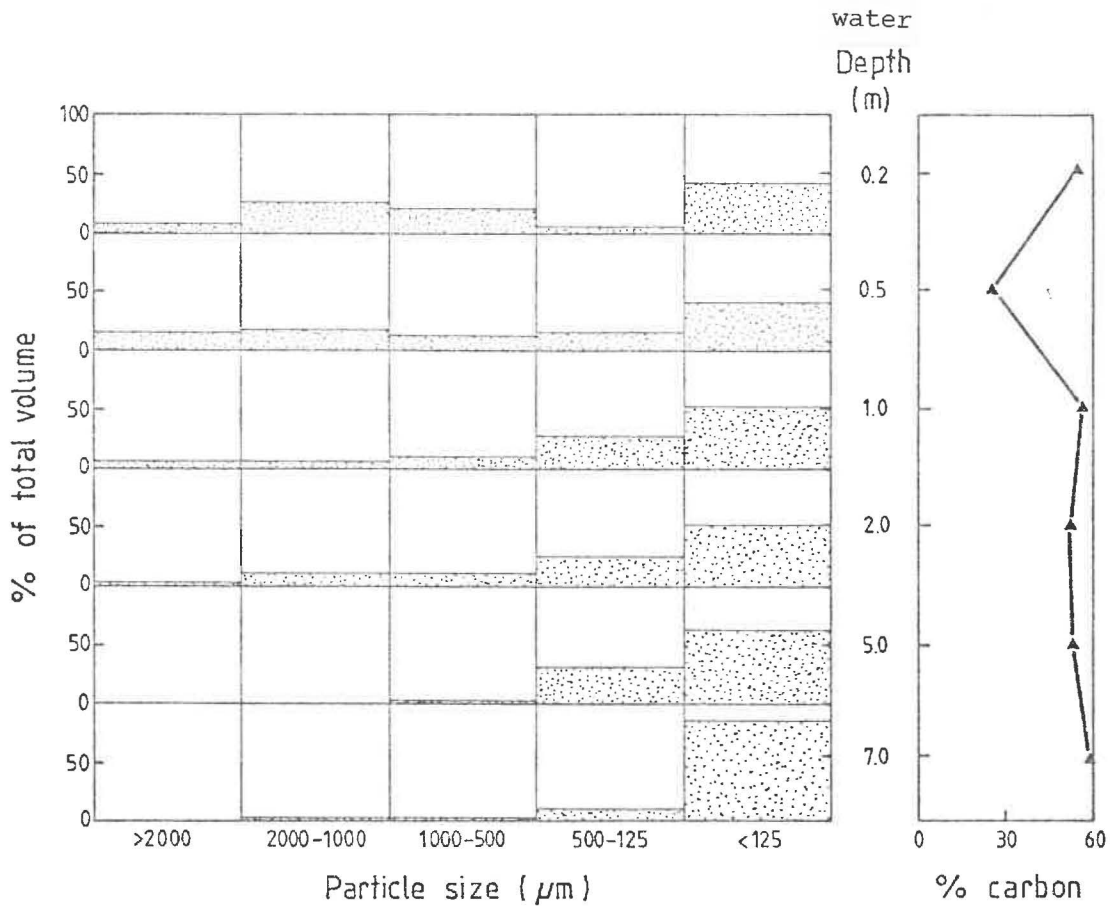


Figure 1.3 Particle size distribution as % total volumne and organic carbon content as % dry weight of typical sediments in L. Maratoto. Samples were collected along transect A in December 1979.

cm thick sandy layer have been uncovered. Hence, at times, only large pieces of wood (including trunks of trees and shrubs) remain on the ash in the zone between 1 m depth and the shoreline. For most of the lake, however, the sediment is composed of fine organic mud with increasing amounts of coarse, plant material as one nears the shore. This material originates not only from the growing vegetation on the edge of the lake but also from the erosion of peat on the shore. On the very edge of the lake, the sediment is made up almost solely of peat closely interwoven with roots and stems - the remains of plants that invade the area at times of low water levels. Depending on weather patterns, wave action may also either deposit or erode from this area significant amounts of material consisting of manuka (Leptospermum scoparium) leaves and seed pods, and other plant material of similar size. This transient material, when eroded from the shoreline, is redeposited around the one metre depth zone.

On the shores exposed to the wind, wave action has cut into the otherwise gently sloping shelf and an 80 cm perpendicular bank has been formed, which remains held together largely by the roots of the shoreline vegetation.

In summary, we may classify the sediment from the lake into four types according to the depth at which they occur.

A. 7 m and 5 m stations: fine organic ooze.

B. 2 m and 1 m : medium organic particles with some coarse woody material.

C. 0.5 m : medium organic particles with large amounts of sand and pumice.

D. 0.2 m : coarse organic material, mainly peat.

1.2.5 Hydrology

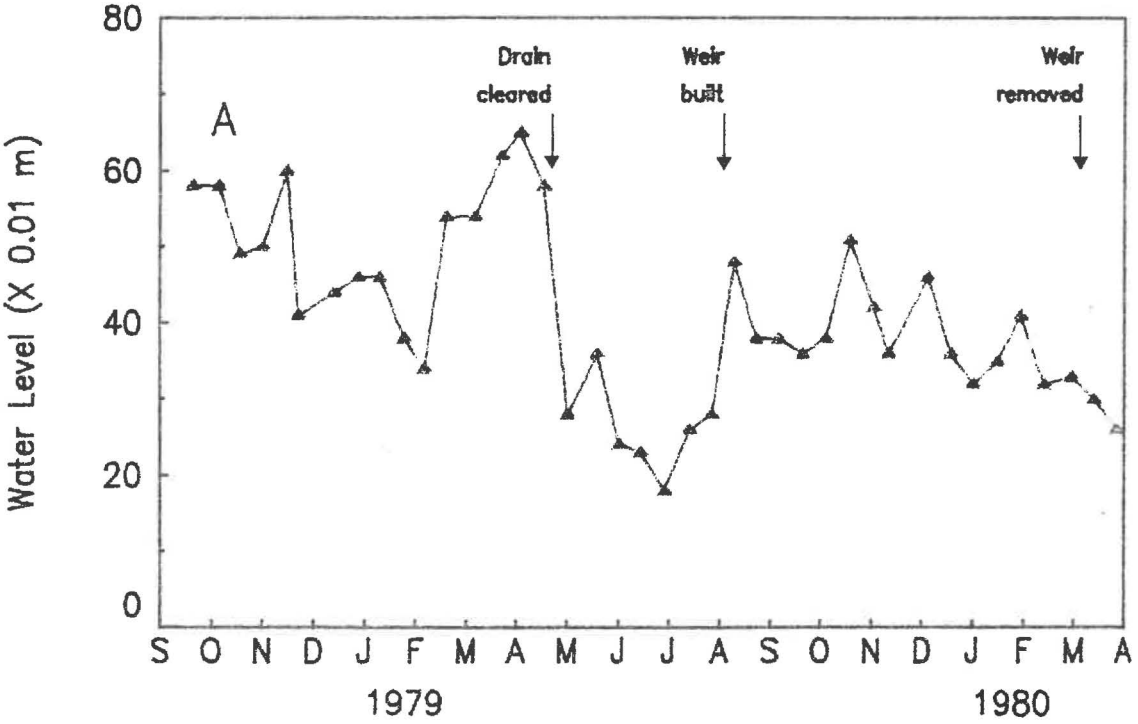
Lake Maratoto has no large inflow and only one regularly maintained inlet drain. The remainder of the water reaching the lake is rainfall run-off, largely from the south and east. No doubt percolation of water through the peat swamp to the west also takes place. The lack of any large watercourse flowing through the lake is of great significance for its limnological characteristics. The outlet drain of the lake has been dug through higher ground to the north east to lower the water table and bring the peatland surrounding the lake into production. Previous to this, flooding was common, most of the excess water having to flow over the swamp to the south or west to reach formed water courses (C. Graham pers. comm.). Continual deepening of the drains has been required because of peat shrinkage, and this has resulted in a significant drop of the lake's water level. One such drain clearing on 19/4/79 resulted in a considerable decrease in the lake's water level (Figure 1.4A). To maintain some water over the shallower areas of the lake, a temporary weir 50 cm high was constructed early in July 1979, and following this, water level fluctuations were largely caused by rainfall (cf. Figure 1.4B). During periods of low precipitation, evaporation exceeds inflow, and no water leaves via the outlet. The lake can then remain cut off from other water systems for some period - this may be of significance to the movement of eels to and from the lake.

1.2.6 Climate

Although Lake Maratoto is close to the New Zealand Meteorological Service recording stations of Hamilton Airport and Rukuhia, there is not always correspondence between events at the lake and those officially recorded. Generally both wind and rainfall are highly variable - both from season to season and year to year (Figures 1.4B and 1.5). The lake

Figure 1.4. (A) Changes in water level of Lake Maratoto over sampling period. Water depth measured from a staff gauge installed by W.V.A. on 13/9/78 (zero = 51.700 m, Moturiki datum).

(B) Mean daily rainfall for period preceding each sampling visit to Lake Maratoto. Data from the Hamilton Airport Meteorological Station, 3.2 km NE of the lake.


A
Drain cleared
Weir built
Weir removed
Water Level (X 0.01 m)
80
60
40
20
0
S O N D J F M A M J J A S O N D J F M A
1979
1980

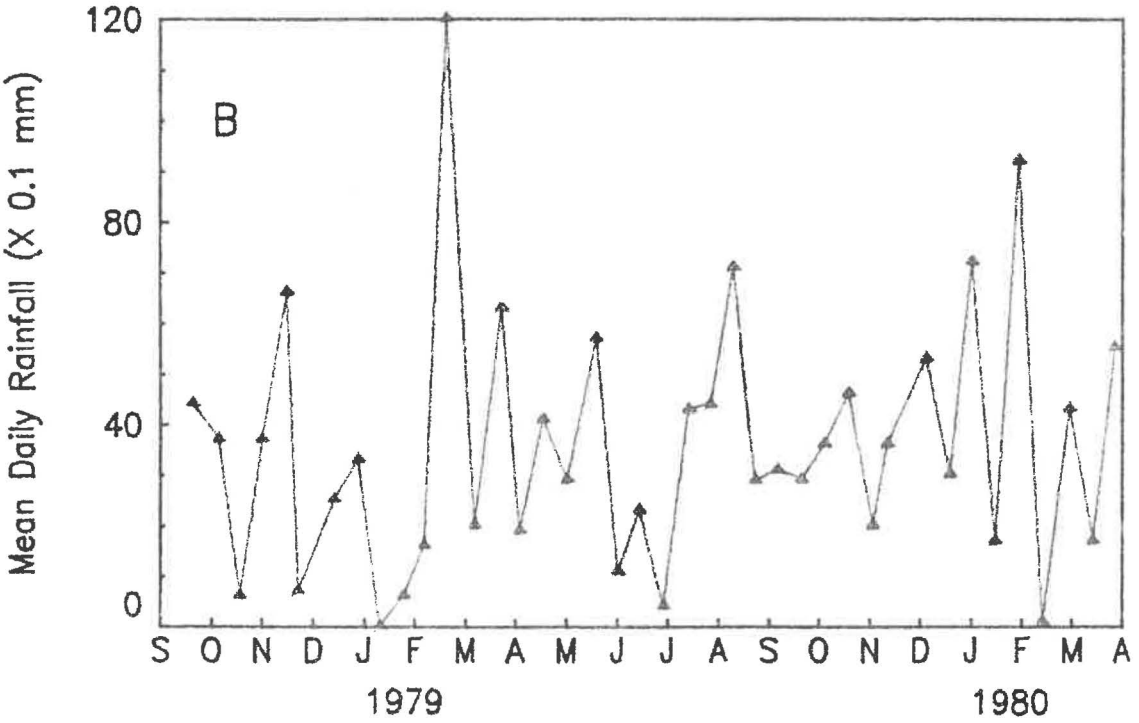
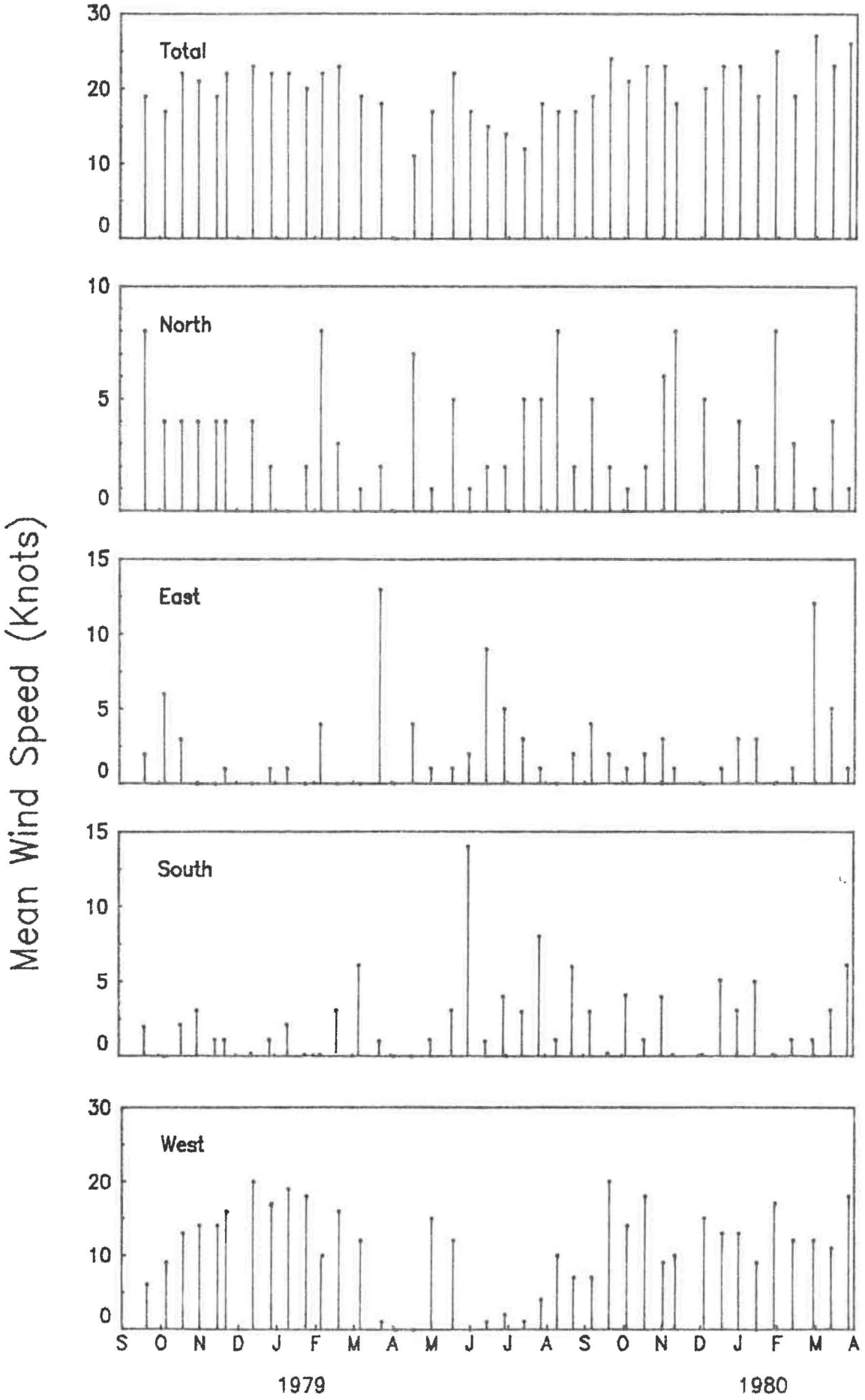

B
Mean Daily Rainfall (X 0.1 mm)
120
80
40
0
S O N D J F M A M J J A S O N D J F M A
1979
1980

Figure 1.5. Mean daily wind speed at ground level for period preceding each sampling visit to Lake Maratoto. Data from the Hamilton Airport Meteorological Station, 3.2 km NE of the lake.


Mean Wind Speed (Knots)
Total
North
East
South
West
30
20
10
0
10
5
0
15
10
5
0
15
10
5
0
30
20
10
0
S O N D J F M A M J J A S O N D J F M A
1979
1980

is exposed to the dominant west wind, but gusting north and north-east winds that run along the main axis of the lake also affect the water circulation. The periodic disruption of stratification in summer is attributable to these winds.

1.2.7 Temperature

Temperature measurements were made with a YSI model 54 oxygen/temperature meter. Readings were taken at half metre intervals over the region of maximum depth, at two weekly intervals from 19 September 1978 to 25 March 1980.

As the water is dark in colour, large amounts of heat are absorbed by the lake and during the summer strong thermal stratification develops. Strong winds nonetheless, can rapidly return the lake to homothermy. The isotherms (Figure 1.6A) give a clear picture of how quickly changes can occur.

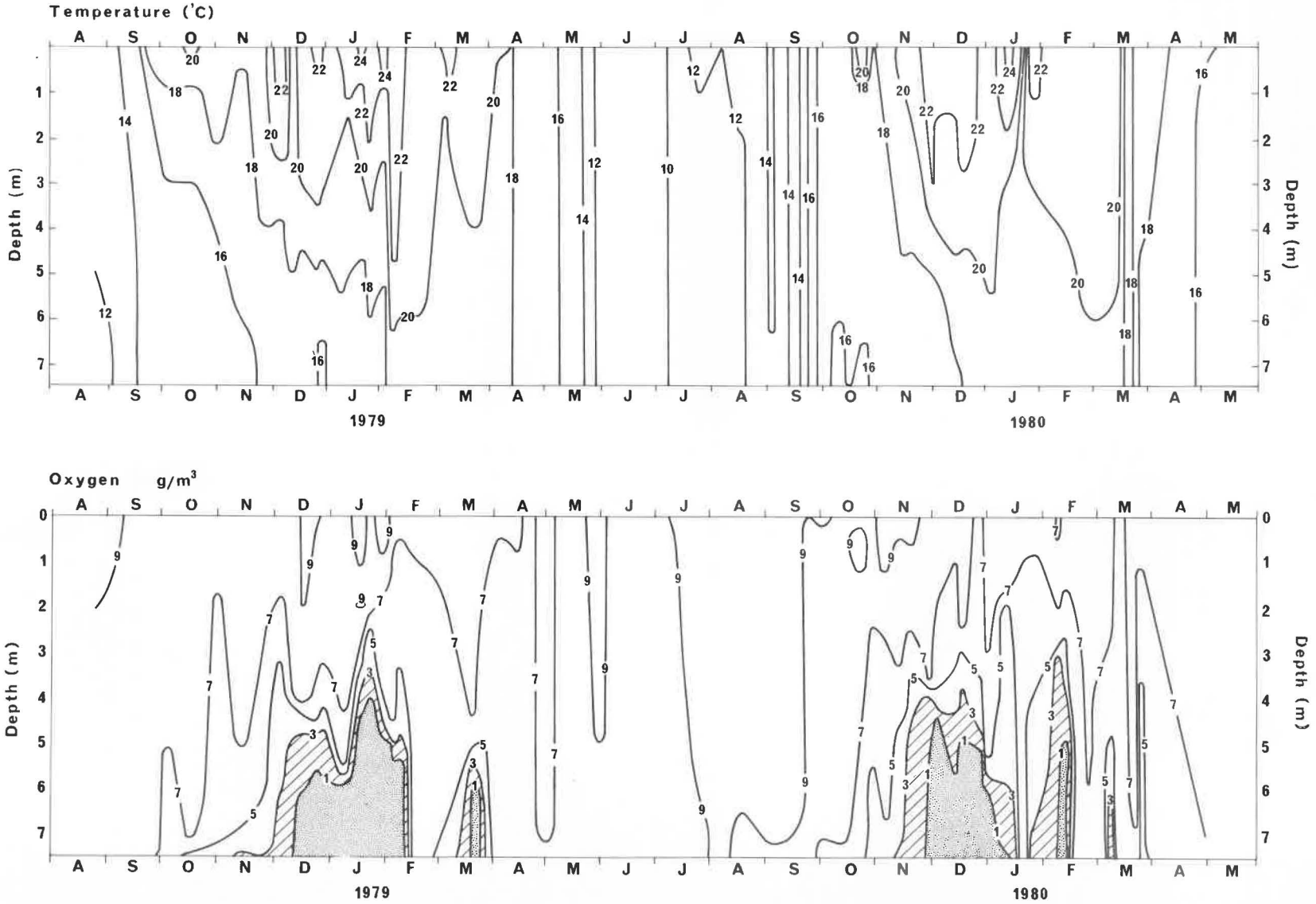
Temperatures at the surface of the lake varied from 10.5 to 31.5 'C and that of the bottom water from 10.2 to 20 'C. The lake was homothermal from about May to September.

1.2.8 Oxygen

As might be expected in a polyhumic lake with periods of thermal stratification, a great diminution of oxygen takes place in the deeper water layers during summer (Figure 1.6B). From 12/12/78 to 12/2/79 and 3/12/79 to 14/1/80 particularly, there was little oxygen in the bottom waters.

Figure 1.6. (A) Isothermal variations of Lake Maratoto, expressed in 'C, from 19/9/78 to 25/4/1980.

(B) Isopleth of oxygen concentration in g/cu. m.


Temperature (°C)
A S O N D J F M A M J J A S O N D J F M A M
Depth (m)
1 2 3 4 5 6 7
1979
1980
Oxygen g/m³
0 1 2 3 4 5 6 7
Depth (m)
1979
1980

At the 7 m station the deoxygenated layer did not usually extend into the top five metres of water. However, in shallower sections of the lake, owing to the high oxygen demands of the sediments, this oxygen deficit layer did encroach into the upper water (Table 1.4).

One important characteristic of the lake is the rapid depletion and replenishment of oxygen which can occur within a day, e.g. 2.1 g/cu. m dissolved oxygen at 7 m on 12/3/80 and 5.5 g/cu. m on 13/3/80; 6.8 g/cu. m on 25/3/80 and 3.9g/cu. m on 26/3/80. Evidently, the lake's exposure to strong winds - especially from the north and east - allows for periodic recirculation of the water during the summer, but it is not until the temperature drops that appreciable amounts of dissolved oxygen remain at all depths (usually from April to at least October).

1.2.9 Water Colour and Clarity

The water of Lake Maratoto is the colour of weak tea, appearing quite black against the dark peat bottom. Spectrophotometric scans of the water show a rapid rise in absorbance at the blue end of the spectrum, this being due to humic compounds. As a result, little light is present in 0.5 m of water, and even red light is almost non existent at 2 m (C. Howard-Williams and W. Vincent pers. comm.).

During the period of study, transparency was measured with a Secchi disc 20 cm in diameter. Light intensity was recorded with a submersible photo cell with maximum sensitivity at the yellow - red end of the spectrum (5,500 - 7,500 A'). From this, the % transmission at 0.5 m was calculated. Results of these measurements are presented in Figure 1.7.

	Station					
	7 m		5 m		1 m	
depth (m)	O2 g/m^3	T 'C	O2 g/m^3	T 'C	O2 g/m^3	T 'C
0	7.8	22.8	7.8	22.8	7.1	23.0
0.5					6.8	22.8
1	7.7	22.5	7.6	22.5	6.6	22.0
2	7.5	22.2	5.5	21.8		
2.5	5.1	21.0				
3.0	4.4	21.0	3.8	20.0		
4.0	0.9	19.5	0.6	19.2		
5.0	0.5	18.5	0.5	17.5		
6.0	0.4	18.0				
7.0	0.4	17.0				
7.5	0.3	16.6				

Table 1.4. Oxygen and temperature levels on 23/1/78 at three stations along transect A in Lake Maratoto.

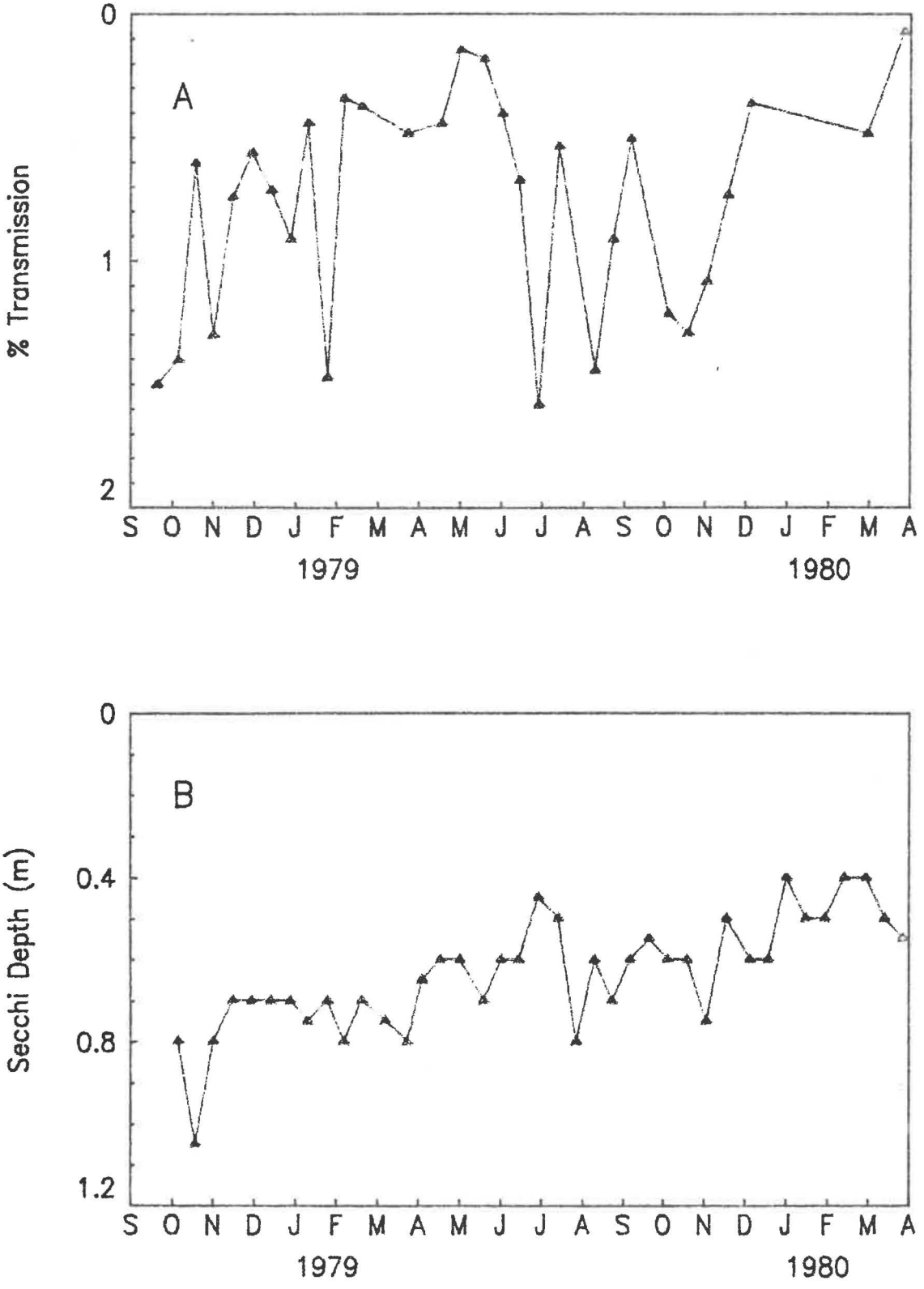


Figure 1.7. Light penetration in Lake Maratoto during the sampling period.

(A) Percentile transmission of light at 0.5 m.
(B) Secchi disc transparency.

The values obtained are comparable to those from the other small dystrophic lakes of the Waikato Valley in which high concentrations of brown humic acids markedly reduce light penetration. Generally in the winter months water was clearer than at other times of the year, though the water clarity decreased over the sampling period. Dilution of the humic material by rain, the flocculation of these compounds under certain conditions, and variation in the quantity of suspended solids are expected to have produced these results.

1.2.10 Chemical Properties

Lake Maratoto is one of the most acid lakes of the Waikato Valley. As a result of the buffering effect of iron complexes, pH values remained between 4.1 and 5.5 (Table 1.5). Only slight changes occurred with increasing depth, even during periods of deoxygenation. The highest pH values were recorded in the summer when algal removal of dissolved CO_2 is at its maximum.

Chemical properties of the lake water are given by Boubée (1978). In addition, samples were taken in May 1978 when the lake was well mixed and in February 1979 during the summer stratification. The samples were analysed by the Soil and Water Centre of M.W.D. and the results are given in Table 1.6. Like many other lakes in the lower Waikato, the total phosphate content is high, indicating eutrophication. Breakdown of organic matter and input from pasture are thought to be the main cause of this. The dissolved reactive phosphate content during the summer time drops markedly. During the bloom of flagellates, which normally occurs from October to February, levels probably become limiting (R. Pridmore pers. comm.).

Date	S	1 m	2 m	3 m	4 m	5 m	6 m	7 m	Id	Is	O	Ns
16 12 77	4.28											
22 12 77	4.60	4.52		4.55		4.50		4.45				
6 1 78	4.50	4.55		4.65		4.55		4.52				
16 1 78	4.75	4.70		4.45		4.40		4.35				
17 1 78	4.75											
23 1 78	4.75	4.65		4.60		4.45		4.45				
2 2 78	4.45	4.38		4.35		4.30		4.55				
8 3 78	4.90	4.95		4.88		4.92		4.95				
14 3 78	4.85	4.90		4.88		4.90		4.85				
9 7 78	4.75	4.70		4.60		4.65		4.75				
31 10 78	4.50											
14 11 78	4.65											
12 12 78	4.55											
9 1 79	4.70											
2 2 79	5.00	5.00	5.00	5.00	5.00	5.00		5.30				
6 2 79	4.70											
8 8 79	4.80											
27 9 79	4.60				4.50			4.50	3.70	4.30	4.60	4.50
27 9 79	4.25	4.20	4.20	4.20	4.15	4.20	4.15	4.10				
23 10 79	4.95											
8 11 79	4.72											
22 11 79	4.80											
28 1 80	4.85											
10 4 80	5.50				5.40			5.40				

Table 1.5. Changes in pH value of Lake Maratoto water over the sampling period. Samples taken over the region of maximum depth and at the following locations: S = water surface at 7 m station; Id = inlet drain; Is = inlet seepage; O = outlet; Ns = surface of northern basin.

Date	Station	Depth (m)	T.P.	T.D.P.	D.R.P.	NH4	NO3	Total Kjeldahl N
3/5/78	7m south	0	65	50	12	219	62	*
	"	1	65	48	14	209	64	*
	"	3	63	48	13	219	66	*
	"	5	53	50	12	219	68	*
	"	7	63	52	12	199	67	*
	Inlet 1	-	288	275	244	915	95	*
	" 2	-	272	265	216	616	141	*
2/2/79	7m south	0	41	26	5	31	13	1237
	"	1	42	29	5	36	*	1313
	"	2	41	31	5	37	14	1237
	"	3	39	29	5	31	26	1188
	"	4	55	39	6	57	8	1295
	"	5	54	36	6	61	15	1147
	"	6	50	26	7	60	27	1420
	"	7	50	42	9	*	*	1527
27/9/79	7m south	0	52	42	7	83	356	1362
	"	4	47	42	9	99	350	1280
	"	7	45	36	9	90	353	1284
	Inlet	-	157	141	128	546	450	2641
	Seepage	-	61	52	21	119	278	1360
	Outlet	-	61	36	6	65	281	1268
	5m north	0	50	31	6	69	246	1226
10/4/80	7m south	0	60	57	13	213	121	1187
	"	4	60	54	15	206	126	1356
	"	7	12	12	14	190	103	1254

Table 1.6. Phosphorus and nitrogen concentrations in Lake Maratoto water. All values in mg/m^3. Analyses by Water and Soil Division M.W.D. Hamilton. (* = missing values)

Nitrogenous compounds on the other hand, are always extremely high. White (1982) states that in New Zealand, waters containing over 300 mg/m^3 total N are rare, occurring only in a few eutrophic lakes. Values obtained in Lake Maratoto and other lakes in the lower Waikato are at least four times as great. The mean Total-N:Total-P ratio in Lake Maratoto is 31. Such a high ratio is unlikely to be the product of organic breakdown, but it is not known if it results from farming practices (Baber and Wilson 1972), or whether water seepage from peat swamps is naturally high in nitrogen.

1.2.11 Suspended Solids

Particles suspended in the water are important, not only in restricting light transmission but are also of significance to filter feeders. These particles include planktonic algae and other micro-organisms, resuspended sediments and flocculated material.

1.2.11.1 Methods -

Water samples were collected regularly during the sampling period by lowering a 7 m open ended flexible hose of 2 cm diameter, into the deepest part of the lake. During December 1978, samples were also taken at metre intervals with a water sampler. The samples were preserved in Lugol's iodine until analysis. Particles were counted with a Coulter Counter (R) using a 100 µm aperture. Details of operation and treatment of the data followed procedures set out by Sheldon and Parsons (1967). Counts were separated into 1 to 10 µm and 10 to 50 µm size classes. These two particle size classes were used, as most of the algae in Lake Maratoto were larger than 10 µm. The 10 to 50 µm size class therefore is thought to represent mainly planktonic algae and some suspended solids while the 1 to 10 µm class will include mainly suspended solids

and some micro-organisms.

1.2.11.2 Results and Discussion -

There were always many more particles in the 1-10 µm size class than in the larger size category (Figure 1.8), but there was not a close correspondence between the fluctuations in phytoplankton numbers (Figure 1.9) and those in particle numbers. In general, particles of both size classes were most abundant in the winter months, probably because of the increased turbulence of the water after the breaking up of stratification. The clearing of the outlet drain and subsequent lowering of the lake's water level which occurred at this time would also have led to an increase in erosion and suspension of particles from the edges of the lake. Although bacterial numbers were not determined, it is possible that these also increased at this time since their growth would be favoured by the mixing of nutrients released from the sediments during stratification in summer. Table 1.7 shows typical examples of the depth distribution of particles during summer stratification.

1.2.12 Submerged Vegetation

Unlike the neighbouring lakes where Characeae at least are common, there is no submerged vegetation in Lake Maratoto. This is probably a result of the pH, low transparency, poor light penetration and disturbance of the soft sediments at shallow depths. There is nonetheless a rich periphyton on the edges of the lake which accounts for a substantial part of the primary production and is an important food source for many organisms. Genera that have been recognised include:

Oedogonium

Zygnema

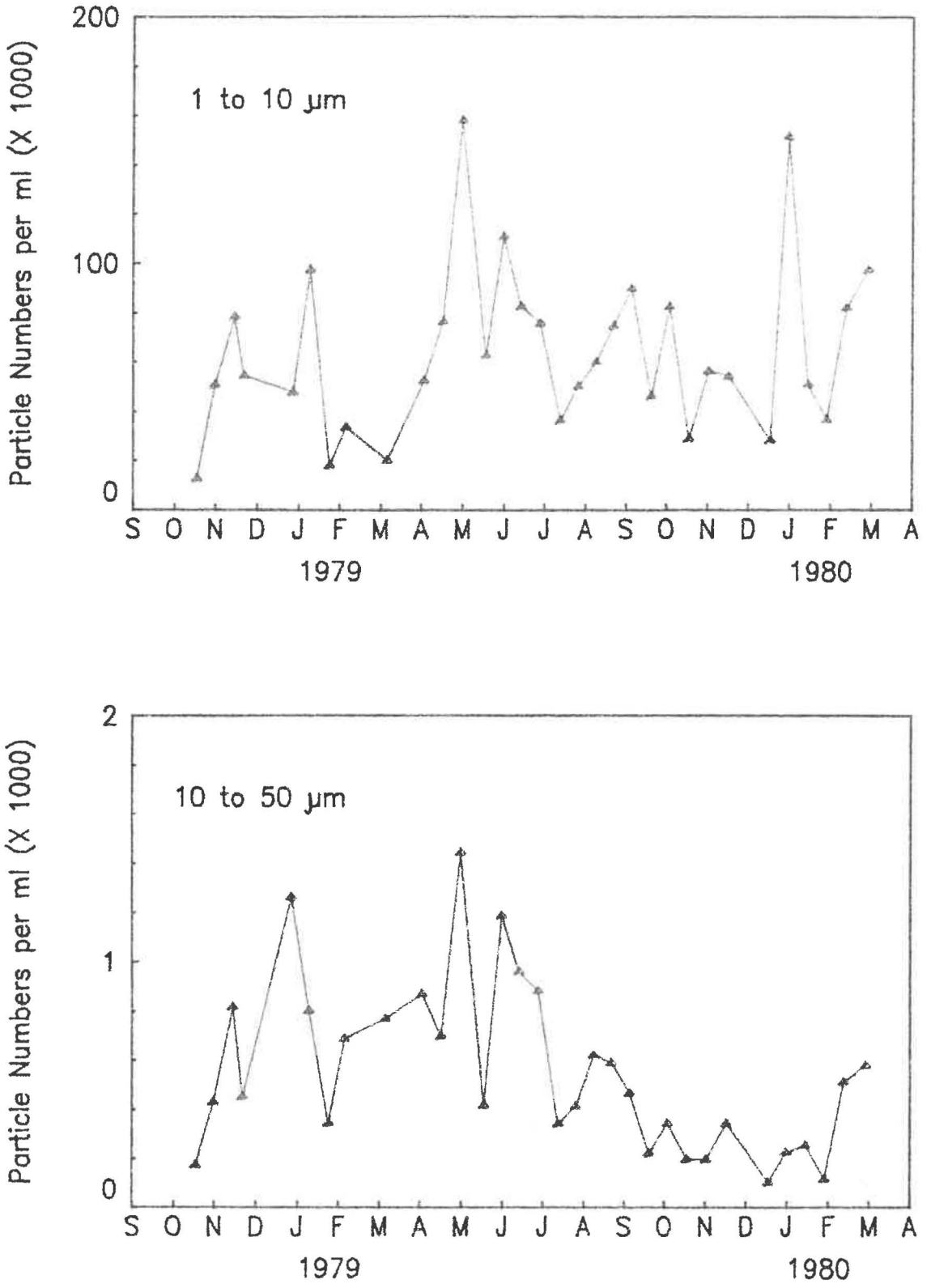


Figure 1.8. Seasonal variation in suspended particle numbers in Lake Maratoto.

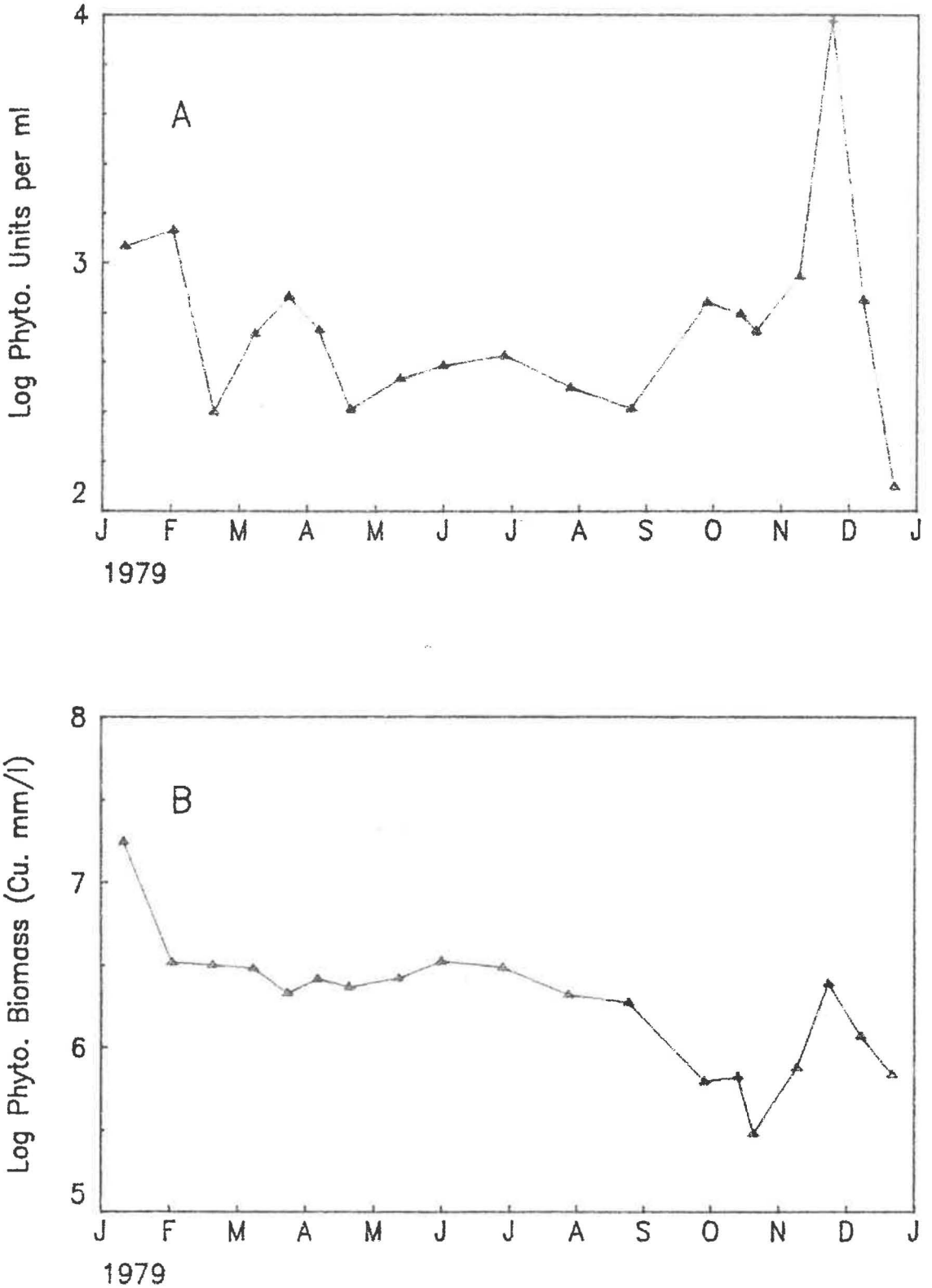


Figure 1.9. Seasonal fluctuation in the phytoplankton population, Lake Maratoto. Data from Etheredge (1983).

(a) Mean number of plankton units per ml.
(b) Mean biomass.

Date	Depth (m)	Particles No./ml 1-10 µm	10-50 µm
5/12/78	0	108090	1370
"	1	123670	640
"	2	51150	450
"	3	86640	300
"	4	12270	300
"	5	36090	350
"	6	21330	290
"	7	51490	250
28/12/78	0	87440	1550
"	1	76130	1140
"	3	35090	960
"	4	99780	420
"	5	21160	880
"	6	45370	410
"	7	30610	250

Table 1.7. Depth distribution of suspended particles as determined by Coulter counting.

Mougeotia

Ulothrix ?

Stigeoclonium

Navicula (chains)

Tabellaria (chains)

1.2.13 Planktonic Algae

The phytoplankton of Lake Maratoto was studied in detail by Etheredge (1983). Numbers and volume measurements are reproduced in Figure 1.9. Of the 61 species found, dinoflagellates were the most common. Although poor light penetration is expected to be a limiting factor, production is high, particularly in the summer months when low turbulence allowed the algae to remain in the photic zone. A Synura sphagnicola bloom of up to 9,000 cells/ml was recorded in November 1979 but the highest volume of algae was found in January 1979 when Botryococcus braunii was abundant. Diatoms dominated the plankton in winter and these were probably kept in suspension by water turbulence.

1.2.14 Epipelic Algae

At least 25 species of algae were found on the sediment of Lake Maratoto but their highly clumped distribution made density estimates difficult. (V. Reid pers. comm.). The dominant group from 0.5 to 2 m water depth were Naviculaceae. At 5 m Melosira spp. followed by Naviculaceae were the most common, while at 7 m there were mainly Eunotia spp. and Melosira spp.

1.2.15 Emergent Vegetation

In the more sheltered areas of the lake there are clumps of the tall spike rush (Eleocharis sphacelata) and Baumea articulata (Figure 1.10). There are also areas of partly submerged rushes (Baumea teretifolia, Baumea rubiginosa, Juncus pallidus and Schoenus brevifolius). During prolonged periods of low water, these rushes, as well as other plant species, tend to invade the exposed shore line, but usually recede as the water rises. For the remainder of the shore line, manuka (Leptospermum scoparium) provides a sharp delineation between water and land (Plate 2B). The absence of raupo (Typha orientalis) is noteworthy as it is present on most other water bodies in the Waipa County. It is possible that pH limits the growth of the plant here.

1.2.16 Surrounding Vegetation

The lake is almost entirely fringed by a band of manuka (Leptospermum scoparium), but there is an increasing encroachment by gorse (Ulex europaeus) and blackberry (Rubus fruticosus) (Figure 1.10). Some willows (Salix fragilis) are also found close to the water's edge. The ground cover is made up of a variety of seedlings and bog plants, including Sphagnum sp. and Drosera binata. A more detailed list of species found near the shoreline is given by Boubée (1978) and Edmonds (in prep.). The remainder of the catchment is in pasture.

Figure 1.10. Lake Maratoto - Vegetation.

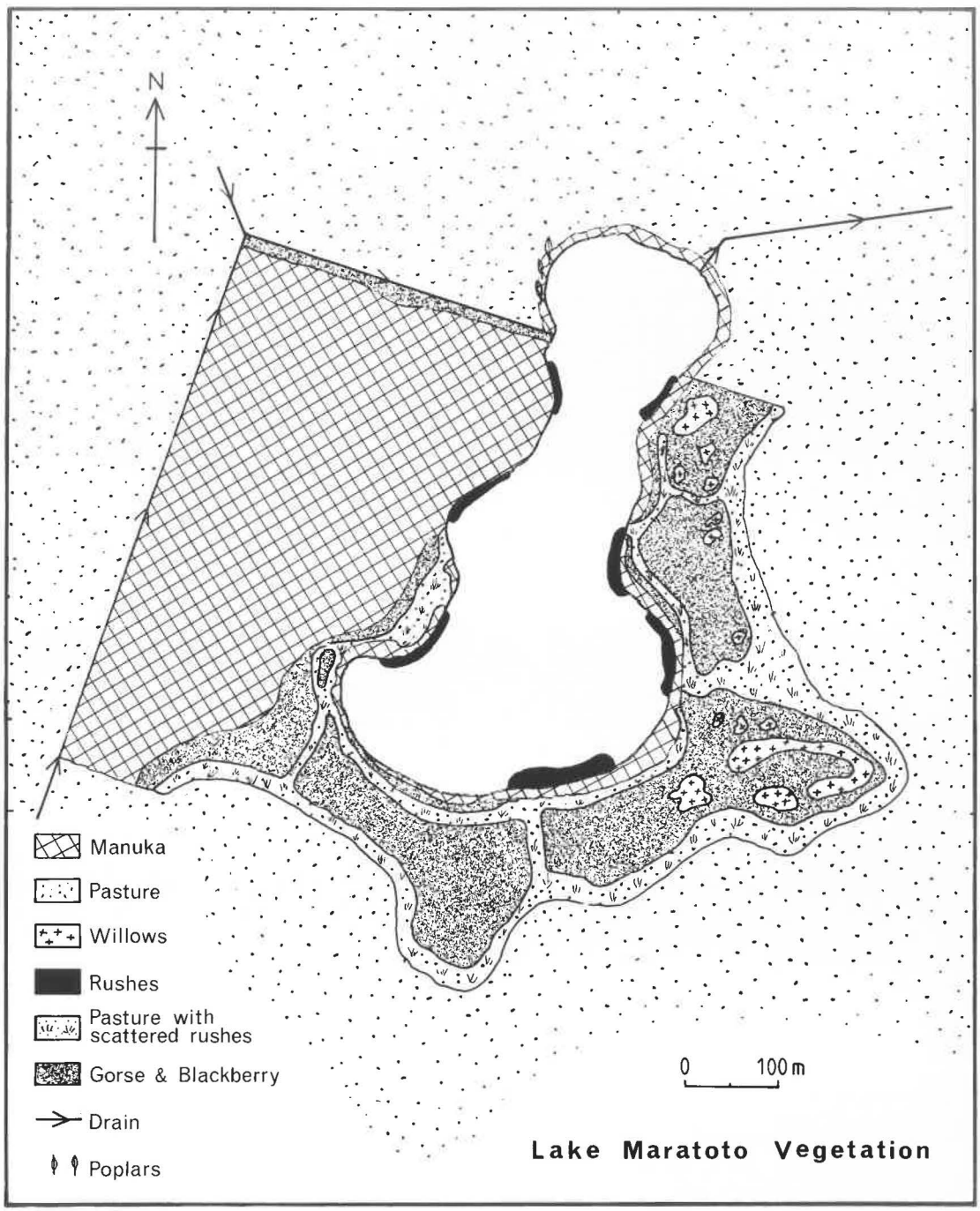

N
Manuka
Pasture
Willows
Rushes
Pasture with scattered rushes
Gorse & Blackberry
Drain
Poplars
0
100 m
Lake Maratoto Vegetation

Plate 2. Lake Maratoto: (A) aerial view;

(B) shoreline showing manuka growing to very edge of lake and Baumea bed.

A

B

CHAPTER 2

THE BENTHIC FAUNA OF LAKE MARATOTO

."Le pouvoir des nombres est d'autant plus respecté que l'on n'y comprend rien"

Voltaire (1764)

2.1 INTRODUCTION

When undertaking a sampling programme, the number of samples taken, the sampling position, type of sampler, frequency of sampling and method of separation of the fauna from the substrate are probably the most important factors that need to be considered.

An aggregated distribution is perhaps the most common pattern exhibited by benthic macro- and micro-invertebrates (Elliott 1971; Paterson and Fernando 1971; Resh 1979). If a satisfactory degree of accuracy is to be obtained, such clumped distribution pattern requires the collection of several benthic samples from each of the habitats that have been recognised. Elliott (1971) suggests that a minimum of 50 sampling units should be taken for quantitative data to be reliable. Realistically, a compromise between statistical accuracy and labour is required, the sampling method used being a determining factor.

In testing the efficiency of samplers, Kajak (1963), and Paterson and Fernando (1971) found that core samplers captured greater numbers of organisms per unit area than did an Ekman grab. This difference is probably largely because the grab sampled a smaller area than assumed, and also created more disturbance of the area being sampled. The grab, however, was capable of collecting more species than the core sampler.

Preliminary sampling of Lake Maratoto using a long handled dip net showed that the benthic fauna was dominated by chironomids, of which only three species were common. It was thus considered that the rarer species were relatively unimportant in the general description of the bottom fauna, and a corer was the favoured sampling device in the lake. Nonetheless, one must remember that with a small sampling unit, the sampling error at the edge of the unit is proportionately greater.

To test the effect of core size on population estimates, a series of samples was taken, using S.C.U.B.A., around the one metre zone, using tubes of 22.7, 44.2 and 81.7 sq. cm. The resulting total counts (Appendix 1) tested by the Kruskal - Wallis one way analysis by rank (Elliott 1971), did not show any significant difference between the sampling devices.

Lloyd (1967) has concluded that small samplers provide the best indication of degree of patchiness in a population. In view of this and the relative efficiency of sorting small samples, the 22.7 sq. cm core was preferred for the collection of benthic invertebrates in Lake Maratoto.

Preliminary work on the lake had shown that large population changes often occurred with small changes in depth. Thus it was important for the sampling device to be positioned accurately at each of the stations. Taking benthic samples with S.C.U.B.A. normally would have been the most effective way of doing this. Unfortunately, the dark colour of Lake Maratoto reduces a diver's visibility range to about 30 cm. Furthermore, on the edge of the lake, disturbance of the sediment by the diver was a serious drawback. Since the maximum depth of the lake was only seven metres, a hand held sampler that could easily be manipulated by one person from a small boat was used.

The principal factor affecting the number of invertebrates recovered from sediment samples after their collection is the mesh size of the sieve used (Jonasson 1955; Kajak 1963; Kajak et al. 1968). If sieves of too fine a mesh are used, the great volume of material retained will result in an underestimation of numbers, since small animals will be more difficult to find. Conversely, if the commonly used 500 or 600 µm mesh sieve is used, much of the small fauna sought

after will be lost. Many authors, including Jonasson (1955), Cantrell and McLachlan (1977), Paterson and Walker (1974), Tudorancea et al. (1979), have selected a 250 µm to 300 µm sieve. As the retention efficiency of the mesh has been shown to be correlated with the width of the head capsule of the chironomid to be separated (Jonasson 1955), it is expected such sieves would only retain any first instar larvae and the second instars of small species of Chironomidae, by chance. However, Ramcharan and Paterson (1978) and Cowell and Vodopich (1981) have noted that excluding these early instars does not change information on the species composition or relative abundance of each species. Only absolute densities are affected.

In deciding the frequency of the sampling programme, the development rates of the larvae whose population one is attempting to measure and describe are important. This development rate in chironomids has been shown to be temperature related. Biever (1965), for example, states that for the Chironomini, the time taken from egg hatch to adult is eight days at 30 'C and 34 days at 15 'C. He also found the duration of emergence to be five to eight days at 30 'C and over six weeks at 15 'C. Cowell and Vodopich (1981) found similar short development times for Chironomini living in the high temperatures of Florida, but were unable to determine accurately the larval length of life for Cladotanytarsus sp. This species, it appears, had continuous rather than cohort reproduction at high water temperatures. In New Zealand, Robb (1966), working with C. zealandicus, found a minimum development time (egg to adult) of 40 days at 15 'C and about 20 days at temperatures of 22.5 to 30 'C. Forsyth (1971) further noted the following minimum development rates:

Syncricotopus pluriserialis	25 days at 20 'C
Corynoneura donovani	12 days at 20 'C

Chironomus zealandicus	20 days at 22 'C
Paratanytarsus agameta	17 days at 20 'C

I have observed similar minimum development rates for animals reared in the laboratory at room temperature, although the maximum development rates were for some individuals, up to ten times longer.

In Lake Maratoto, since water temperatures are relatively high (Figure 1.6A), short development times can be expected for most of the year. However, the time taken to process all the samples that were collected made a shorter than fortnightly interval between sampling unrealistic.

2.2 METHODS

Qualitative samples of the fauna were collected with a long handled sweep net, 50 cm in diameter and 0.6 mm mesh. A number of plastic pot scrubbers were also deposited as artificial substrates in various positions in the lake. These were collected at intervals and the attached fauna determined.

Quantitative core samples were taken at approximately fortnightly intervals from 19/9/78 to 17/3/80 at four stations at depths of 7 m, 5 m, 2 m and 0.5 m along transect A (Figure 1.2). By early 1979, it was evident that the highest concentration of larvae and the greatest changes in population densities occurred on the edge of the lake, so that from 6/2/79 two extra stations (at 1 m and 0.2 m) were also sampled.

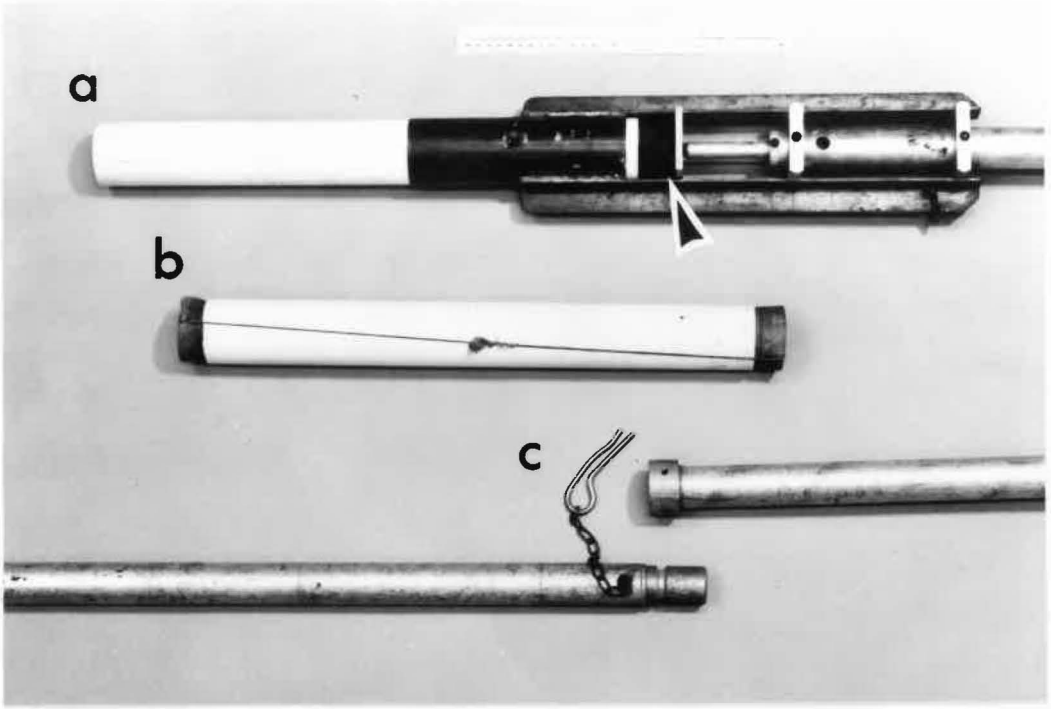
At each station, five samples were obtained with a hand operated corer similar in design to that described by Boubée (1977). Essentially this device (Plate 3A) consists of a brass casing and handle to which

Plate 3. A: sediment corer; (a) coring head with coring tube in place. Arrow points to sliding steel plate with rubber gasket

(b) sealed coring tube

(c) design of joints in handle extensions.

B: light trap. One of the pannels has been removed to show the collecting vessels. The ballast and switching device are sealed in the pottle - note light sensor at centre of the right pannel.



A

B

P.V.C. tubes can easily be attached and detached. The P.V.C. tubes (50 cm long, 3 mm gauge walls, 22.7 sq. cm cross sectional area) have the lower edge tapered to assist penetration into the substrate. The handle is composed of several two metre sections made of 5 cm diameter light gauge aluminium tubing that can be held together with steel pins. In the body of the corer, there is a sliding steel plate with a rubber gasket affixed, which covers the upper end of the P.V.C. tube in its closed position. As the core descends through the water column, this plate moves upward and allows water to flow unimpeded through the tube. This reduces the bow wave in front of the moving core that would otherwise tend to disturb the sediment and the organisms therein, although some disturbance of the sediment surface will still occur, for even an open ended tube will disperse the surface layers before penetrating the substrate. On withdrawal of the core from the sediment, the steel plate closes, forming a pressure seal that prevents loss of material through the lower end of the corer. Once at the surface, a rubber bung is inserted in the lower end of the P.V.C. tube before lifting it out of the water. In the boat, the P.V.C. tube can be detached from the body of the corer and sealed with a second rubber bung. A 1 mm hole drilled near the top of the tube allows the excess water to flow out as the bung is inserted. The hole is then sealed with plasticine.

The sediment samples were brought back to the laboratory in their P.V.C. tubes and either processed immediately or kept in a cool room at 5 'C until the next day. The samples were washed in a standard 225 µm mesh sieve, 20 cm in diameter and 7 cm high, with an inner lining of a 15 cm high sheet of clear acetate of 1.5 mm thickness extending above it. This allowed the use of a spray of water to wash the fine sediment through the screen without loss of animals. This not only considerably

shortened processing time, but the action of spraying also tended to break up the midge tubes, thus making the larvae more visible.

Only the top few centimetres of the cores were sieved, since preliminary work showed that animals were confined to this semi-liquid upper layer. Below this, the sediment was more compact and the anoxic conditions that prevailed excluded animals from it.

Screened residues ranged in volume from 5 ml to 500 ml and were preserved in 10% formalin. To ease the sorting process, a few drops of a 10% aqueous solution of Rose of Bengal were added to each sample.

Although various sorting aids were tried, such as elutriators (Lauff et al. 1961; Magdych 1981), flotation (Whitehouse and Lewis 1966; Kajak et al. 1968; Flannagan 1973; Karlsson et al. 1976), electric currents (Fahy 1972) and fluorescent dyes (Hamilton 1969) (these being totally unsuitable as the dyes leached from the sediment following staining), only Rose of Bengal stain (Mason and Yevich 1967; Williams and Williams 1974) was found suitable for Lake Maratoto samples. This stain is picked up by exposed animal tissue and a few plants, thus making it easier to differentiate the organisms from the debris.

The animals were eventually hand sorted in white trays using a magnifying glass and strong lighting. Many samples, especially those from the 0.2 m station, contained a large volume of coarse, peaty material that would not wash through the sieve. Hand sorting of such samples was time consuming and arduous, and required considerably more time than the average sample which could be sorted in 40 to 60 minutes.

Counting and identification were carried out after mounting the animals in P.V.A. lactophenol and examining them with a compound microscope. With practice, it became possible to identify many larvae during sorting with a stereo microscope at 80X magnification without having to mount them. To place larvae into age groups, head capsule length was taken as the most convenient parameter (see also section 3.2). Measurements were made with a graticule eyepiece at 80X.

Light trapping was also carried out on several occasions. The trap used (Plate 3B) was constructed of aluminium sheeting and was fully collapsable. The electrical components were taken from a fluorescent torch. A UV tube (a 6 Watt 23 cm Actinic 5 (BL) tube) was held over the collecting funnel by four perspex veins. A solar switch was incorporated in the device to turn the unit on after nightfall. Power was supplied by a 12 volt 10 AH battery.

Because migration of animals between different depths has frequently been observed (e.g. Deevey 1941; Bay *et al.* 1966; McLachlan 1970), it is necessary when dealing with seasonal population changes to look at the lake as a whole. In the quantitative treatment of the distribution and abundance of fauna therefore, the following terms and equations were used.

$$1) \qquad \text{Mean total number} = \frac{\Sigma\, n_i . a_i}{\text{Total area of lake}}$$

Where n_i = mean number of individuals per square metre at depth interval i.

a_i = area of depth interval i as given in Table 1.1. Since the 1 m and 0.2 m stations were not sampled prior to 6/2/79, the mean total numbers before that date were calculated assuming that the 0.5 m station

was representative of the fauna found between 1.5 and 0 m water depth.

2) Mean annual standing crop = $\frac{\Sigma \text{ mean total number}}{n}$

Where n = 27 = number of sampling dates from the end of stratification in 1979 (5/3/79) to the same period in 1980 (12/3/80).

All computations were carried out on a VAX computer using BMDP (Dixon and Brown 1981), SPSS (Nie et al. 1981) and MINITAB (Ryan et al. 1981) statistical computing systems.

2.3 RESULTS

A complete list of organisms collected from Lake Maratoto is presented in Table 2.1. Of these, 20 taxa were recovered quantitatively and the full data are given in Appendix 2. These 20 taxa represent species or groups that are widespread in the 0.2 to 7 metre zone of the lake. A further 10 taxa were found in this zone but were too small to recover quantitatively. Sampling with sweep nets in the outlet drain, amongst the reeds, and in flooded areas just behind the shoreline (including seepage water), yielded an additional 18 taxa. Two more species were collected by light trapping. Of the benthic macroinvertebrates found, two groups, the chironomids and the oligochaetes, were by far the most common.

2.3.1 Sampling Variability

Since natural benthic populations are rarely random in their distribution, an appropriate transformation of the data is generally required before "normal" methods of statistical analysis can be applied. Several methods are available for deriving these transformations and

TABLE 2.1. List of microinvertebrates collected from Lake Maratoto between 19/9/78 and 25/3/80. L = light trapped adults; O = outlet drain; S = seepage and flooded areas; E = edges; R = reed stalks; C = cores (usually widespread).

PLATYHELMINTHES		
TRICLADIDA		
Planariidae	indet.	C
NEMATODA	indet.	C
ANNELIDA		
OLIGOCHAETA		
Tubificidae		
Limnodrilus		C
MOLLUSCA		
GASTROPODA		
Physidae		
Physa (*Physa*) sp.		O
ARTHROPODA		
CRUSTACEA		
CLADOCERA		
Bosminidae		
Bosmina (*Eubosmina*) *meridionalis* Sars, 1904		C
Chydoridae		
Alona quadrangularis (Muller), 1785		C
Daphniidae		
Ceriodaphnia dubia Richard, 1895		C
Simocephalus sp.		C
Macrothricidae		
Ilyocryptus sordidus (Lieven), 1848		C
OSTRACODA		
Darwinulidae		
Darwinula repoa Chapman, 1963		C
COPEPODA		
CALANOIDA		
Centropagidae		
Calamoecia lucasi Brady, 1906		C
CYCLOPOIDA		
Mesocyclops leuckarti (claus), 1857		C
HARPACTICOIDA	indet.	C
MALACOSTRACA		
AMPHIPODA		
Eusiridae		
Paraleptamphopus sp.		C
ISOPODA		
Asellote	indet.	C
ARACHNIDA		
Arrenuridae		
Arrenurus (*Arrenurus*) sp.		C
Hydrachnidae		
Hydrachna (*Anohydrachna*) *maramauensis* (Stout), 1953		C
Limnocharidae		
Limnochares (*Cyclothrix*) sp.		C

Table 2.1. (Cont.)

INSECTA		
LEPIDOPTERA		
	Nymphula sp.	S
ODONATA		
	Xanthocnemis zealandica (McLachlan), 1873	C
	Austrolestes colensonis (White), 1846	C
	Hemicordulia australiae (Rambur), 1842	C
EPHEMEROPTERA		
	Leptophlebiidae	
	Zephlebia versicolor (Eaton), 1899	L
TRICHOPTERA		
	Hydroptilidae	
	Oxyethira albiceps (McLachlan), 1862	R
	Leptoceridae	
	Triplectides cephalotes (Walker), 1852	C
	Oecetis unicolor (McLachlan), 1868	C
	Polycentropodidae	
	Polyplectropus sp. (? *puerilis*) (McLachlan), 1868	C
HEMIPTERA		
	Corixidae	
	Sigara sp.	C
	Notonectidae	
	Anisops wakefieldi White, 1878	C
	Veliidae	
	Microvelia macgregori (Kirkaldy), 1899	E
COLEOPTERA		
	Dytiscidae	
	Liodessus sp.n.	C
	Elmidae indet.	S
	Hydrophilidae	
	Paracymus pygmaeus Macleay, 1871	S
	Gyrinidae	
	Gyrinus convexiusculus Macleay, 1871	O
DIPTERA		
	Culicidae indet.	S
	Tipulidae indet.	S
	Ceratopogonidae	
	Palpomya sp.	C
	Chironomidae	
	Tanypodinae	
	Ablabesmyia mala (Hutton), 1902	S
	Pentaneura sp.	S
	Gressittius antarcticus (Hudson), 1892	C
	Macropelopia spp.	C
	Podonominae	
	Parochlus sp. (*araucanus* group)	C
	Orthocladiinae	
	Syncricotopus sp.	C
	Eukiefferiella sp.	C
	Metriocnemus spp.	C
	Chironominae	
	Chironomus zealandicus Hudson, 1892	C
	Chironomus analis Freeman, 1959	L
	Kiefferulus opalensis Forsyth, 1975	C
	Cladopelma curtivalva (Kieffer)	C
	Tanytarsinae	
	Calopsectra funebris (Freeman), 1959	C

Elliott (1971) recommends one based on Taylor's power law. This power law (Taylor 1961) states that the variance (S^2) of a population is proportional to a fractional power of the mean ($\bar{x}$):

$$S^2 = a\bar{x}^b$$

Parameter a is mainly dependent on the size of the sampling unit, while parameter b is an index of dispersion which varies continuously from zero for a regular distribution, to infinity for a highly contagious distribution (a = b = 1 for a random distribution, while for a log-normal distribution b = 2), (Elliott 1971). Both a and b can be obtained by plotting log S^2 against log $\bar{x}$. Once these values are determined for the population under study, each count is replaced by x^p where p = 1-b/2. Methods applicable to normal distribution are then appropriate.

If, as in most biological systems, the negative binomial can be established as a suitable model for the population under study (see Elliott 1971), the index of precision D%, expressed as a decimal may be calculated using the following equations:

$$D^2 = 1/n\bar{x} + 1/nk \qquad 1)$$

Where n is the number of replicate samples used and k is the dispersion parameter of the negative binomial estimated from:

$$k = \frac{\bar{x}^2}{S^2 - \bar{x}} \qquad 2)$$

If no relationship exists between 1/k and $\bar{x}$, a common k (k_c) may then be calculated using equation (3):

$$\frac{1}{k} = \frac{y'}{x'} \qquad 3)$$

Where $x' = \bar{x}^2 - \frac{S^2}{n}$ and $y' = S^2 - \bar{x}$

Note that 1/k = 0 for random samples while for maximum contagion 1/k = n - $1/\bar{x}$, i.e. in this study would approach 5, the number of replicate samples taken at each station.

For the oligochaetes, the log - log regressions of variance against mean for each station were similar and the data were pooled (Figure 2.1A). The slope of the resulting regression line gives b = 1.7822. This value approximates 2 and a logarithmic transformation is suitable. Such distributions are common amongst oligochaetes (Brinkhurst et al. 1969). As 1/k and $\bar{x}$ were found to be independent, the calculation of a common k is justified. The slope of the regression line of y' on x' gives k_c = 1.14 (Figure 2.1B). From equation 1 the standard error is then established to be 108 % for the lowest density of oligochaetes detected (about 90 animals per square metre). This error reduces with increasing population size (e.g. 61% for 400/sq. m, i.e. an average of 1 worm per core) and tends towards 42%.

As with the oligochaetes, the log - log plots of variance against mean for the chironomids were similar for each station and the data was pooled (Figure 2.2A). The value of b in the regression line is also close to 2, and a logarithmic transformation is again appropriate. Since some samples contained no animals, the transformation log (x + 1)

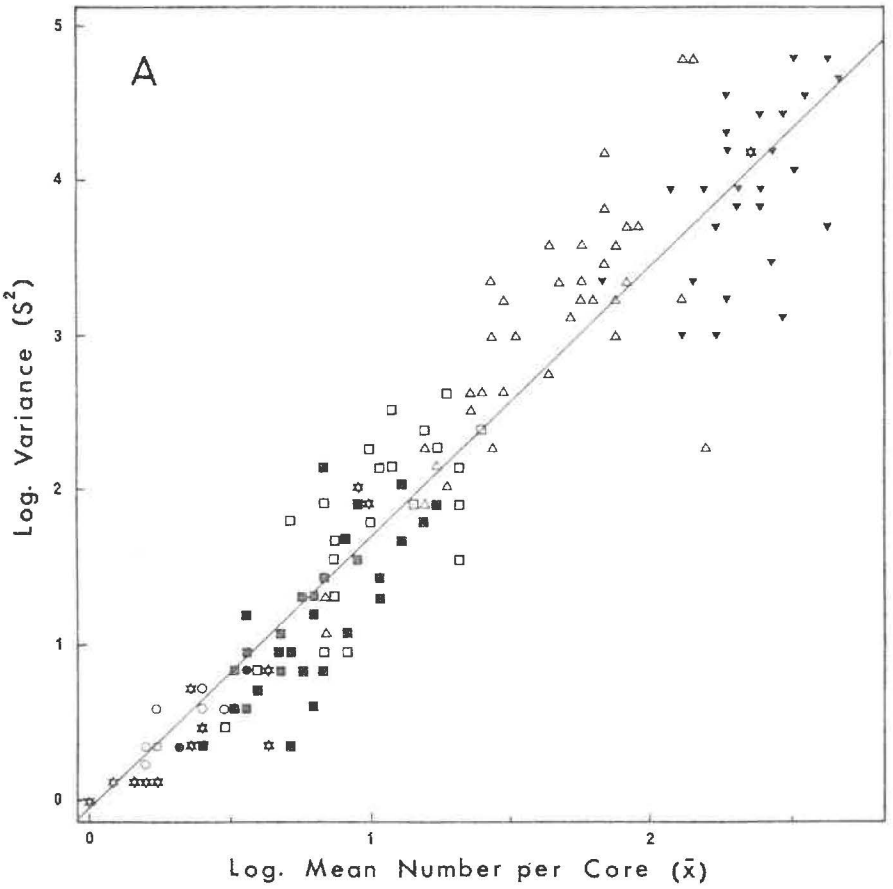
Figure 2.1. (A) log-log regression of variance against mean number of oligochaetes per core. Samples collected fortnightly from Lake Maratoto at six stations along transect A. Regression line, $\log S^2 = 1.782 \log \bar{x} - 1.209$ ($r = 0.973$).

(B) log-log regression of x' on y' for oligochaetes.

Regression line, $\log y' = 0.885 \log x' - 1.221$ ($r = 0.951$).

● = 7 m; ○ = 5 m; ■ = 2 m; □ = 1 m; △ = 0.5 m; ▼ = 0.2 m;

✡ = overlapping points.


A
Log. Variance (S^2)
Log. Mean Number per Core ($\bar{x}$)
0
1
2
3
4
5

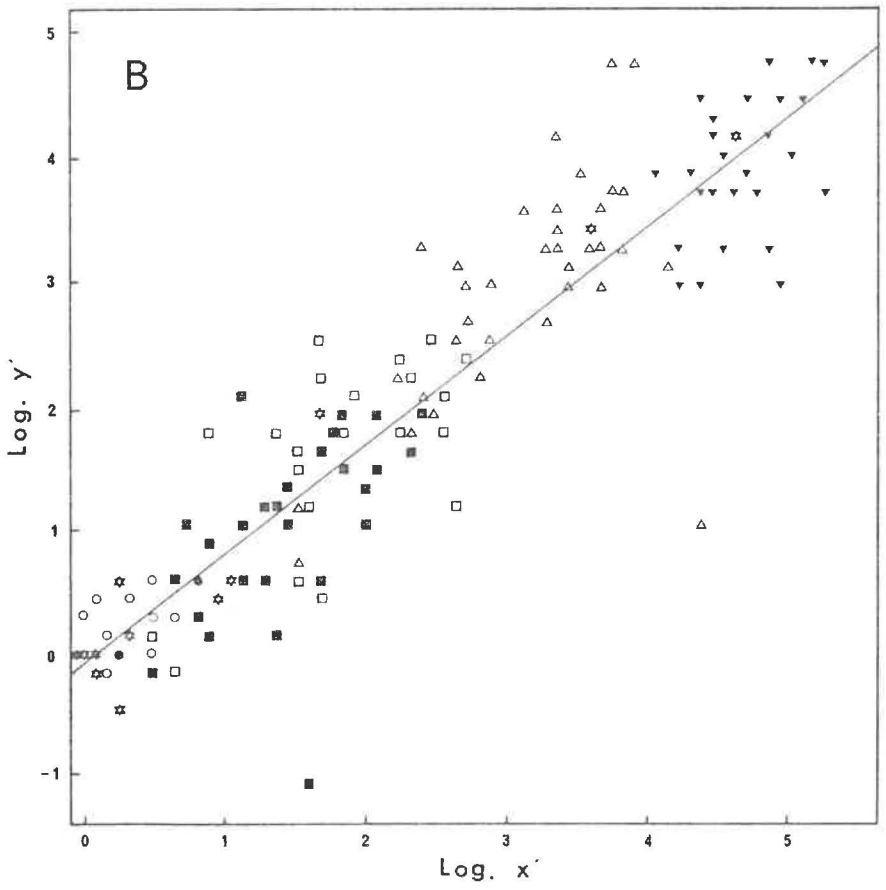

B
Log. y'
Log. x'
-1
0
1
2
3
4
5

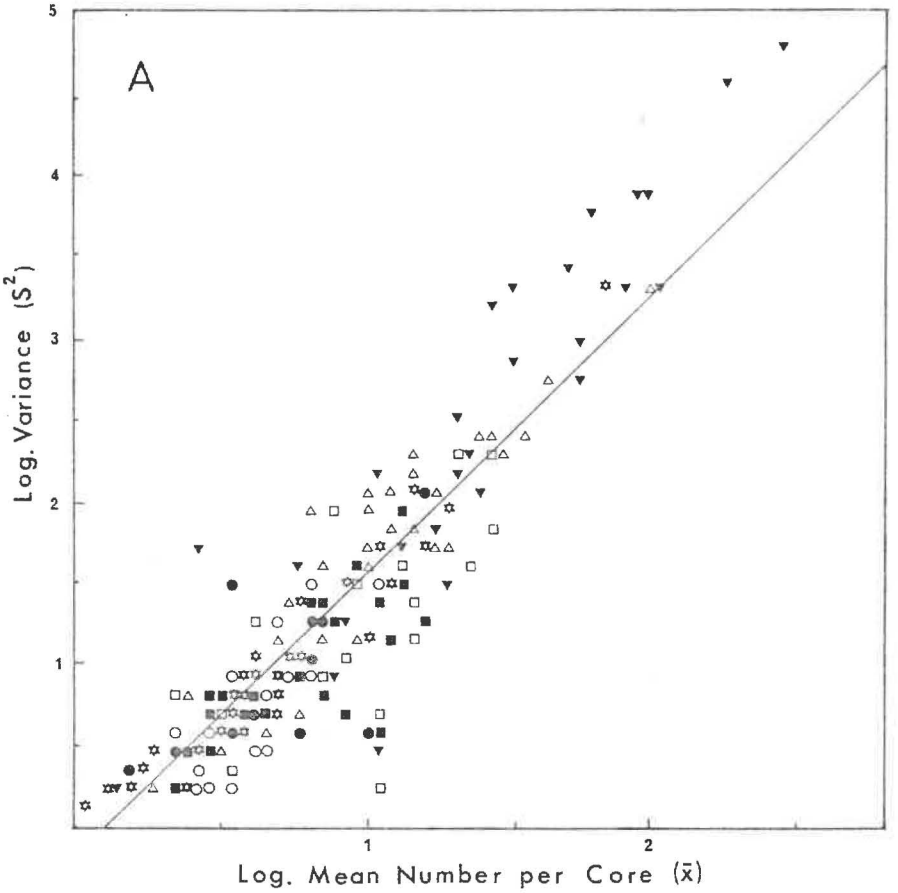
Figure 2.2. (A) log-log regression of variance against mean number of chironomids per core. Samples collected fortnightly from Lake Maratoto at six stations along transect A. Regression line, $\log S^2 = 1.812 \log \bar{x} - 1.98$ ($r = 0.924$).

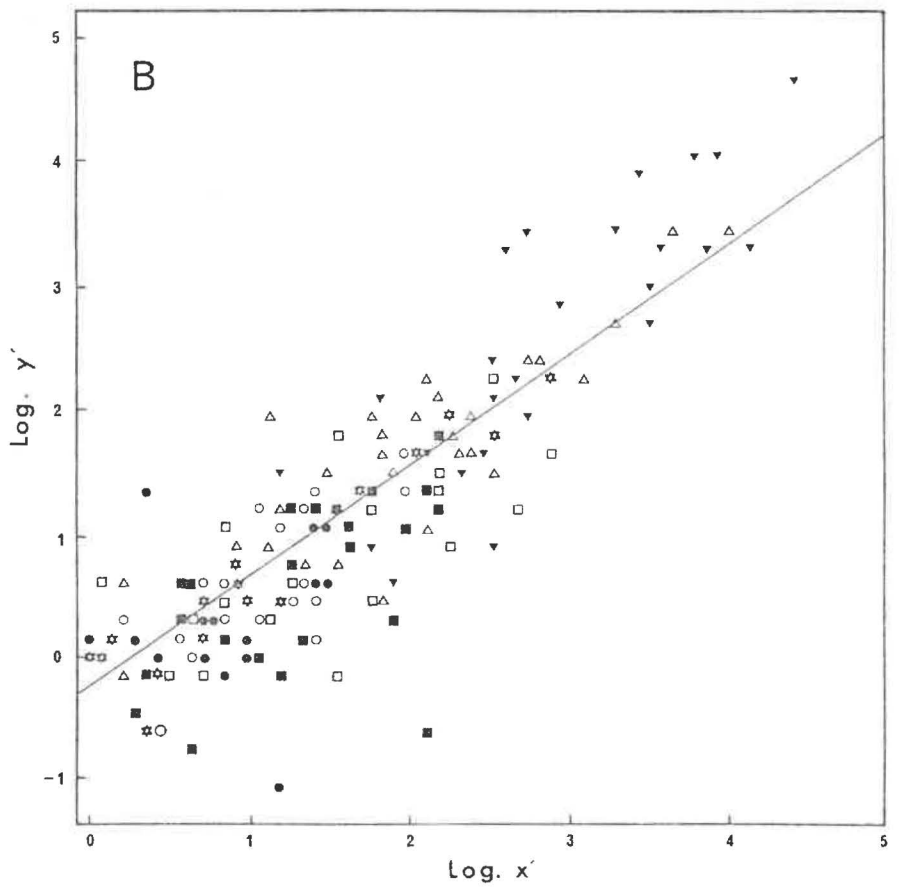
(B) log-log regression of x' on y' for chironomids.

Regression line, $\log y' = 0.951 \log x' - 2.04$ ($r = 0.891$).

● = 7 m; ○ = 5 m; ■ = 2 m; □ = 1 m; △ = 0.5 m; ▼ = 0.2 m;

✡ = overlapping points.


A
Log. Variance (S^2)
Log. Mean Number per Core ($\bar{x}$)
5
4
3
2
1
1
2


B
Log. y'
Log. x'
5
4
3
2
1
0
−1
0
1
2
3
4
5

has been used throughout this thesis.

No relationships were found between 1/k and $\bar{x}$, so a common k of 1.09 was calculated (Figure 2.2B) and used in equation 1 above. This determined the standard error as being equal to 109 % at the lowest larval densities but was found to reduce significantly to approach 43 % with increases in population size.

For both the oligochaetes and the chironomids therefore, the standard error of the population estimate varied between 110 % for the lowest and 43 % for the highest density of animals recorded. Larger numbers of samples would have improved this accuracy, but the time needed for analysis would have been prohibitive.

2.3.2 Suitability of Sampling Sites

Although preliminary field work had shown that samples taken along transect A appeared sufficiently representative of the whole lake, there were small areas to the south of the lake where the sediment from about 1 m to 0.2 m in depth consisted almost solely of fine sand/pumice. This 2 cm layer of volcanic ash overlaid the normal peaty sediment and had little, organic matter on its surface (see also Section 1.2.4). Two extra transects were therefore taken on 25/10/79 across some of these areas (transects B and C in Figure 1.2), and samples collected at approximately 2 m, 1 m and 0.5 m water depth.

The resulting counts (Appendix 3) were compared to those obtained along transect A on the 17/10/79 and 1/11/79 using MINITAB "AONONEWAY" analysis of variance. Because of the large variance recorded at each of the stations, no significant difference ($P > 0.05$) could be detected between the total number of oligochaetes collected at the same depth along the various transects. Similar results were obtained with the

total number of chironomids. As there were also no major differences in species composition between these three transects, taking samples only along transect A was considered adequate for the description of the benthic fauna of Lake Maratoto.

2.3.3 Spatial and Seasonal Abundance

PLANARIANS

Although planarians are common in other lakes of the Waikato Valley (pers. obs.), they rarely occurred in Lake Maratoto. They were found mainly on logs and vegetation at the very edge of the lake.

NEMATODES

Two unidentified species of nematodes were collected by core sampling. They were found in up to 5 m of water, but their numbers greatly increased towards the edges of the lake and they were most common at the 0.5 m station. No seasonal or population size estimations were attempted as the animals were too small to recover quantitatively.

OLIGOCHAETES

The most common worm was a Limnodrilus sp. Unfortunately, most, if not all, of the specimens collected were immature, making further identification impossible. It is likely that other species were also present.

Together, these worms constituted 61% of the mean annual standing crop of the lake. This dominance of the fauna is principally due to the very large population existing on the edge of the lake, where a maximum of 205,000 per sq. m was recorded on 28/1/80. The density of worms decreased rapidly with increasing distance from the edge, and was very

low in the centre of the lake (Table 2.2). This depth distribution of oligochaetes is unusual in that these animals with their resistance to anoxia are generally most numerous in the profundal (Brinkhurst 1974). Their absence from the deepest part of a lake is usually the result of serious deoxygenation (e.g. Forsyth and McColl 1975), while their exclusion from the shore can be explained through the presence of dense macrophyte beds. The lack of aquatic plants in Lake Maratoto, combined with the high oxygen demand of the sediment at the centre of the lake are probably the cause of the depth distribution of oligochaetes. In addition, there appeared to be a close relationship between particle size and oligochaete numbers, with higher numbers of worms within coarse sediments, particularly where remains of rushes and rhizomes were present.

	DEPTH (metres)					
	0.2	0.5	1	2	5	7
Mean No/m^2	105625	20138	3731	2439	255	39
% Total Fauna	81.3	67.8	49.9	47.4	12.3	3.5

Table 2.2. Annual mean density of oligochaetes and percentage of the total fauna within different depth zones of Lake Maratoto.

The mean annual standing crop of oligochaetes was 4,900 per sq. m (max. 12/7/79: 7,800 per sq. m; min. 17/10/79: 1,200 per sq. m). This value is higher than those reported by Timms (1980) for Lakes Rotoroa (3,067 per sq. m) and Rotoiti (1,585 per sq. m), while Forsyth (1978) recorded the highest mean standing crop in his study of seven Rotorua lakes, from Lake Ngapouri as 1,680 oligochaetes per square metre.

From the oligochaete densities obtained at each station, no overall seasonal trends are apparent, but the low population usually present at the 7m and 5 m stations was reduced to zero during periods of very low oxygen concentrations (Figure 2.3).

Despite the lack of trends in seasonal density changes between each of the depths sampled, the total oligochaete population of the lake peaked in winter and summer with the lowest numbers recorded both in autumn and spring. Pennak (1978) states that oligochaete egg cocoons may be deposited in late summer and early autumn and that this usually results in a mid winter population peak. Although egg cocoons were not specifically searched for, they were encountered throughout the year, with the highest numbers recorded in spring and early summer. The presence of mainly immature worms throughout the year further suggests that reproduction in Lake Maratoto is continuous.

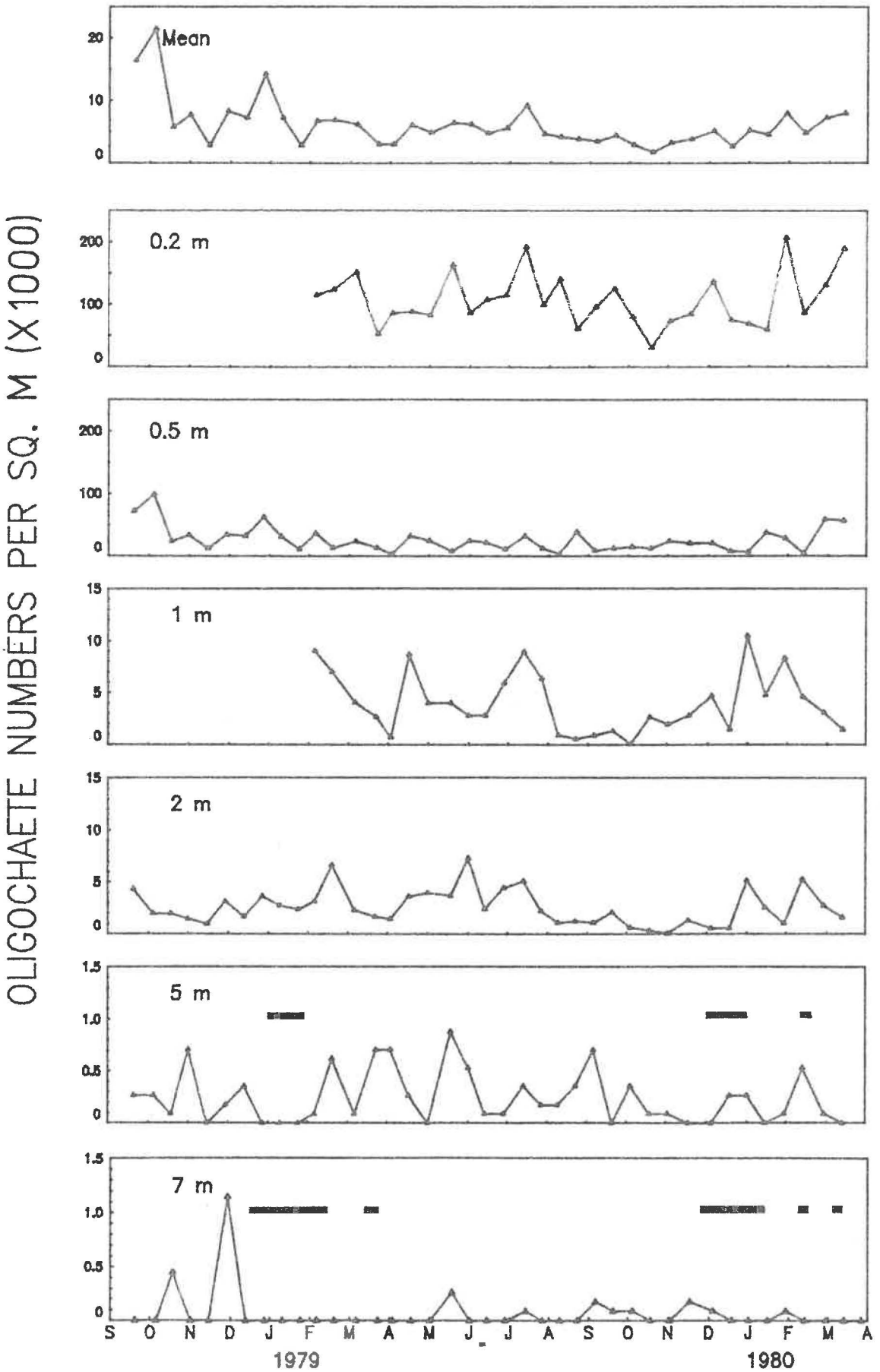
GASTROPODA

Physa sp. was present in the outlet drain and along the lake shore adjacent to it. No other living gastropods were found, but remains of Hyridella were collected at the south end of the lake. It is likely that these were brought to the lake by water birds or during pre-European occupation of the lake. The lack of shell bearing animals can be attributed to the low pH of the lake, most molluscs being unable to survive a pH of less than 4 (Wiederholm and Eriksson 1977).

CRUSTACEA

Due to their small size, cladocerans, copepods and ostrocods were not sampled quantitatively. A list of species found is given in Table 2.1. Of the copepods, Calamoecia lucasi was common at the 5 m and 7 m stations but was absent from the shallower stations, while Mesocyclops

Figure 2.3. Seasonal changes in population density of oligochaetes. Horizontal black bars indicate periods when the oxygen concentration above the sediments was below 3 g per cubic metre.


OLIGOCHAETE NUMBERS PER SQ. M (X1000)
Mean
0.2 m
0.5 m
1 m
2 m
5 m
7 m
S O N D J F M A M J J A S O N D J F M A
1979
1980

leuckarti was present at all depths. Ceriodaphnia was similarly present at all depths, but was most common on the edges of the lake. The remaining cladocerans ostracods and harpacticoid copepods were mainly restricted to the edges of the lake. Most were true benthic forms.

In the inflow and outlet of the lake an undescribed Asellote isopod (M. Lewis pers. comm.) and the amphipod Paraleptamphopus sp. were common.

No decapods were either collected or seen while S.C.U.B.A. diving in the lake, but a specimen of Paranephrops planifrons was seen in an eel fisherman's baited net. As the pH of Lake Maratoto is low, it is most unlikely that these animals are able to survive for long periods in the lake. It is probable that the animal in question entered the net at some other fishing location.

ACARINA

Water mites were common on the edges of the lake, but few were collected by core sampling. Limnochares (Cyclothrix) sp. were particularly numerous amongst the reeds and rushes. This large, red coloured mite was seen in the laboratory to feed on chironomid larvae. Feeding was only observed when the larvae were in their tubes. The mite usually spent long periods near the entrance of the chironomid tube waiting for the larva to protrude from its case. The mite would then dart forward and attach itself in the region of the clypeus, out of range of the prey's mandibles (Plate 4B). A violent struggle usually ensued in which the mite was either pulled into the larval tube, or the larva came out, continuing to struggle for some time before being overcome - probably by the injection of a poison. The mite would then gorge itself by sucking up the body contents. As the prey was usually larger than the mite, only part of its body was ingested before being

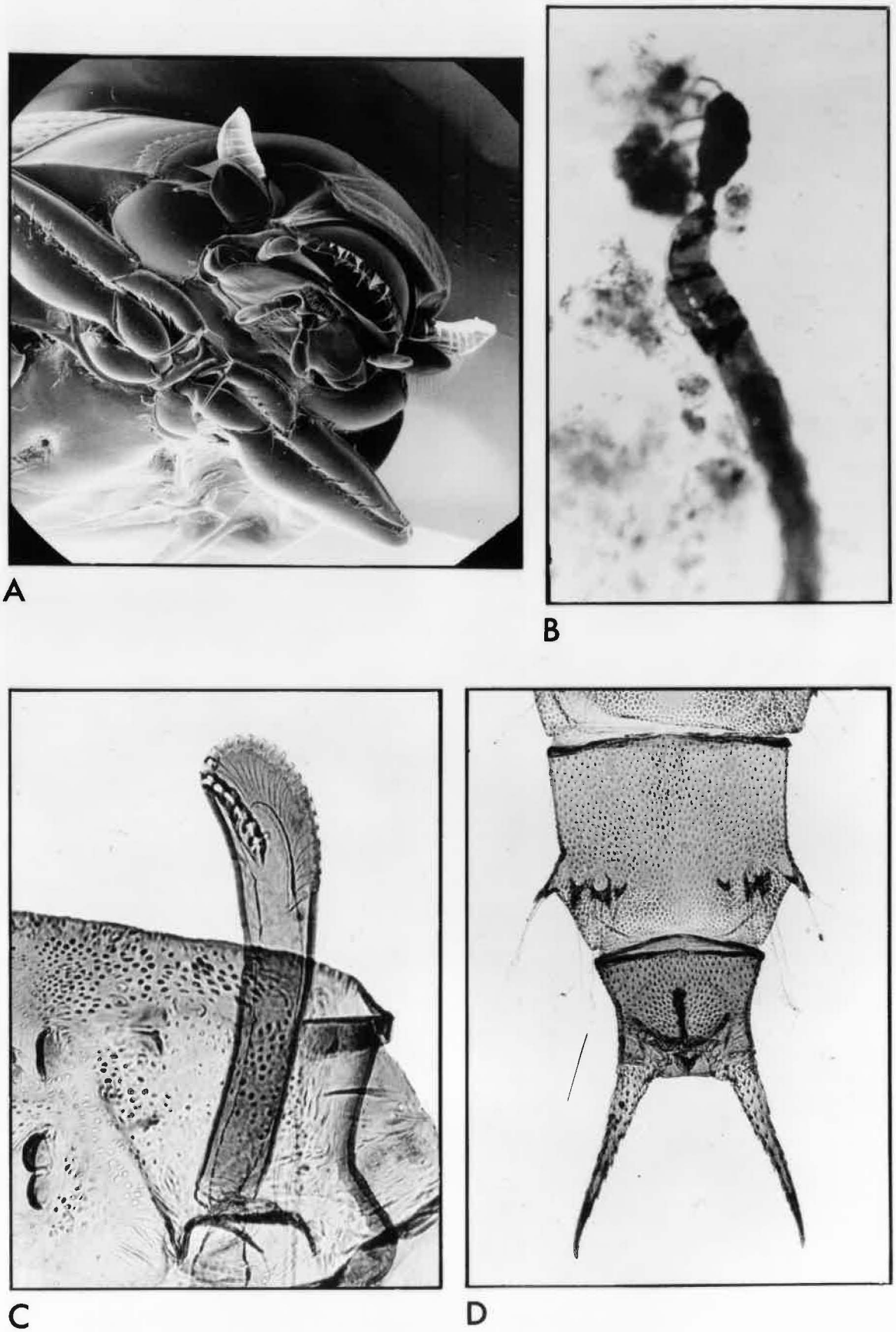


Plate 4. *Gyrinus convexiusculus*: (A) SEM photo of adult head, anterior view (M.A. Chapman, C. Beltz). *Limnochares* (*Cyclothrix*) sp.: (B) adult feeding on *Calopsectra funebris* larva. *Palpomya* sp.: (C) pupal respiratory organ; (D) caudal end of pupa.

discarded. Larvae were never observed to survive an attack.

Other mites, including Arrenurus sp. and Hydrachna (Anohydrachna) maramauensis, were present in the lake, but in much smaller numbers than in other Waipa lakes (pers. obs.).

LEPIDOPTERA

A few larvae of Nymphula sp. were found amongst the vegetation of the inlet drain and other seepage flows.

ODONATA

The most common damselfly was Xanthocnemis zealandica. A few specimens only of Austrolestes colensonis were collected. Both species were most numerous amongst the littoral vegetation. They were also collected on artificial substrates in 7 m of water, during winter and early spring. Their distribution is therefore probably restricted by the lack of suitable substrata.

A small population of the dragon fly Hemicordulia australiae was found amongst the littoral vegetation. Like the damsel flies, they were collected in too small numbers to give any indication of seasonal changes in population size.

EPHEMEROPTERA

A single specimen of Zephlebia versicolor was collected by light trapping in December 1981. This species has been collected from enriched streams (P. Summerhays pers. comm.) and may have come from one of the many drains surrounding the lake.

TRICHOPTERA

Oecetis unicolor was the most commonly occurring caddis. Cowley (1978) states that they are common in shallow areas of many lakes that have clear sandy areas of beach. In Lake Maratoto, although they occurred throughout the lake, they were most common at the 0.5 m station (Figure 2.4) where wave action had exposed a volcanic ash layer.

The maximum number of larvae occurred in winter (Figure 2.5), but in the summer there appeared to be a second generation since smaller animals again became abundant particularly on the edges of the lake. Cowley (1978) has recorded adults from October to at least April. In Lake Maratoto, adults, pupae and young larvae were common in November and December. These young larvae could therefore have emerged in the autumn to give rise to a second generation whose numbers would have peaked in mid winter.

Larvae of Triplectides cephalotes were most common on the very edge of the lake. Although rarely found in the deepest part of Lake Maratoto, a number were collected from artificial substrates placed in 7 m of water. They were also common on the sandy volcanic ash layers exposed at the southern end of the lake. As the larvae are phytophagous (Cowley 1978), they are likely to be restricted to areas where algae and weeds abound.

Numbers were generally low along the chosen transect, so seasonal trends are unclear. Cowley (1978) found their life cycle to be short, such that the young larvae which I collected in late spring could mature to give a second generation of larvae in winter.

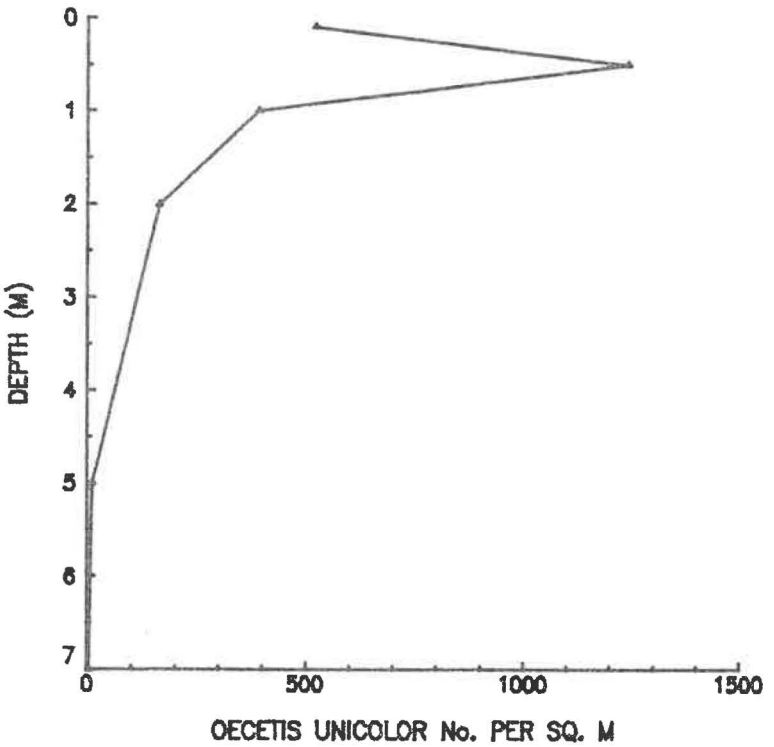
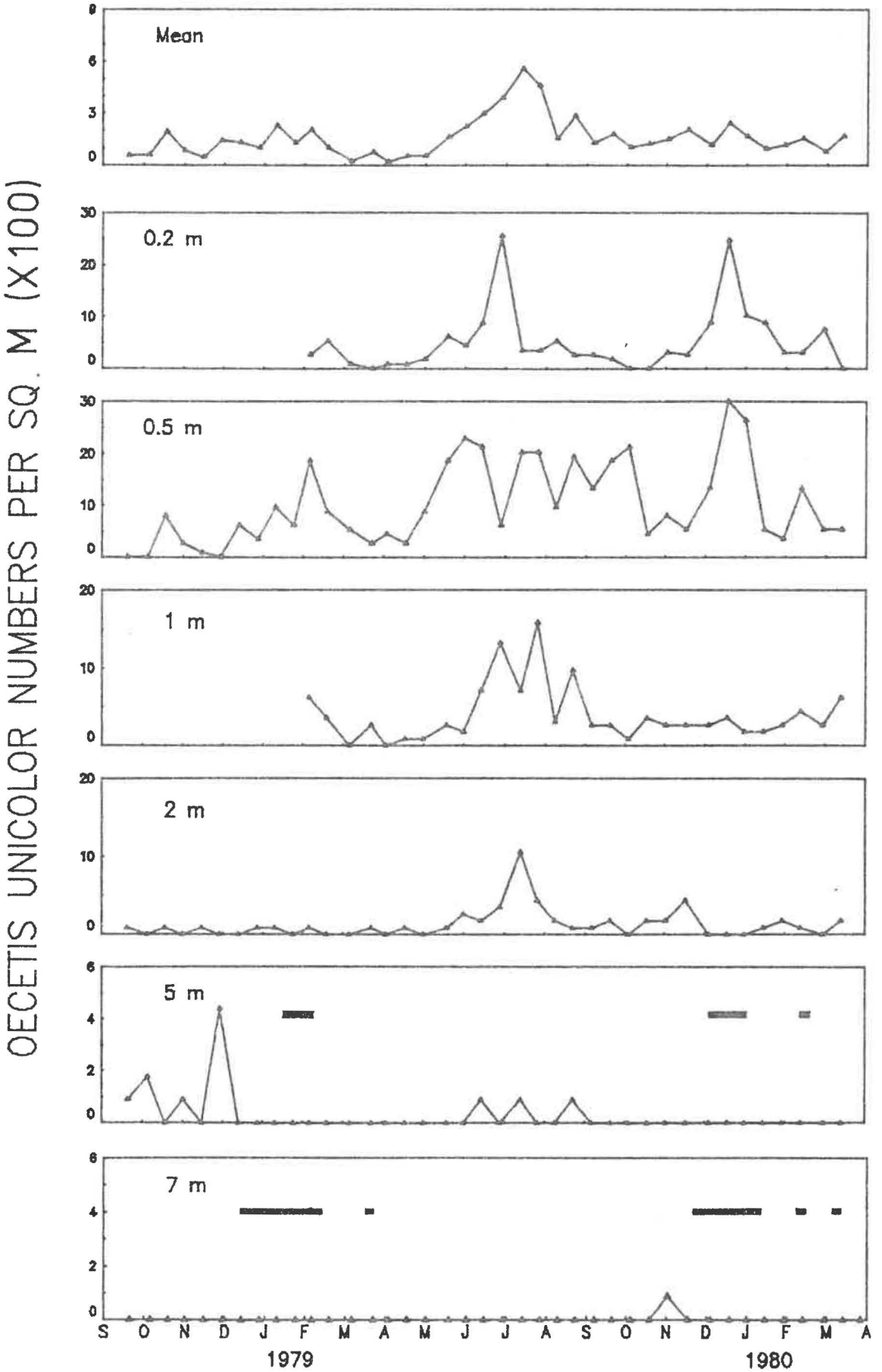


Figure 2.4. Mean depth distribution of Oecetis unicolor from 5/3/79 to 12/3/80.

Figure 2.5. Seasonal changes in population density of Oecetis unicolor. Horizontal black bars indicate periods when the oxygen concentration above the sediments was below 3 g per cubic metre.


OECETIS UNICOLOR NUMBERS PER SQ. M (X100)
Mean
0.2 m
0.5 m
1 m
2 m
5 m
7 m
S O N D J F M A M J J A S O N D J F M A
1979
1980

A few larvae of Polyplectropus sp. (?puerilis) were collected from the edge of the lake, and in up to two metres of water. The largest number of larvae were collected on artificial substrates. The larvae are free living and usually hide within an untidy cover of silk and detritus. In these tunnels, the larvae spend a large amount of time irrigating, but immediately investigate movements transmitted to them by the silk line laid around the hide. It would appear that a certain level of movement must reach the caddis before a reaction is recorded, as stage I chironomids and encased larvae were left untroubled. Later stages of chironomid larvae which were moving freely were always killed, even if the caddis was not hungry. These larvae, which were particularly prone to becoming tangled in the mass of silk, were usually first given a single bite. This resulted not only in the larvae rolling over and becoming even more entangled in the silk, but at the same time there appeared to have been an anaesthetising affect as struggling soon stopped. With the larger chironomids, attempts were then made to pull the prey under the cover of the hide where the body was eaten. Small chironomid larvae were swallowed whole. Decomposing chironomid larvae were never seen to be eaten, while freshly killed larvae were only accepted if moved in front of the caddis.

Very few specimens of Oxyethira albiceps were collected from the reed stems of the lake. It is surprising not to have found more specimens as this species is common in other Waikato lakes (pers. obs.). Cowley (1978) states that the distribution of this species is determined primarily by their food, and that they are most frequent where filamentous green algae are plentiful. Since these algae are abundant in Lake Maratoto it is possible that low pH also restricts the distribution of this caddis.

HEMIPTERA

Both Sigara sp. and Anisops wakefieldi were extremely common throughout Lake Maratoto. Some individuals of both species were trapped during core sampling, particularly on the edges of the lake during the summer when both populations peaked. Their densities were much higher than suggested by the numbers collected in these samples. Their presence made the use of underwater emergence traps for collecting chironomids impossible as when the water boatmen and back swimmers rose to the surface to breathe, many were trapped.

Anisops eggs were found on sticks and twigs on the edges of the lake but were also extremely dense on the polystyrene marker buoys anchored at the centre of the lake, particularly in late spring to early summer. Young (1970) found that eggs of both Notonectids and Corixids were laid from mid winter to late summer, larvae being present from spring to autumn. He also states that adults were present throughout the year but bugs that moulted to the adult form after late summer did not lay eggs before mid winter. This pattern agrees with what occurred in Lake Maratoto.

Notonectids are known carnivores, preying largely on chironomids (Forsyth and McColl 1974), but also on zooplankton. Corixids are supposedly phytophagous (Young 1970), although there are numerous indications of predatory habits (Henrikson and Oscarson 1981). The occurrence of high numbers of corixids in acid lakes has been attributed to a lack of fish predation (Henrikson and Oscarson 1981). Since there are no fish in Lake Maratoto, their abundance in this lake is not surprising.

Microvelia sp. were common at the surface of the water, particularly amongst the vegetation on the lake's edge.

COLEOPTERA

Beetle larvae that were collected along transect A were counted as one group. The most common species, Liodessus sp.n., were found from September to December on the very edge of the lake. Other coleopterans were rare. They included Paracymus pygmaeus and unidentified species of Elmidae which were found amongst moss and plants in seepage water.

Several specimens of Gyrinus convexiusculus (Plate 4A) were seen in the outlet drain throughout the sampling period and on one occasion a number were sighted on the edges at the southern end of the lake. Despite a thorough search, no larvae were found here. Two larvae were collected in mid November 1979 amongst submerged grass stems in the water at the edge of Lake Mangahia. The situation in which the larvae were found was not unlike that existing in the drain and on some edges of Lake Maratoto. It is therefore assumed that gyrinids also breed here.

DIPTERA

Ceratopogonidae

Larvae and pupae of Ceratopogonidae were common throughout the year amongst the mosses and plants of inlet drains, and in seepage flow. A number were also collected from the 0.2 m station and during the dry summer period (March to April) from the 0.5 and 1 m stations.

The majority of known New Zealand Ceratopogonidae have been described by Ingram and Macfie (1931) and Macfie (1932). Further species were described by Tonnoir (1924), Tokunaga (1964), Dumbleton (1971) and Sublette and Wirth (1980). Nothing is known of the aquatic

stages of these species. Of the larvae collected in Lake Maratoto, only two females and one male were successfully reared to the adult stage. Using the keys of Wirth et al. (1977) and Lee (1948), the species appears to be a Palpomya sp. but colour and measurements do not match described Australasian species (Macfie 1932; Lee 1948). The pupa is shown in Plate 4.

In the laboratory larvae of Palpomya sp. were seen to feed both on freshly killed and on partly decomposed chironomid larvae. There was a preference for recently killed and maimed larvae. Ceratopogonid larvae seem to be incapable of piercing the skin of their food for it is only where this has been damaged that the animal is able to prod with its head and burrow into the food mass while ingesting it. Several ceratopogonid larvae were seen burrowing deeply into the body and skin of dead chironomids.

Culicidae

Mosquito larvae were present behind the reeds and in stagnant pools on the edges of the lake. No identification was attempted.

Chironomidae

Next to the oligochaetes, this group of animals was the most common in Lake Maratoto, representing about 40% of the mean standing stock of the lake. The largest population was found on the edges of the lake. Although numbers were relatively small in deeper water, they contributed 96% and 87% of the annual mean total benthic population at the 7 m and 5 m stations. Thirteen species were found, including predators, deposit feeders and filter feeders. Because of their importance in the lake, the group is dealt with in detail in Chapter 3.

PISCES

Short fin (Anguilla australis) and long fin eels (A. dieffenbachii) are fished for commercial purposes in Lake Maratoto and a reasonably large population is therefore presumed to exist. A number of elvers were caught in the outlet drain in early December. After that date, little migration could take place due to lack of water flow.

No other fish species inhabit the lake. This is probably because of the low pH of the water which is thought to disturb the normal ion and acid base balance in fish, causing their death (Wiederholm and Eriksson 1977). In the outlet drain there is a small population of the mud fish Neochanna diversus. Eggs of the common bully Gobiomorphus cotidianus were also collected here in June 1980.

2.4 GENERAL DISCUSSION

Polyhumic or dystrophic lakes such as Lake Maratoto normally have a low species diversity and a concentration of the fauna on the very edge (e.g. Brundin 1949; Berg 1955; Wiederholm and Eriksson 1977). However the total of 20 macrobenthic species recorded quantitatively in Lake Maratoto cannot be compared with a mean of 12.4 species per lake (max. 26, min. 1) for 20 South Island lakes (Timms 1982) and 11.4 (oligochaetes not identified) in seven Rotorua lakes (Forsyth 1978), because these authors used different sampling methods and did not include the littoral zone. The paucity of species in Lake Maratoto is better shown by comparison with Lake Grasmere, a mesotrophic lake in Canterbury, where Stark (1981) found 113 macroinvertebrate species or groups in the macrophyte beds, including 17 chironomid species.

Taxonomic problems prevent adequate comparisons of species diversity between New Zealand lakes at present but even when the fauna is fully known, it is likely to be less diverse than in continental lakes. New Zealand's geographic isolation, climatic vagrancy and lack of refuges during the Pleistocene glaciation, have prevented the establishment of a rich fauna, and the survivors tend to occupy broad rather than specialised niches (Forsyth 1978; Timms 1980). Thus, the low species diversity found in Lake Maratoto is not solely the result of the characteristics of the lake, but also reflects the overall low species richness of the New Zealand fauna.

Despite difficulties in comparing the species diversity of Lake Maratoto with that of other lakes, the absence of fish, gastropods and Malacostraca, as well as the presence of large numbers of *Kiefferulus opalensis* (see Chapter 4), is considered to be significant, and a result of the humic characteristics of this lake.

The concentration of the majority of the fauna on the lake shore is also of note. McLachlan and Dickinson (1977), who recorded a comparable distribution in a Northumberland bog lake, found that peat particles entering the lake as a result of wave erosion of the shore constituted an important and highly nutritious input. These peat particles while in suspension became well colonised by micro-organisms, and resettled only a short distance from the shore, where they were the major food source of the fauna.

Algae, particularly epiphytic and benthic species, also constitute a significant proportion of the diet of many invertebrates. Due to poor light penetration in humic stained lakes, photosynthesis is restricted to shallow depths. Benthic animals dependent, either partially or completely, on this food source, will thus be restricted to the shore line.

The oxygen levels in the water do also contribute to the uneven depth distribution of the fauna. The relationship between the population size of chironomids and the oxygen concentration of the water above the sediments is shown in Figure 2.6, and in spite of the considerable scatter of points which reflects the clumped distribution of the fauna, the relationship is significant. Oxygen levels may limit the population size for two reasons. Firstly, low oxygen levels, combined with the low pH may severely limit the development of the microfauna, especially that of heterotrophic aerobic bacteria. As these form the bulk of the diet of many invertebrates, particularly of worms (Brinkhurst et al. 1969), a decrease in their numbers will consequently affect the macrofauna. Secondly, not only will low levels of oxygen in the water exclude animals from the sediment surface, but oxygen deficits within the sediments can also prevent its colonisation by burrowing animals, even if levels of oxygen above the sediment are not limiting.

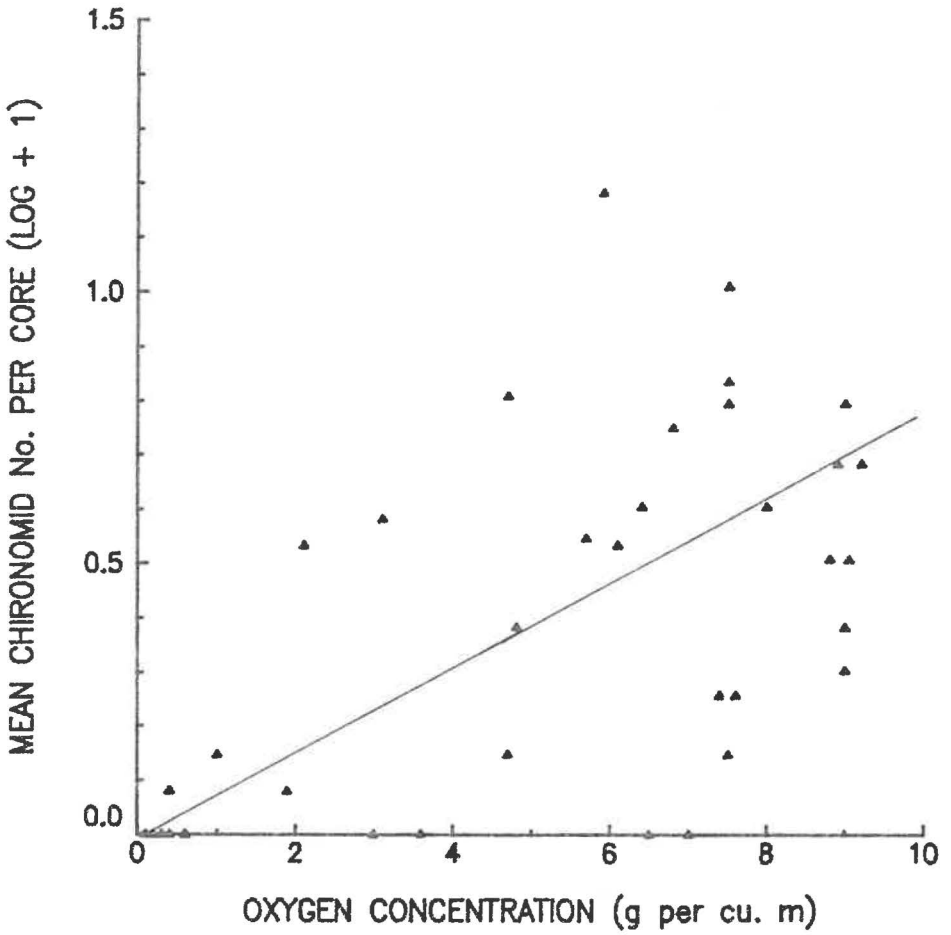


Figure 2.6. The relationship between mean chironomid numbers at the 7m station and oxygen concentrations in the water immediately above the sediments. Regression line, $Y = 0.0605 + 0.0627\ x$, $r^2 = 34.5\%$, $p < 0.001$.

This may explain why, despite their higher tolerance of low oxygen concentrations, oligochaetes were always excluded from the centre of Lake Maratoto, while chironomids, which can build tubes above the sediments, were present there for most of the year.

The decrease with depth of both the number of individuals and of the number of taxa can also be attributed to the changes in sediment type with depth. The stone cased caddis Oecetis unicolor for example, was most common when volcanic ash was also present in the sediment. On the edges, the substrate is generally coarser and more diverse (Section 1.2.4) and offers numerous hides and crevices that may be exploited. Conversely, the sediment in the centre of the lake is fine and uniform. Further examples of the importance of substrata are found in the colonisation of artificial substrates (plastic pot scrubbers) by species not otherwise expected in a particular area - damsel flies in the deeper water of Lake Maratoto for instance.

The low species diversity of humic lakes is probably an indication of the general uniformity of the bottom sediments, which lack the variety present in other lake types where various aquatic macrophytes and different sediment particle sizes contribute to the substrate diversity.

In summary, the major causes of the distribution pattern described in Lake Maratoto are: concentration of the food source on the lake shore, low oxygen concentrations at the centre of the lake, and a more diverse sediment on the edges. This makes the shore line, particularly the area which floods during periods of high water, extremely important. These areas, which when flooded may be covered with 10 to 50 cm of water, deserve greater attention in future studies, for they are highly productive. It is unfortunate that efficient man-made drainage now

prevents major and prolonged flooding of swamp land surrounding the many lakes in the Waikato, for these areas, which were widespread in the past, are extremely important habitats.

CHAPTER 3

CHIRONOMIDAE FROM LAKE MARATOTO AND OTHER WAIKATO LAKES.

"In Chironomidae there is rarely anything particular to say about the fifth tarsal segment"

Brundin (1966)

3.1 NOMENCLATURE

In New Zealand, as in America and Britain, systematists have in the past largely based the taxonomy of chironomids on imaginal characters (Hudson 1892; Hutton 1902; Kieffer 1921; Tonnoir 1923; Pagast 1947; Freeman 1959). The result has been an overlap of genera, a lack of association between adult and immature stages, and a consequent paucity of ecological information.

Over the past decade a preference has developed for smaller genera, with classification based on characters of all life stages (Brundin 1966; Forsyth 1971; Sublette and Wirth 1980), but there is still much inconsistency in the application of the classifications (e.g. Martin 1982). Despite major efforts, notably those of Forsyth (1971, 1975b, 1979) and the recent publication of a key to the larvae (Stark 1981), the New Zealand chironomids remain for the most part unexplored.

To clarify the nomenclature used in this thesis, a brief description of the chironomid taxa encountered is given.

3.1.1 Methods

Larvae and egg cases were collected from a wide range of habitats and reared in the laboratory to the adult stage. High mortality rates resulted in the summer, but rearing of larvae in winter and early spring was more successful. Larvae were normally placed singly in 3 cm diameter covered petri dishes with a small amount of sediment and water and, for some species, moss and filamentous algae. This was usually enough for the larvae to develop to adults. Small amounts of yeast and/or commercial goldfish food were added to the rearing chamber at the beginning of the study, but better survival rates were obtained without this additional food. The emerged adults were allowed to remain in the

rearing chamber for at least 6 hours, as teneral specimens are less suitable for taxonomic purposes. The adults were killed by blowing chloroform vapour into the chamber, and were eventually stored with their exuviae in vials of 70% ethanol to which a few drops of glycerol had been added to prevent desiccation.

To identify chironomids accurately, slide mounts must be prepared. P.V.A. lactophenol, to which chlorazol black had been added as a stain, was found to be the most satisfactory mounting medium. With adults, some preliminary clearing of the body in hot KOH was required but all other material was mounted directly.

Photomicrographs were taken to illustrate distinctive features. Examination of some of the material under the S.E.M. also helped clarify some of the taxonomy. Keys that were found particularly useful include those of: Edwards (1929), Johannsen (1937), Freeman (1959, 1961), Bryce and Hobart (1972), Mason (1973), Beck (1976) and Coffman (1978).

3.1.2 Description of Taxa

TANYPODINAE

Identification of larvae of this group is difficult, genera and species only being easily separable as adults. All larvae from this sub-family were therefore dealt with as one group.

Four taxa have been recorded either as adults, pupae or larvae from Lake Maratoto. These are *Ablabesmyia mala* (Hutton) (Plate 5A), *Pentaneura* sp. (Plate 5B), *Gressittius antarcticus* (Hudson) (= *Macropelopia antarctica* Forsyth 1978) (Plate 6) and *Macropelopia* spp. (probably *M. apicinella* and *M. umbrosa*) (Plates 5C, 5D).

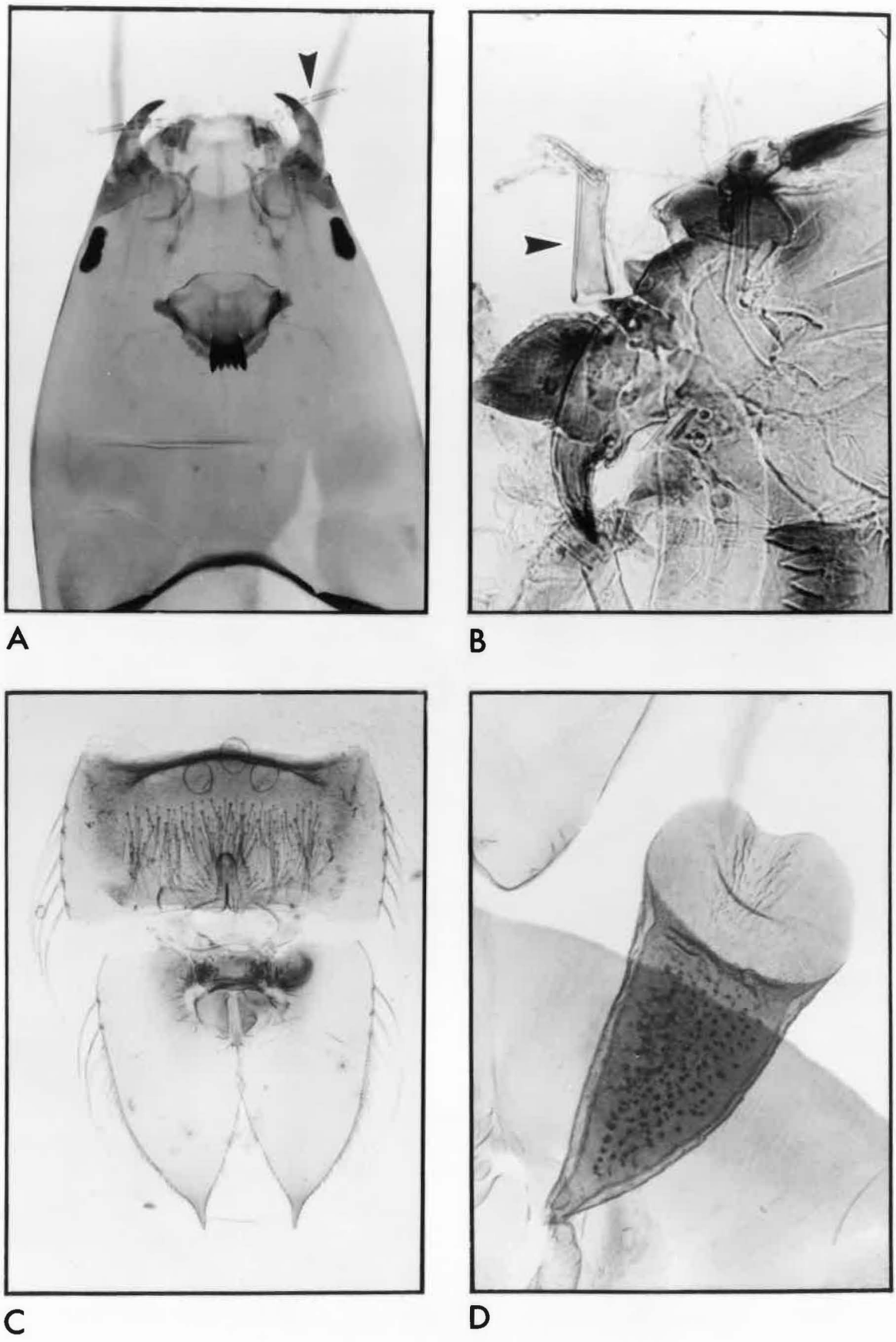


Plate 5. *Ablabesmyia mala:* (A) larval head capsule - note multisegmented base of maxillary palp. *Pentaneura* sp.: (B) larval head capsule - note maxillary palp with single basal segment. *Macropelopia* sp.: (C) pupal swim fin; (D) pupal respiratory organ.

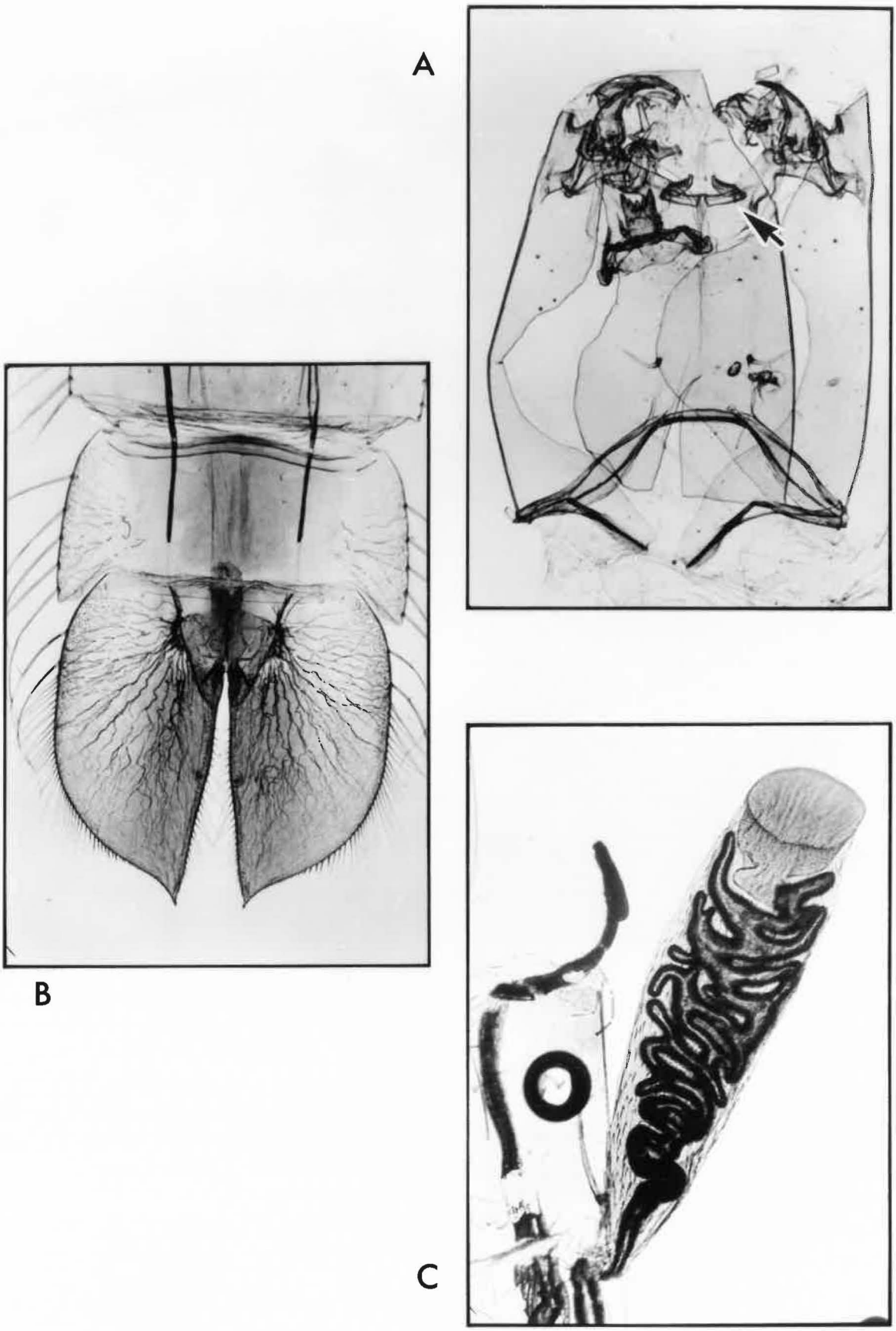


Plate 6. *Gressittius antarcticus*: (A) larval head capsule - note paralabial combs; (B) pupal swim fin; (C) pupal respiratory organ.

PODONOMINAE

On the basis of male genital characters, the podonomids collected from Lake Maratoto cannot be separated from some members of the Parochlus (araucanus group). Brundin (1966), has named several species based on pupal descriptions only, but none resemble species collected here. The presence of closely set denticles on the anal spurs of my pupa is distinctive (Plate 7).

ORTHOCLADIINAE

Despite the collection and association of larvae, pupae and adults, the generic placement of the orthoclads collected in the Waikato lakes remains tentative. Three taxa were separated but it is likely that a thorough examination and description of animals in the district will separate more species.

Syncricotopus sp.

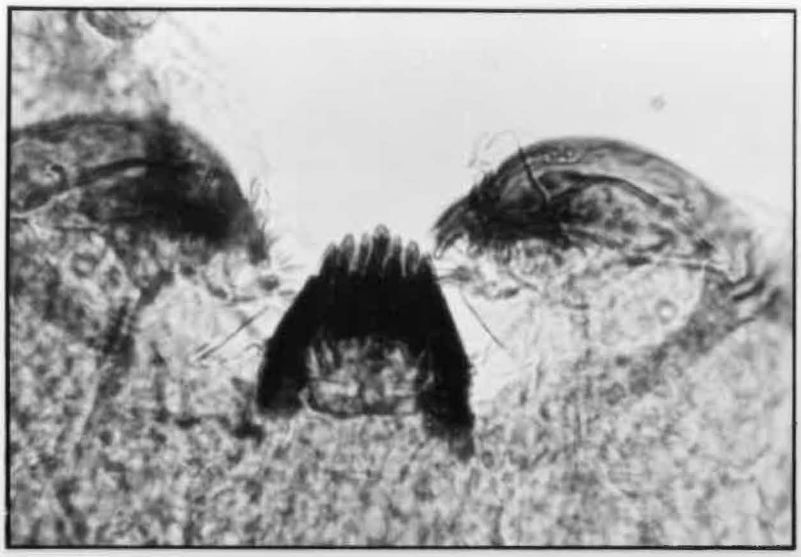
These larvae have a single tooth at the centre of the labial plate (Plate 8A) and are free living.

Eukiefferiella sp.

The middle teeth of the labial plate project and are narrowly separated (Plate 8B). It is possible that at least two species have been included here since larvae and pupae of differing coloration, notably of the eye, have been collected.

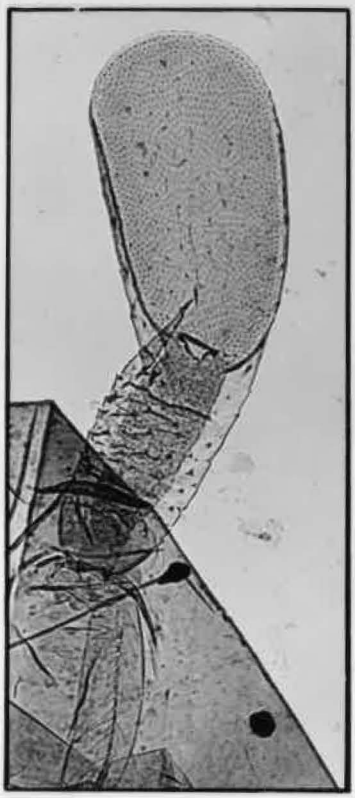
Metriocnemus sp.

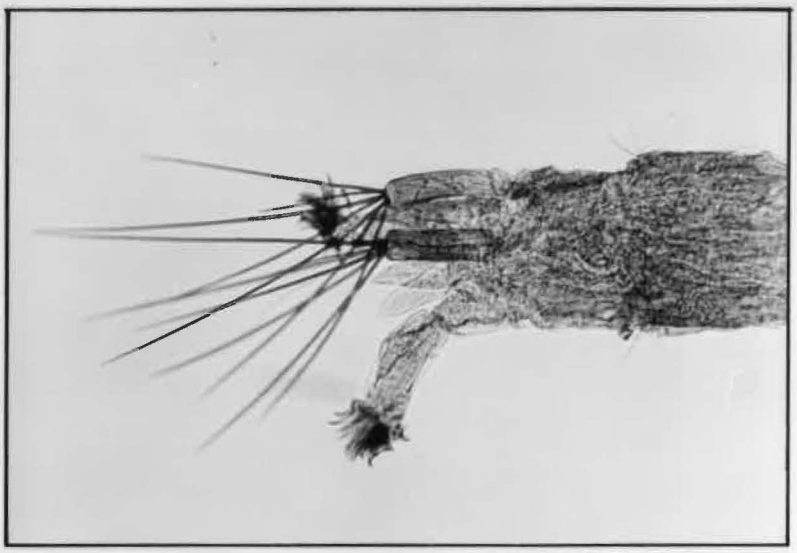
These larvae are free living and have a violet tinge. The head capsule (Plate 9A) is more sclerotised than that of the other orthoclads. In the pupae there are well developed spinules along the



A

B





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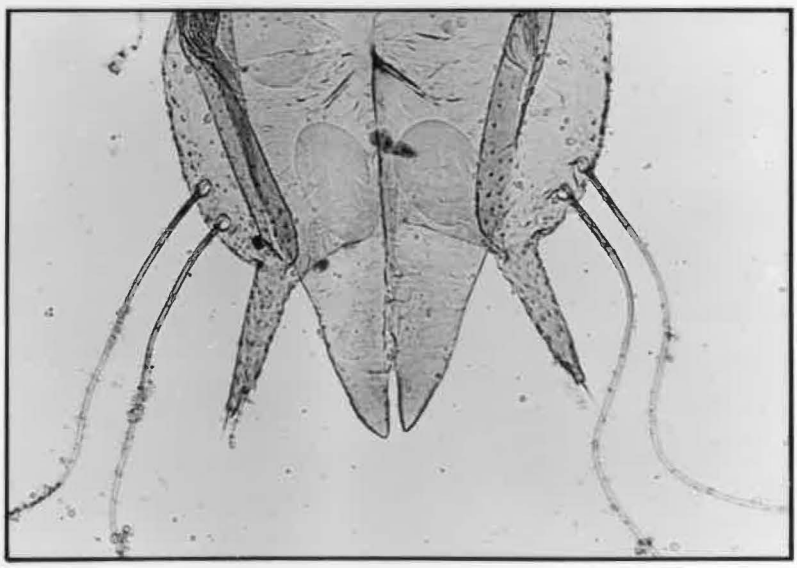

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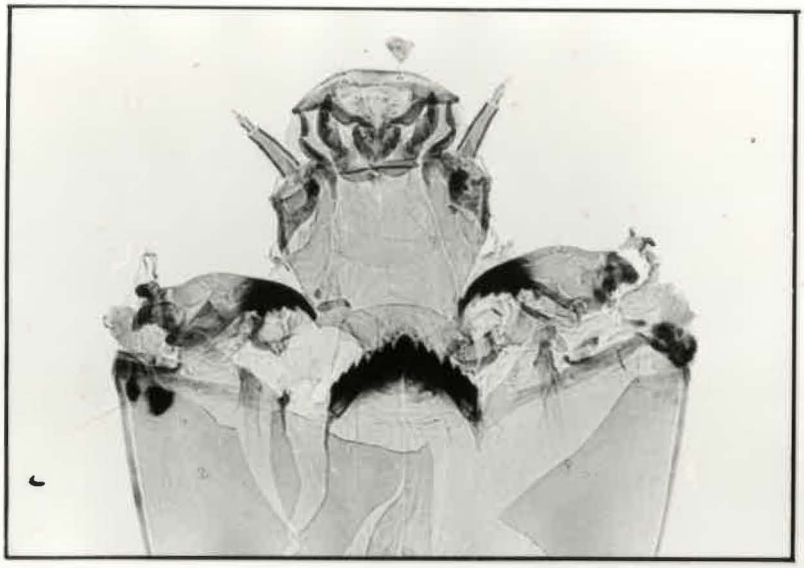
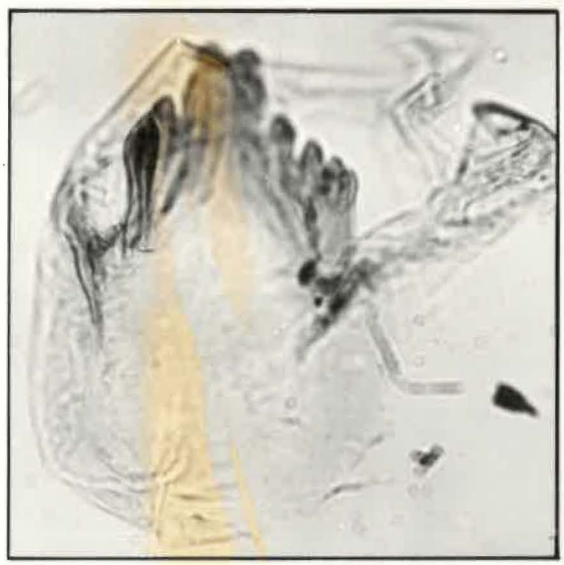
Plate 7. *Parochlus* sp.: (A) larval labial plate and mandibles; (B) caudal end or larva; (C) pupal respiratory organ; (D) caudal end of pupa.



A

B



C

D

Plate 8. *Syncricotopus* sp.: (A) larval head capsule. *Eukiefferiella* sp.: (B) larval labial plate and mandibles. Unidentified orthoclad I: (C) larval labial plate. Unidentified orthoclad II: (D) larval labial plate.

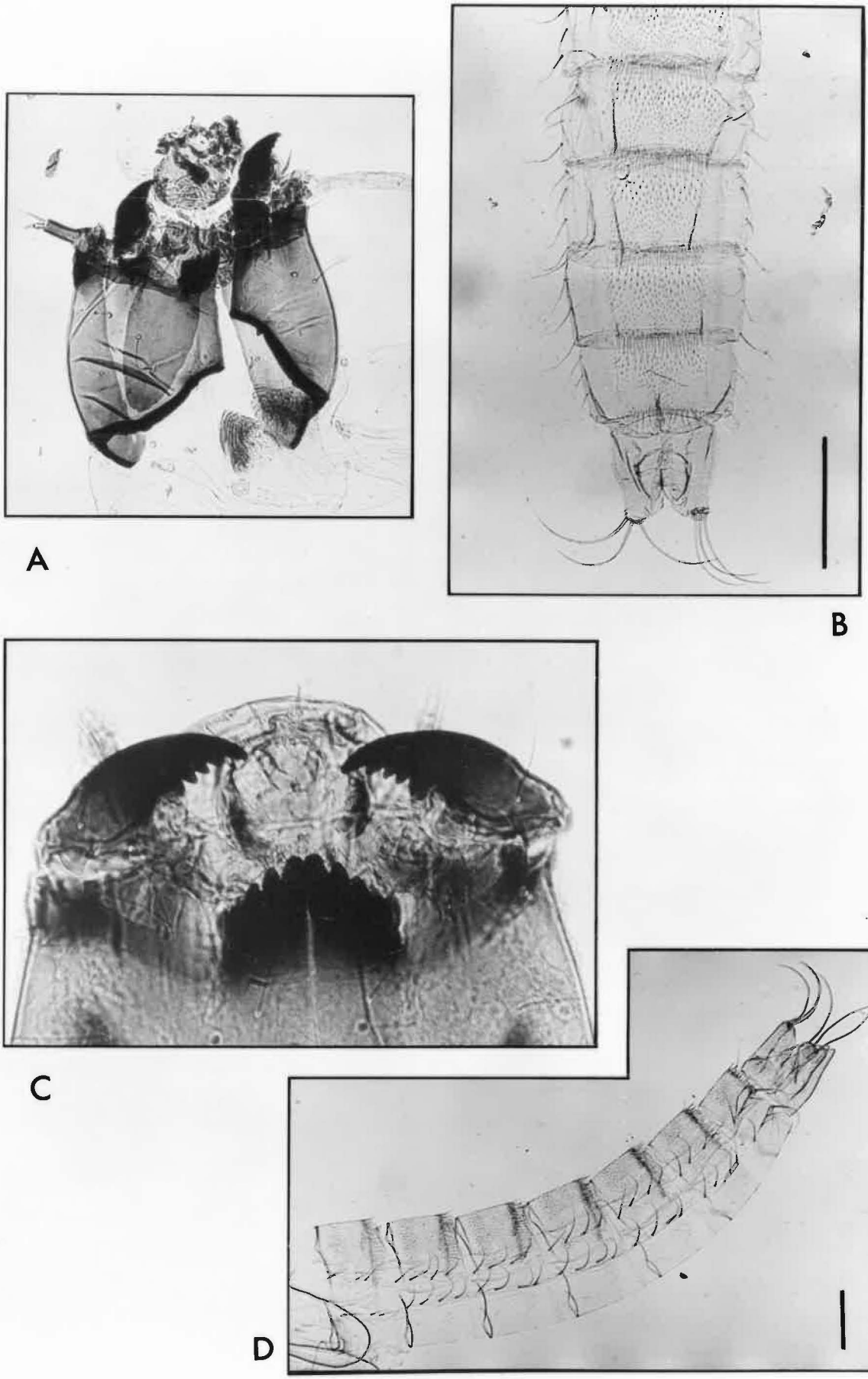


Plate 9. *Metriocnemus* ? sp. 1: (A) larval head capsule; (B) pupal exuviae. *Metriocnemus* ? sp. 2; (C) larval head capsule; (D) pupal exuvium. Scale bar = 0.2 mm.

posterior margins of tergites 2 to 8 (Plate 9B, 9D). Pupation takes place within a sealed case constructed of detritus and silk.

Possibly two species may have been included here. One of these is parthenogenetic (a laboratory culture produced several generations without the appearance of a single male). Differences in size of all instars (Plate 9) and in the morphology of the larvae, notably in the length of the antennal blade, were observed, but insufficient animals were reared for complete description.

Unidentified Orthoclad I

This orthoclad was only found as microfossils in Waikato lake sediments. It can be separated from other orthoclads by the two middle teeth of the labial plate that project well above the others (Plate 8C).

Unidentified Orthoclad II

As with the above orthoclad, this taxa has only been found as a microfossil. The labial plate has three central teeth projecting above the others (Plate 8D).

CHIRONOMINAE

Chironomus zealandicus Hudson

This species group is the only one in New Zealand for which field and laboratory data on larvae are available - perhaps a reflection of its large size and widespread geographical and bathymetric distribution. A review of the literature as well as personal observations suggest that C. zealandicus type larvae represent a complex of species that have not as yet been separable morphologically. Species whose larvae closely resemble each other include C. antipodensis and C. subantarcticus (Sublette and Wirth 1980), C. analis and possibly several distinct

cytological forms of C. zealandicus. Only the presence/absence of gills has so far been used as grounds for the separation of larvae (Lamb 1961; Robb 1966; Forsyth 1971; Sublette and Wirth 1980). These gills were found by Robb (1966) to develop according to salinity and oxygen levels, while overseas work on related species has shown that pH is also involved (Ueno 1938). Taxonomic use of gills therefore may not be reliable.

Differences in coloration and marking both in the larvae and pupae have been noted from material obtained in varying localities, but I have been unable to determine if these were real morphological differences or if they were simply environmental or age differences. In Lake Maratoto all larvae collected had two pairs of ventral blood gills and a trifid middle tooth of the labial plate (Plate 10A). Adults that were reared or caught on the wing fitted the description of C. zealandicus Hudson given in the review of Freeman (1959). In Lake Rotomanuka, larvae similar in appearance to the one figured here have been associated with C. analis (Plate 10D).

Cladopelma curtivalva (Kieffer)

Larvae of C. curtivalva (= Chironomus cylindricus Forsyth 1971) are best distinguished from the other Chironomini by the large outer, lateral pair of teeth of the labial plate (Plate 11A). The mandible is also distinctive (Plate 11B). The pupae can be recognised by the posteriolateral spurs of tergum VIII (Plate 11C), but more easily by the presence of a mace on the sixth abdominal segment.

A

B

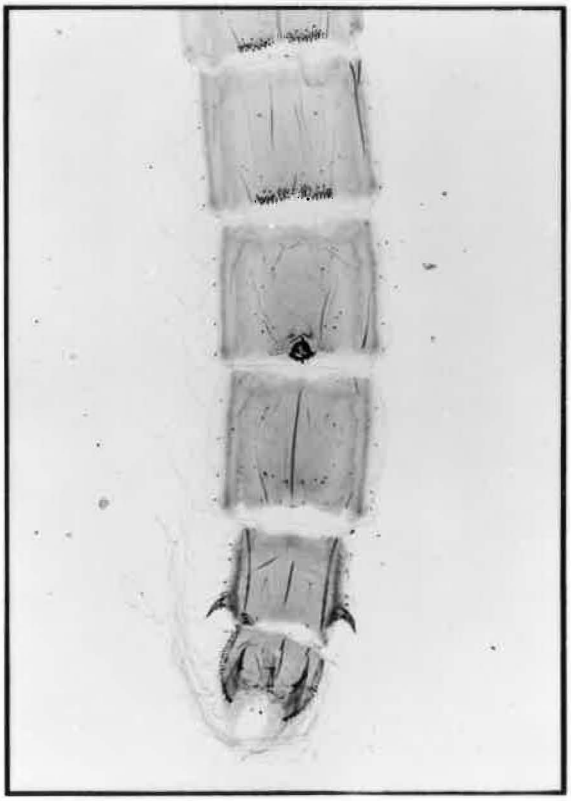
C

D

Plate 10. *Chironomus zealandicus*: (A) SEM photo of larval head, ventral view; (B) pupal posteriolateral spur of segment VIII; (C) SEM photo of male genitalia. *C. analis*: (D) SEM photo of male genitalia.

A

B



C

D

Plate 11. *Cladopelma curtivalva*: (A) larval head capsule; (B) larval mandible; (C) pupal exuvium; (D) SEM photo of male genitalia.

Kiefferulus opalensis Forsyth

Only one species of Kiefferulus has been recognised so far in New Zealand. A full description of all life cycle stages is given by Forsyth (1975b). In Australia where three species have been recorded, two species can be separated only with difficulty (Martin 1964). Cytological studies on the New Zealand species would be of help in confirming the present state of identification.

K. opalensis may be differentiated from other New Zealand Chironomini by the racquet shaped appendage 1 of the adult (Plate 12E) and by the shape of the posteriolateral spurs of the pupa (Plate 12D). The larva has one pair of ventral blood gills (Plate 12B) and the paralabials have serrated anterior edges (Plate 12C). The middle tooth of the labial plate is notched (Plate 12A).

Polypedilum pavidus (Hutton)

Polypedilum species are difficult to separate as larvae but can easily be distinguished as pupae and adults.

The large, paired, central teeth of the labial plate flanked by much smaller first laterals (Plate 13A) are distinctive of the genus. The pupal spurs (Plate 13B) which I associate with P. pavidus do not resemble those figured by Forsyth (1971, Figure 10G). Whether this is because of morphological variation awaits further clarification.

Paucispinigera approximata Freeman

The paired medial teeth of the labial plate are much smaller than the first lateral teeth. The second laterals are shorter than, and fused to, the third laterals (Plate 13C).

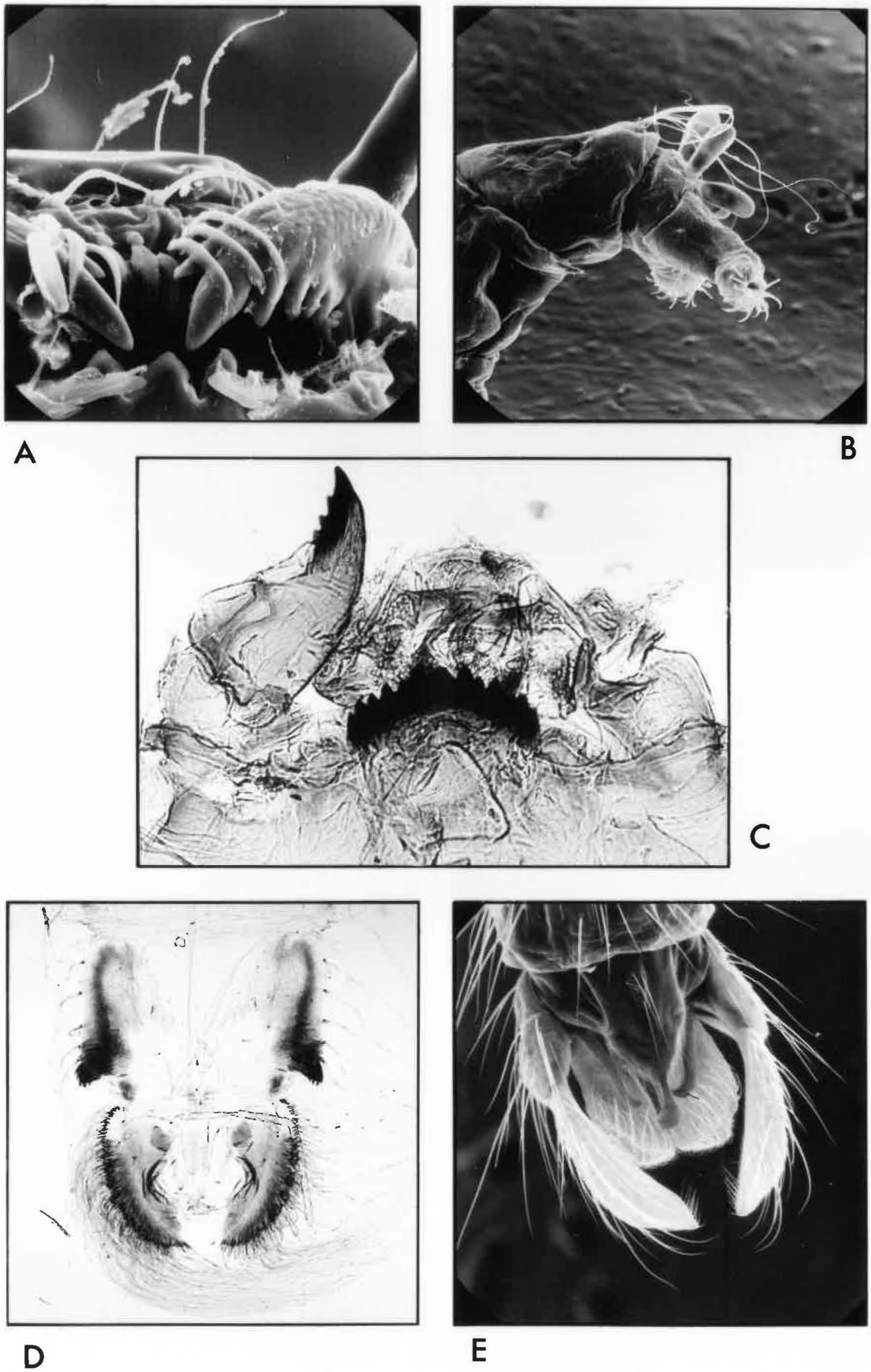


Plate 12. *Kiefferulus opalensis*: (A) SEM photo of larval head, anterior view; (B) SEM photo of caudal end of larva; (C) larval head, ventral view; (D) caudal end of pupa; (E) SEM photo of male genitalia.

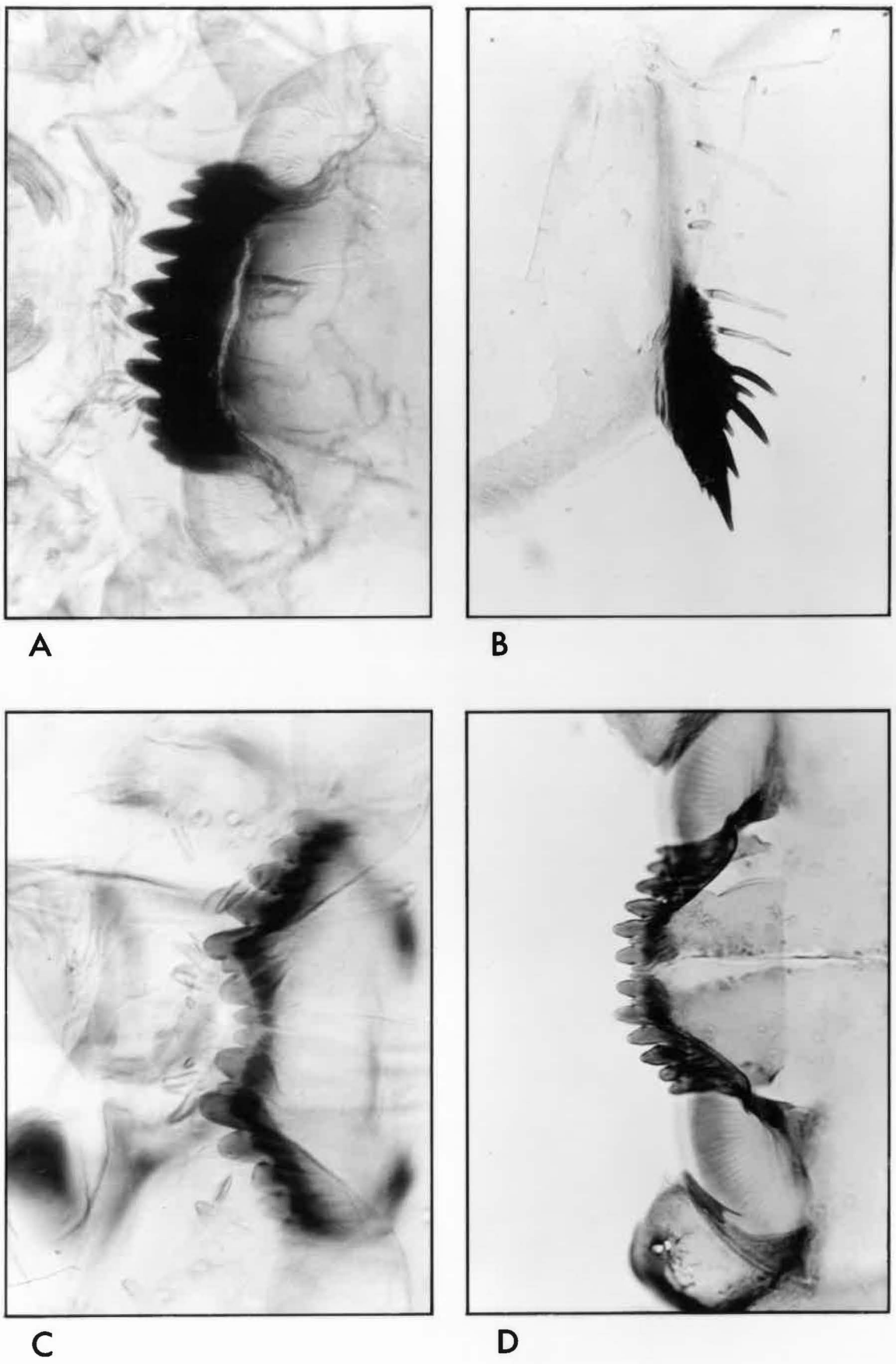


Plate 13. *Polypedilum pavidus:* (A) larval labial plate; (B) pupal posteriolateral spur of segment VIII. *Paucispinigera approximata:* (C) larval labial plate. *Paucispinigera* sp.: (D) larval labial plate.

Paucispinigera sp.

The paired medial teeth and second lateral teeth of the labial plate of this species are minute. The first and third laterals are of equal size (Plate 13D).

Cryptochironomus sp.

I have collected larvae of this genera in the Waitomo Stream but in the Waikato region only fossilised remains of the larvae have been found. The labial plate is shown in Plate 14B.

Harrisius pallidus Freeman

Only a few adults of this species were collected by light trapping on Lake Rotomanuka. Stark (1981) found some larvae inside partly decomposing wood in mountain streams, and it is probable that the imagines I collected came from a neighbouring stream.

Parachironomus ? cylindricus (Freeman)

This species is only known as microfossils in the Waikato but has been recorded in South Island lakes. The labial plate is shown in Plate 14C.

Unidentified Chironomini I

Since this taxa is known only from a few fossilised larval remains, its generic placement is uncertain. The labial plate is shown in Plate 14A.

A

B

C

Plate 14. Unidentified Chironomini I: (A) larval labial plate. *Cryptochironomus* sp.: (B) larval labial plate. *Parachironomus ? cylindricus*: (C) larval labial plate.

TANYTARSINAE

Calopsectra funebris (Freeman) (= Tanytarsus funebris Forsyth 1971)

All stages of C. funebris have recently been redescribed by Sublette and Wirth (1980), although it is likely that the name Calopsectra has been wrongly applied by these authors (D. Forsyth pers. comm.; L. Sawedal pers. comm.).

The larvae can be separated from other Tanytarsini larvae by the clear medium tooth of the labial plate (Plate 15A) and the long Lauterborn stalks (Plate 15B). Other characteristics of the larvae, pupae and adults are shown in Plates 15A-D.

Calopsectra sp.

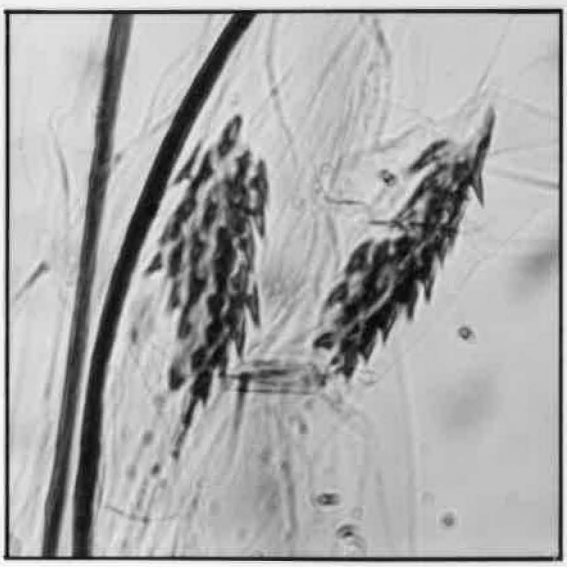
This species was only recorded as macrofossil remains in the Waikato but mouth parts closely resemble those of a larvae collected from the Waimangu Valley (Rotorua). These larvae have attributes of both Calopsectra funebris and Corynocera sp. (Plate 16A). Adults and pupae of this species closely resemble those of C. funebris and Corynocera sp. and so far cannot be separated from them.

Corynocera sp. (= Dryadotanytarsus ? duffi Deevey 1955)

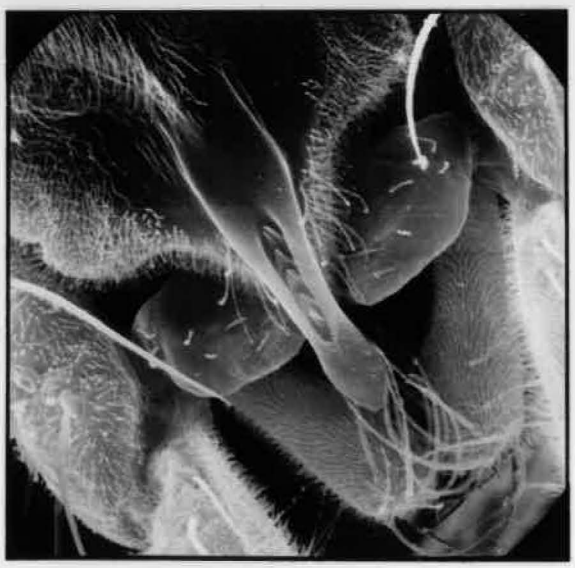
The larvae collected in the Waikato look similar to the northern hemisphere Corynocera spp. (Hirvenoja 1961; Linevitsh 1962; Lehmann 1973). The labial plate and mandibles (Plate 16B) are distinctive. The pupae and adults which were all reared from larvae, closely resemble C. funebris to which they are probably related.

A

B



C



D

Plate 15. *Calopsectra funebris:* (A) larval labial plate; (B) antennae; (C) pupa, abdominal tergum IV; (D) SEM photo of male genitalia.

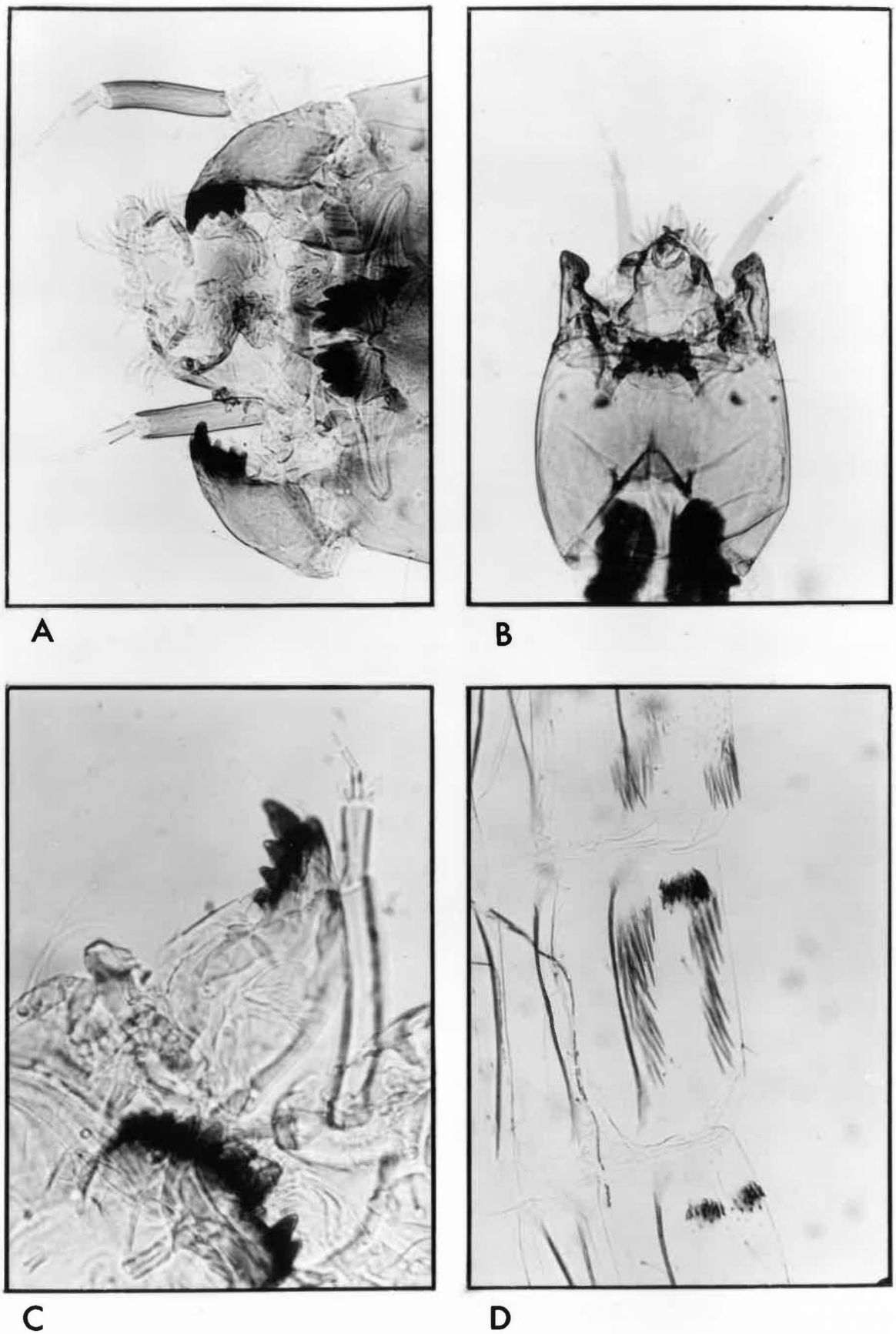


Plate 16. *Calopsectra* sp.: (A) larval head capsule. *Corynocera* sp.: (B) larval head capsule. *Paratanytarsus agameta:* (C) larval mandible, antenna and labial plate - one of the first laterals is broken; (D) pupa, abdominal tergites III to V.

Some variations in the size of the adults and in the number of spines on the anal points of the males were noted between the species, but with the Tanytarsini these characters are not considered useful taxonomically (Reiss 1968; Paasivirta 1972). Precise relationship to the other Tanytarsini species must therefore await cytological examination.

Paratanytarsus agameta (Forsyth)

P. agameta (= Lundstroemia agameta Forsyth 1971) is parthenogenetic, no males ever having been collected or reared. The pupae have long spinules on most tergites that distinguish them from the other Tanytarsini (Plate 16D). The antennae of the larvae have only short Lauterborn stalks and the labial plate is unicoloured (Plate 16C).

3.2 DETERMINATION OF CHIRONOMID INSTARS

The recognition of larval instars in the Chironomidae is essential to the description of their biology. With these larvae, as with those of many other insects, the soft body steadily increases in size as the animal grows, but the sclerotised head capsule changes in size only at the time of each moult, and so can be used for instar determination. However, if growth rates differ greatly between seasons or habitats, the head capsule size ranges of different instars may overlap and cause errors in determining the age structure of populations. Although McCauley (1974) stated that the effects of temperature on the head capsule sizes in chironomids are only important in extreme cold or in tropical situations, Iovino (1975) has shown that larvae of Chironomus attenuatus reared at 15 'C were considerably larger in all instars than larvae reared at 25 'C. In any chironomid population study, it is therefore essential to determine the reliability of separating larval instars by measurements of the head capsule and body. Furthermore, the few previous instar determinations that have been obtained for Chironomus zealandicus (Robb 1966; Forsyth 1971; Forsyth and McColl 1974; Graham 1976), Polypedilum pavidus (Stephens 1978), Paratanytarsus agameta (Stephens 1978; Towns 1981) and Maoridiamesia harrisi (Towns 1981), may not be applicable to larvae in Lake Maratoto.

3.2.1 Methods

Chironomid larvae were obtained at regular intervals from various depths of Lake Maratoto (see Chapter 2). Further material was also collected, mainly for comparison, from other Waikato lakes. As numbers of first instar larvae collected in the field were low, where possible, additional larvulae were obtained by hatching eggs in the laboratory.

Animals were examined under a stereo microscope at 80X magnification. Measurements were made of the length (posterior rim to tip of labrum) and maximum breadth of the head capsule, and of the body of unmounted specimens. If necessary, larvae were subsequently mounted in P.V.A. lactophenol and identified under a compound microscope.

3.2.2 Results and Discussion

In all but two of the taxa investigated, four distinct size classes could be recognised using head width or length measurements (Table 3.1). The occurrence of four larval instars in the Chironomidae is probably universal (Oliver 1971) and the failure to find very small Parochlus sp. is probably because they were absent from my sample.

The size classes that have been determined here for Lake Maratoto are probably applicable to that lake only. Size differences have been found between Lake Maratoto Chironomus zealandicus and those from Lake Ngaroto (Waikato) and Blue Lake (Rotorua). Measurements given by Robb (1966) and Graham (1976) also show some variations from those given here (Table 3.2). Although these differences could be due to the presence of different Chironomus species in these lakes, it is likely that they were caused by temperature and food availability.

Although the various chironomid taxa were expected to show some differences in the shape and growth rate of their head capsule, this was not found. Logarithmic plots of head length versus head width of each taxa gave linear relationships with no significant differences between the slopes for each taxa (Figure 3.1).

Taxa	Stage	Head width (µm)					Head length (µm)					Body length (mm)				
		$\bar{x}$	S	min	max	n	$\bar{x}$	S	min	max	n	$\bar{x}$	S	min	max	n
Tanypodinae	I	137	14	87	175	44	189	16	175	225	39	1.7	0.3	1.6	2.8	42
"	II	248	23	175	325	83	330	29	250	450	77	2.8	0.7	1.5	6.3	82
"	III	473	33	425	550	34	590	45	475	675	31	5.1	1.0	3.3	7.2	30
"	IV	865	60	712	1000	29	1045	63	900	1175	30	9.4	2.0	5.0	13.0	27
Parochlus sp.	II	107	7	100	112	7	145	10	125	150	7	1.5	0.2	1.4	2.0	7
"	III	159	11	150	175	13	212	25	175	250	13	2.4	0.2	1.9	2.8	13
"	IV	223	12	200	250	29	305	24	275	375	30	3.7	0.6	2.7	4.7	29
C. zealandicus	I	101	3	100	112	26	129	7	125	150	26	0.9	0.2	0.8	1.5	25
"	II	175	7	150	200	59	231	18	175	275	59	3.3	0.7	1.9	5.6	57
"	III	320	26	250	425	137	415	41	300	500	139	6.2	1.9	2.6	14.4	112
"	IV	561	45	445	775	150	731	72	512	925	150	12.8	3.1	5.7	19.4	112
C. curtivalva	I	85	10	75	100	5	110	13	100	125	5	1.4	0.0	1.4	1.4	4
"	II	113	8	100	125	227	143	10	125	150	28	1.9	0.3	1.3	2.3	28
"	III	175	11	150	225	379	219	27	165	275	81	2.9	0.6	1.8	4.0	73
"	IV	260	18	225	325	159	340	30	275	425	159	4.6	0.8	2.8	6.3	142
K. opalensis	I	99	13	62	137	41	123	18	75	150	41	1.3	0.4	0.6	2.2	40
"	II	168	11	150	200	67	218	20	175	262	72	2.4	0.4	1.6	3.1	66
"	III	293	26	250	400	69	384	41	300	500	70	3.9	0.8	2.5	5.5	65
"	IV	508	57	362	675	90	653	81	500	925	90	6.9	1.7	3.1	11.0	85
C. funebris	I	75	0	75	75	6	100	0	100	100	6	0.8	0.1	0.7	1.0	6
"	II	100	4	87	112	20	129	9	125	150	21	1.4	0.3	1.0	2.2	18
"	III	150	9	125	175	66	204	20	175	250	66	2.3	0.4	1.3	3.1	61
"	IV	230	14	200	275	123	323	25	250	375	123	4.0	0.8	2.3	5.7	131

TABLE 3.1. Body dimensions of chironomid larvae from Lake Maratoto.

$\bar{x}$ = mean, S = variance, n = number of larvae examined.

Stage				Habitat	Reference
I	II	III	IV		
60- 80	120-150	300-360	580-660	Christchurch ?	Robb (1966)
		350-425	600-750	L. Hayes	Graham (1976)
100-112	150-200	250-425	445-775	L. Maratoto	Own study
	200	312-450	675-775	L. Ngaroto	" "
		325-350	575-675	Blue L.(Rotorua)	" "

TABLE 3.2. Head capsule width measurements (µm) for Chironomus zealandicus larvae.

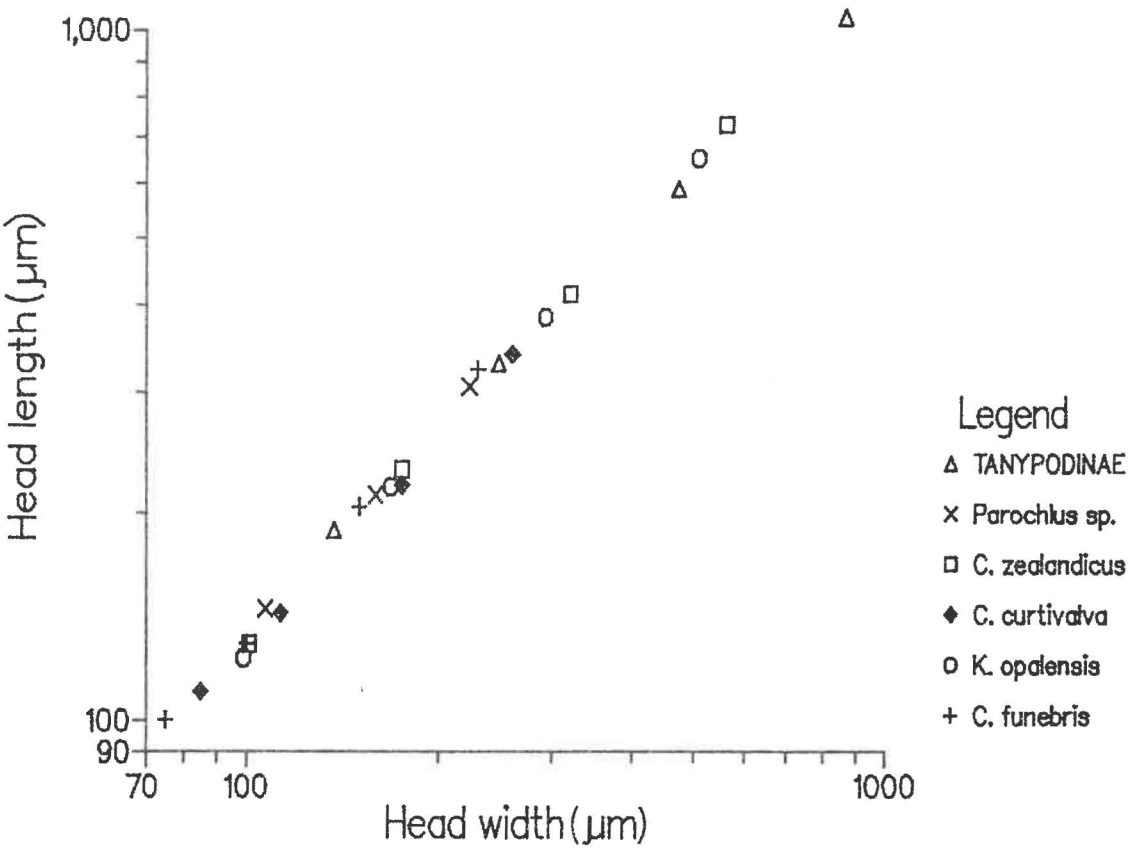


FIGURE 3.1. Log - log plot of average head width against head length for each chironomid larval instar.

After egg hatch there is a large increase in body length but in later instars this is more gradual (Figure 3.2). There was a large overlap in size ranges of the different instars which made body length measurements unreliable for instar determination. Nevertheless, since some differences in body size exist between instars and between species, it is a useful parameter for rapid identification and ageing of larvae.

The most satisfactory means of separating instars however, is to use head measurements. The size differences in head capsules between instars were sufficiently great for instar determination by eye to be readily possible once a little experience was gained. Since the larvae when viewed under the stereo microscope are usually on their sides it is most convenient to use head length.

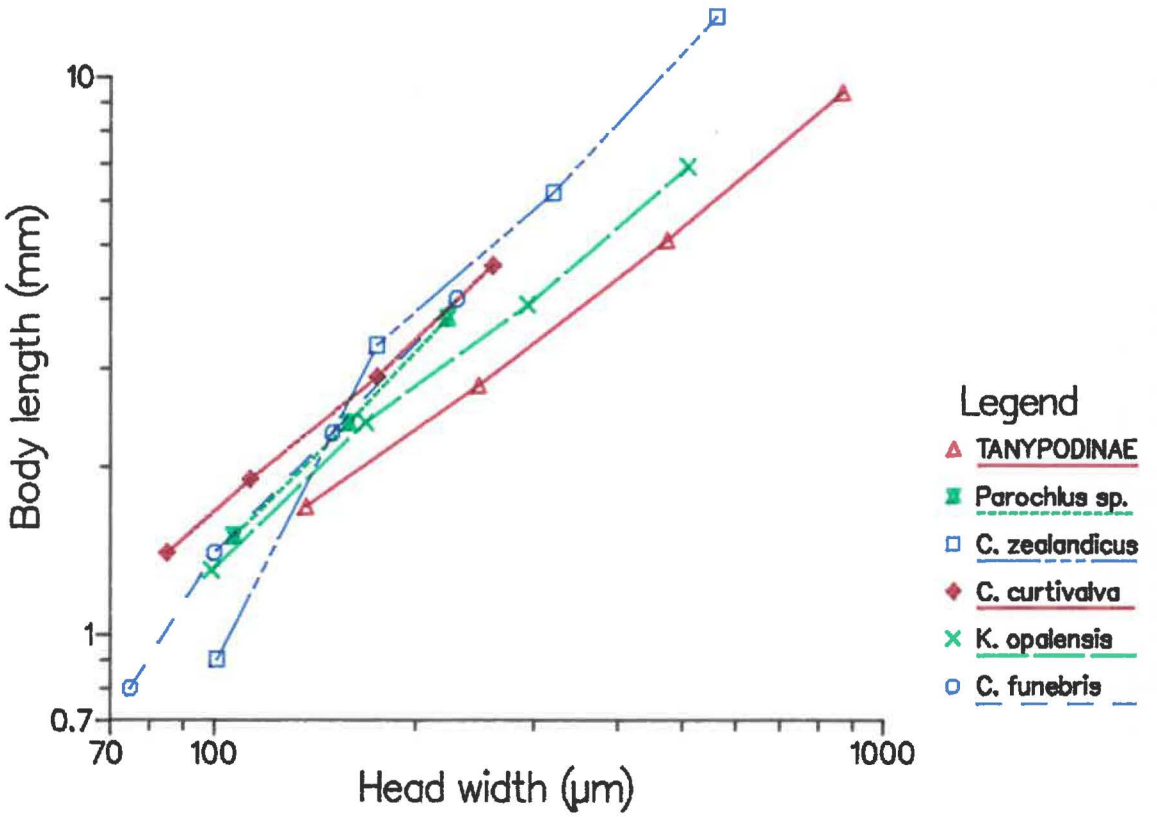


Figure 3.2. Log - log plot of average head width against body length for each chironomid larval instar.

3.3 FEEDING AND LIFE HABITS

3.3.1 Introduction

Food is often implicated as a causal factor in determining life history strategies (Lellak 1965; McLachlan et al. 1978; Anderson and Cummins 1979; Ward and Cummins 1979). Ideally, to determine feeding patterns and requirements, direct field observations of the larvae should be made. However, poor light penetration in most benthic environments and the size of the larvae would make any such attempts difficult. Laboratory studies employing artificial or enriched substrata on the other hand, are usually more fruitful but extrapolations to natural conditions can be misleading.

Gut content analyses allow the general nature of the food ingested to be determined but they have the serious drawback of not giving much indication of the food quality which for detritus feeders in particular, may be a critical factor. Nevertheless, determining gut contents of freshly collected or preserved larvae is particularly useful when comparing several species from the same environment. These, combined with behavioural studies, such as those of Walshe (1951) and Leathers (1922), allow many species to be classified into groups having a common type of feeding, (Leathers 1922; Izvekova 1971). The task is a large and difficult one with chironomids, for in no other group of aquatic insects are there such variations in the feeding mechanisms of morphologically close species (Monakov 1972). Difficulties are further compounded by the ability of some species to obtain varying types of food in a number of ways (Izvekova 1971). Under unfavourable conditions some larvae may also alter their diet (Kajak and Warda 1968) and a detritus feeder can for example, when pressed for food, become carnivorous (Loden 1974; pers. obs.).

The animals available for analysis were the same as those collected for the population study. The material was unavoidably roughly handled during sieving and was preserved in 4% formalin - treatments that Davies and McCauley (1970) have shown to cause regurgitation of the foregut contents. This, they say, occurs especially when the gut is full, tanypods being particularly susceptible. It would be of little consequence if food items were regurgitated in the same proportions as they occurred in the gut. The work of Davies and McCauley (1970) and Tarwid (1969), on predatory chironomids did show that the regurgitated material consisted mainly of algae, such that, from a gut content analysis, tanypods would appear to be predominantly carnivorous. The problem is further complicated by their report of increased predation by tanypod larvae if there is a delay in sorting or preserving samples after collection.

One possible method of overcoming the above difficulty would be to freeze rapidly the sediment sample, using either solid carbon dioxide or liquid air, as suggested by Davies and McCauley (1970). However, the extra work entailed was not felt to be warranted in this study which aimed to to carry out qualitative gut content analyses and make only general assessments of quantitative relations. These were combined with observations on live animals to provide a general picture of feeding strategies.

3.3.2 Methods

The methods used here were essentially those of Mecom and Cummins (1964). To extract the gut from the body wall, the head of the larva was severed and a scalpel or dissecting pin moved anteriorly whilst the caudal end was held with forceps. Microdissection was carried out under a stereo microscope. Where possible in larger animals, foregut contents

were preferentially selected. All extraneous tissue, including gut wall, was then removed with forceps and pins.

Gut contents tended to be present as a series of hard aggregates which were then dispersed into their components by ultrasonic treatment, as done by Coffman et al. (1971). To achieve this, the gut contents were washed with filtered water into a 10 ml beaker and dispersed for 30 to 45 seconds with a Kontes micro-ultrasonic cell disrupter (frequency 25 KHZ and 5.58 Watt setting). Tests were made at various intensities for different periods of time, but no measurable alteration to the material concerned was found at the settings used. It should be stressed that this use of ultrasounds may have caused disruption of naturally occurring aggregates, but the technique was essential to provide a standard treatment of the contents for comparisons.

Sonified material was then filtered through a 0.45 µm, 13 mm Millipore filter using a syringe as an aspirator and a micro analysis filter apparatus. Gut contents from the larger individuals were collected on separate filters, but for smaller animals, up to seven animals of similar size were pooled. Filters were placed over a drop of "Leitz" immersion oil on ordinary microscope slides and dried under a lamp until clear. A drop of oil was then placed over the filter before the cover slip was dropped in place.

Slides were examined at 200X magnification with a phase contrast microscope. Contents were assessed on an areal basis using the following particle size categories.

A. Diatoms

S = < 12 µm

M = > 12 µm < 40 µm

L = > 40 µm

B. Detritus S = < 12 µm

M = > 12 µm < 45 µm

L = > 45 µm < 250 µm

These categories were chosen as they appeared to accommodate conveniently the three diatom size classes of about 12, 24 and 72 µm and detritus found in the gut.

Observations were made with a Whipple grid. Ten fields of view were chosen randomly on each slide. In each field, the area covered by particles in the respective size category was estimated on the following one to five scale:

1	2	3	4	5
0%	0-25%	25-50%	50-75%	75-100%

Results were expressed as the average percentage cover of the total particle area.

Where present, filamentous algae and other extraneous material were recorded separately. Diatoms were identified to genus using the keys of Belcher and Swale (1977), and Ward and Whipple (1966).

Further observations were made on whole animals mounted for taxonomic study. These were mounted in P.V.A. lactophenol which cleared them sufficiently for the gut contents to be examined and recorded qualitatively.

Time was also devoted to the observation of live animals under a stereo microscope. The usual procedure was to introduce the larvae with a few ml of water into a petri dish and provide them with algae and detritus as substrate. Observations were then made at intervals over several days. In some instances, pieces of glass tubing, 20 mm in

length and of various diameters were presented as a "case" to the larvae, (Plate 17A). Here, no substrate was provided but yeast or a small amount of phytoplankton was added as the food source. These glass tubes were readily accepted by the larvae of most of the species and allowed clear observation of the feeding and irrigation motions.

3.3.3 Results

A summary of quantitative gut contents analyses of some chironomid larvae from Lake Maratoto is given in Table 3.3. In addition, a selection of qualitative observations of gut contents of larvae collected from various habitats is given in Appendix 4. Time constraints and the large numbers of animals that would have been required, prevented detailed analysis of seasonal, depth or instar changes in the diet.

The particles present in the gut consisted mainly of detritus and algae (dominated by diatoms in some species and green algae in others.) In addition to these particles there was at times a large quantity of a green/brown amorphous material of unknown origin, which was only seen in fresh specimens. Many of the animals dissected had empty guts, either because of regurgitation or the time and location of collection.

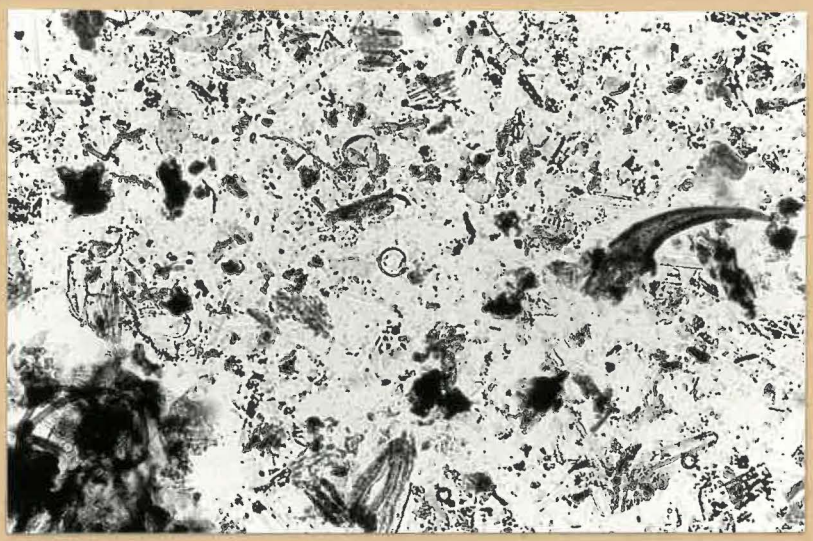
Since detritus and green algae predominate in the water in both winter and summer, (K. Etheredge pers. comm.), they can be regarded as representing material in suspension. Diatoms, on the other hand, are rare in the open water, but are abundant on the mud surface and so can be taken to represent deposited material. Using these criteria, only Kiefferulus sp. and Polypedilum sp. could be classified as filter feeders (Plate 17C). The other species were either deposit feeders (Plate 17B), grazers or carnivorous.

Plate 17. (A) Polypedilum sp. in glass tube used to observe feeding.

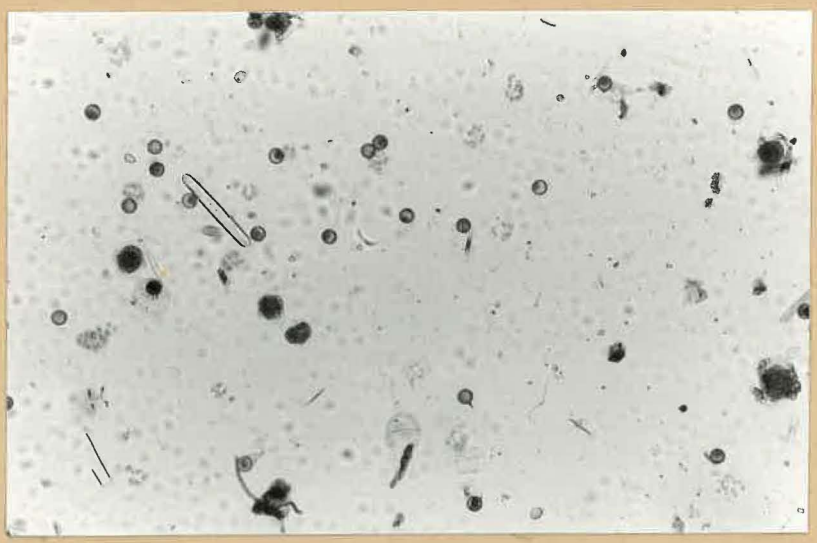
(B) Gut contents of Chironomus zealandicus, a detritus feeding chironomid.

(C) Gut contents of Kiefferulus opalensis, a filter feeding chironomid.

A



B



C

Table 3.3. Summary of quantitative analyses of gut contents in some Lake Maratoto chironomid larvae. TPO = Tanypodinae, POD = Podonominae, ZEA = Chironomus zealandicus, CUR = Cladopelma curtivalva, KIE = Kiefferulus opalensis, FUN = Calopsectra funebris. Algae: S = <12 µm, M = >12 µm <40 µm, L = >40 µm. Detritus S = <12 µm, M = >12 µm < 45 µm, L = >45 µm < 250 µm. D = dominant, p = present, i = mostly empty guts.

Taxa	TPO	TPO	POD	ZEA	ZEA	ZEA	ZEA	ZEA	ZEA	ZEA	CUR	CUR	CUR	CUR	CUR	KIE	KIE	KIE	FUN	FUN	FUN	FUN
Date	2/79	2/79	2/79	2/79	2/79	2/79	2/79	2/79	7/79	7/79	2/79	2/79	2/79	7/79	7/79	2/79	7/79	3/81	2/79	7/79	7/79	7/79
Depth	0.5	5.0	5.0	0.5	0.5	0.5	1.0	7.0	0.5	7.0	0.5	0.5	0.5	0.5	7.0	0.5	0.5	0.5	0.5	0.5	1.0	0.0
Instar	4	4	4	4	4	3	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
No. in sample	1	2	3	1	1	2	3	1	2	3	7	4	2	4	7	1	1	1	3	7	1	6
% Algae	p			40	37	45	26	35	40	50	66	37	0	60	33	73	22	45	40	53	33	46
% Detritus	20	p		60	63	55	74	65	60	50	34	63	100	40	66	27	78	55	60	47	67	54
% Animal remains	80					p			p													
Algae % S				30	19	31	30	18	34	25	22	23		0	0	30	0	0	29	22	17	43
Algae % M	p		p	36	34	48	70	36	37	52	49	35		30	50	17	25	50	33	33	75	43
Algae % L	p			33	47	31		45	29	22	29	41		70	50	11	75	50	37	44	8	14
Detritus % S	p	p	p	44	47	32	73	50	48	58	43	55	55	70	25	46	36	29	42	42	44	29
Detritus % M				34	40	47	27	25	29	29	34	38	20	50	25	41	57	40	37	46	40	36
Detritus % L				22	13	20		25	23	13	17	7	25	0	50	12	7	40	23	12	25	25
Filamentous algae													p									
Detritus filaments														p							p	p
Fungal hyphae																				p	p	p
Sponge spicules				p	p	p				p									p			p
Sand		p								p			p									
Adult insects									p	p										p	p	p
Chironomid larvae	p								p	p												p
Oligochaetes	p					p																p
Crustacea	D																			p	p	p
Other invertebrates									p													
Undetermined		D	p																			
Anomoeneis				p	p	p	p	p	p	p	p	D			p	p			p		D	p
Chroococcus?							p	p											p		p	
Cyclotela				p	p	p	p	p	p	p												
Cymbella				p	p	p	p	p	p	p	p			p	p	p			p	p		p
Eunotia				p	p	p	p	p	p	p										p	p	
Frustulia																p			p			
Melosira				p	p	p	p	D	p	D	p				D	p	p			p	p	D
Navicula				p	p	p	p	p	p	p	p			p	p			p	p	p	p	p
Peridinium					p	p	p	p		p	p	p				p	p	p	p			
Pinnularia				D	D	D	D	p	D	p	D	p		D	p	p	p	p	D	D	p	p
Staurastrum																p						
Surirella				p	p	p	p	p	p	p	p	p			p	p		p		p	p	p
Synedra				p	p	p	p	p	p	p												
Tabellaria				p	p	p	p	p	p	p	p				p	p			p	p		p
Trachelomonas				p	p	p	p	p		p	p	p				D			p		p	p
Note		i	i											i	i							

Of the material that could be classified according to size, the majority was smaller than 50 µm, thus fitting into the two smallest size categories - namely FPOM (.45 - 75 µm) and SPOM (75 - 250 µm) - proposed by Boling et al. (1975). A few particles longer and/or wider than the 250 µm maximum size category used here were found on occasions. These were probably ingested as clump material or as pliable strands that could easily become folded within the gut of the animals.

Although selection of material was expected, because of varying filtration abilities, (McLachlan et al. 1978), size and shape of tube and many other factors connected with the size (Kajak and Dusoge 1970) and species of the larvae, there appeared to be little or no differentiation of food items between species or instars. This non selectivity of feeding among the Chironomidae has been widely reported e.g. Leathers (1922), Walshe (1947), Kajak et al. (1968), Alfred (1974), McLachlan et al. (1978). Consequently attention was directed more to the method of capturing food, and the results are presented below for the separate taxa.

TANYPODINAE

The larvae in this sub-family do not build tubes but move around, pushing their heads at random amongst the organic debris, apparently in search of food. They are commonly regarded as predators, but detritus, filamentous algae, sand and desmids were common in their guts. Only occasionally were the remains of animals found (chydorid cladocerans, copepods, oligochaete worms and eggs, chironomid larvae and chironomid eggs). In many larvae, there was a coloured substance which may have been of animal origin. A large number of guts were also found empty. As I have seen larvae of this group with everted foregut and as tanypods are known to regurgitate their food when handled (e.g. Davies and

McCauley 1970), it is possible that gut content analysis does not give a full indication of the food consumed by this group.

Observation of live animals showed that when tanypod larvae are starved they will consume smaller chironomid larvae without hesitation; several being swallowed whole in quick succession (see also Leathers 1922). The larval prey are apparently uninjured initially and can be seen for some time, still wriggling within the gut of the predator. When offered larger prey, the tanypods were usually slower to attack, but if the prey was judged to be of suitable size, it would be grasped and restrained by the mandibles. The body contents of the prey, including the gut, are then sucked in, leaving behind only the head, some skin and the hind limbs. This method of feeding, although not often observed, may well explain the presence of detritus and algae in the gut of tanypods, for it forms part of the prey ingested. It is possible also that detritus and algae are ingested at the same time as the prey. The rapid striking reaction of starved tanypods to a moving prey would certainly make this possible. Other workers, although not discounting the carnivorous habit of some tanypods, have suggested that animal food content has often been overestimated in this group (e.g. Tarwid 1969). It is evident that the food composition greatly differs, depending on the accessibility and abundance of prey. The younger stages, it would seem, feed exclusively on algae. In older and/or hungry larvae, animal food is important and supplements the diet of algae (Kajak and Dusoge 1970; Loden 1974). This animal food includes cladocerans, copepods, ostracods, tubificids and other chironomid larvae. They are also known to feed on mites and larger pieces of plant detritus and on the cast skins of chironomid larvae (Kajak and Dusoge 1970; Thut 1969). Armitage (1968) found them also to be capable of actively selecting algae, and noticed them eating the remains of

invertebrates. This would suggest that tanypods can be carrion feeders. Yet, even when the larvae were starved, I never observed them to accept such food nor to feed on detritus or algae.

PODONOMINAE

Larvae of Parochlus sp. were rare in Lake Maratoto, and feeding was never observed. Examination of guts showed that the content varied from 95% detritus and 5% algae (mainly diatoms) to 95% diatoms and 5% detritus. This suggests that the larvae graze on the sediment, eating what is available there at the time. Brundin (1966) states that the group feeds on unicellular algae, mainly diatoms, and on algal detritus.

ORTHOCLADIINAE

Eukiefferiella sp.

These larvae inhabit tubes made of detritus, algae and sand. They appear to feed from the case, chewing indiscriminately on larger detrital material as well as on feeding nets and cases of neighbouring chironomids. The cases may be perforated at various places by the larvae so that feeding is not restricted to the ends. Gut contents of a large number of larvae were examined. Some consisted predominantly of amorphous material with few diatoms, others were composed mainly of sand and broken diatoms with a little detritus, yet others were for the most part diatoms with some planktonic algae.

It is not clear whether these variations reflect catholic feeding habits or include examination of more than one species.

Syncricotopus sp.

The larvae of this group are usually free living but do form tubes of algae and detritus, just before pupation. They have similar feeding habits to Group V of Leathers (1922), that is, the larvae feed by "chomping" through masses of filamentous algae. In the gut, chains of Tabellaria and Navicula as well as filaments of Stigeoclonium and Oedogonium were always predominant. A small amount of other algae (including diatoms), sand and detritus was also found. These were probably ingested along with the filamentous algae.

Metriocnemus sp.

This group was extremely rare in Lake Maratoto, and only a few specimens were ever collected. The larvae are free living and tended to spend a large amount of time crawling on hard surfaces close to the water surface. They fed by scraping on surfaces of weeds and sticks and prodding in cavities of aquatic plants, depressions in twigs etc. The gut content of the few animals examined consisted predominantly of diatoms.

CHIRONOMINAE

Chironomus zealandicus

As noted previously, more than one species may be included under this name. Variations in feeding that were observed, therefore, may be the result of unsatisfactory identification.

Larvae of this type were usually found buried in rich mud, normally in tubes whose openings at times projected well above the sediment. When the oxygen level was low, the larvae were seen irrigating, with their bodies projecting up to two thirds out of these tubes.

In the laboratory, when introduced into a petri dish of sediment and water, the larvae simply buried themselves within the detritus and accumulated as much material as possible around themselves. It was usually several days before a well defined tube was constructed, but one was always built before pupation. As buried larvae had food in their guts it is presumed that they feed directly on the material surrounding them. It is also possible that the loose nature of the sediment does allow some movement of water and hence of suspended particles which can be trapped and eaten by the larvae. The habits of the larvae, unfortunately never allowed clear observation.

Graham (1976) remarked that C. zealandicus graze the surface of the sediment while Forsyth (1971) says that they filter feed. I have never observed them to behave in either of these ways.

Glass tubes of various shapes and sizes were never readily accepted by the larvae as cases and were certainly not preferred to detritus. If the larvae were provided with both a wide diameter glass tubing and a little detritus or food, the interior of these tubes was soon plastered with particles (including faeces) making viewing difficult. Within such tubes, the larvae spent most of their time irrigating in the normal way but also attending regularly to the side wall of the tube using prolegs and head, presumably spreading silk and binding particles together.

To show the importance of the irrigation current, one end of the glass tube was blocked with sealing wax. This resulted in the larvae immediately leaving the tube and not re-entering it until the obstruction was removed. It is presumed that an open ended tube is necessary not only to aerate effectively but to also bring in food items which then adhere to the wall of the tube, from where they may be eaten.

Jonasson (1972), found that for Chironomus plumosus, tube shape, oxygen concentration and feeding type were interrelated. The varying tube shapes that were observed with Chironomus zealandicus may also result in similar variations in feeding. The gut contents of many mounted larvae collected from various habitats showed little difference from those of the animals analysed in more detail. These latter gut analyses show that C. zealandicus feed mainly on detritus (50% to 70% of gut content) and diatoms (25% to 50%).

Most of the detritus was in the medium to small size range (12 µm to 45 µm) but in the gut there were also some strands of material up to 1.2 mm in length. Of the algae consumed, the assemblage of taxa is the same as that found on the lake bottom (V. Reid, pers. comm.).

Diatoms consumed were for the most part in the small size range (12 µm to 40 µm), these being mainly the smaller species and broken frustules of the larger ones.

In the stomach, sand particles, oligochaetes, crustaceans, insect remains and sponge spicules were also found, all suggesting that C. zealandicus is a sediment feeder.

Cladopelma curtivalva

Larvae of this species are usually found in short cases of detritus and algae, either on the sediment or on stems of plants, particularly Characea. Rearing of the larvae is difficult and it is likely that they have specific requirements.

The larvae are usually inactive in their cases but the smallest disturbance will dislodge them. They then move energetically about the substrate and may not re-enter the cases or build new ones for some time. Glass tubes were never accepted as cases, even though varying

sizes were offered.

As C. curtivalva is sparse in Lake Maratoto, and the larvae small, only a few animals could be analysed in detail for gut content. Food was scarce or lacking in most of them. The analyses revealed a variable content ranging from 100% detritus to 100% diatoms. The detritus was predominantly made up of small particles and the diversity of algae was the same as that found in the sediment.

Observation of the gut content of a number of larvae collected from a wide range of environments showed that diatoms were the most common component in the food of C. curtivalva. The diatom, Pinnularia, at times made up all the gut content, in which case the long slender frustules were found in small bundles placed one behind the other within the gut of the animal. When detritus was present, it was mainly in the small size range, the largest particles seen being 90 x 90 µm in size. Sand was present in some animals and the remains of one copepod were seen in another.

It is postulated that C. curtivalva actively searches and grazes on Pinnularia or at least lives in an environment where the latter is plentiful. Grazing possibly occurs during dark periods, although even when observed under red lighting, feeding was not witnessed.

Polypedilum

This genus was never found living in Lake Maratoto but the large number of fossilized remains found within the lake sediment necessitated knowledge of their feeding habits.

Larvae of P. pavidus were collected mainly from Lake Waahi, where they are the dominant Chironomini, but also from Hamilton Lake and Lake Rotokauri. The larvae of this group appear to be particularly numerous

in the littoral of eutrophic lakes. Forsyth (1981) attributes this to a response to the deposition of wind blown blue-green algae (largely Anabaena sp.) at the edge of these lakes.

The larvae are usually found in short tubes that protrude a short distance above the surface of the substrate. These tubes are made up of sand, detritus and other material held together by silk and mucus. As the larvae readily accept glass tubing as cases, their feeding could be easily observed.

Within the larger diameter glass tubes, the larvae may build a secondary thin lining of silk to reduce the size of the case. This presumably increased the efficiency of irrigation movements made by the larvae.

Three types of feeding were observed: 1. The larvae protruded from the tube and fed on a silk net laid at the entrance of the case. 2. Feeding occurred on the walls of the tube and on the nets built within the case. The case was at times consumed entirely in places, then repaired. 3. A net was built within the case and irrigating movements took place. The net was then eaten and the process repeated. This method of feeding was common when large numbers of particles were present in the water.

With each of these three methods of feeding, the larvae often carried out irrigation movements - possibly for respiration, but also for bringing in a fresh supply of water and hence food. In newly colonised tubes the larvae usually fed at both ends, but eventually one end would be used predominantly for feeding and the other for faecal disposal.

If one end was blocked, irrigation would take place at the open end, the larvae protruding from the tube. In larger glass tubes, however, the water current was able to run along the silk case that the larvae had built then back along the wall of the glass tube. As the silk case usually projected out in front of the glass tube, mixing of the inhalant and the exhalant water current did not take place.

Gut content analyses reflected the mode of feeding of the larvae. Planktonic algae such as Melosira and Trachelomonas were dominant. Other diatoms such as Pinnularia were also found to be numerous in the gut content of certain animals. Inorganic particles were prominent at times, particularly in animals from Lake Waahi which has several coal mines in its watershed.

Of the detritus present, a large proportion was in the fine range but with some large particles up to 120 µm in length.

Polypedilum species were also collected from streams where they were found either buried within stems of dead leaves or within tubes of mucus and detritus. Here, filter feeding, as described, also took place.

Kiefferulus

The larvae of this genus were numerous on the margin of Lake Maratoto where they construct tubes or inhabit crevices on almost every object. They were also found on the surface of marking buoys and anchor lines. Cases were for the most part made up of algal material and detritus cemented together. Within these tubes the larvae irrigated and fed in the manner well described by Walshe (1947) for Chironomus plumosus. This behaviour closely resembles that of Group I larvae described by Leathers (1922). When presented with glass tubing of varying sizes, the larvae, within minutes, entered them and started

irrigating. In tubes larger than or equal to 2 mm I.D., stage IV larvae usually accumulated material along the tube walls to reduce the internal diameter to between 1.2 and 1.6 mm. If one end was partly blocked, irrigation would continue as normal. However, if fully blocked the larvae frequently responded by moving out of the tube and searching for or constructing a new case. With the larger diameter glass tubing, the larvae generally constructed their filtering nets at the entrance of the tube and would irrigate there also to produce a strong water current through the net.

During the summer, the material gathered by the larvae consisted mainly of Trachelomonas, Peridinium, an unidentified colonial green algae (Chroococcus?) and Staurastrum. Detritus and "benthic" diatoms were also present, but few in number. In winter, the larvae were rare and the few animals that were collected almost all had empty guts.

These observations, together with the lack of other observable feeding modes, suggest that Kiefferulus relies solely on suspended material as a source of food.

TANYTARSINAE

Calopsectra funebris

Larvae of this species can be found in puddles, ponds and lakes where the larvae build long, narrow tubes of algae and detritus on the surface of the sediment. While feeding, nearly four fifths of the body protrude from the end of the case. The animal then sways from side to side, feeding energetically on the sediment surface, "bobbing" from spot to spot as if it were actively selecting particles. To gather food, the head is first stretched outwards, then withdrawn with a downward "raking" motion, while the antennae continually test the substrate.

In general, diatoms and algae made up a higher proportion of the gut content than in Chironomus zealandicus, but this was extremely variable. Individual contents ranging from 20% to 90% algae and from 10% to 80% detritus were recorded. As with C. zealandicus, most of the particles gathered were in the small size range. It is possible that the larvae can gather large conglomerate lumps of food which could not be recorded by the method used. Fungal hyphae and spores, as well as thin strands of material 1.8 x 1.8 mm and 2.5 x 0.025 mm in size, were also seen in the gut. The algal species gathered by the animal were in the same proportion as in the sediment, which implies that there was no selection for any particular algae.

Observation of the animals, and gut content analyses suggest that they graze the surface sediment for algae and detritus with its associated micro-organisms. Presumably the antennae are used to locate suitable grazing areas. Besides feeding and irrigating, larvae also spent some time extending their tube to reach new grounds and the antennae here probably help in locating building material and in detecting new feeding localities.

Corynocera sp.

Larvae of this species were not found in Lake Maratoto. The few lakes and ponds where they occurred had clear water up to one metre in depth, and a distinct substrate consisting of a flocculant organic layer up to 20 cm thick with a very high concentration of algae (mainly diatoms) and decaying reeds (Plate 18B). Within this material, the larvae build tubes up to 10 cm in length. The tubes are of debris fastened together (with saliva?) and have a distinct silk lining. These cases overlay each other and form an intricate series of tunnels, one end opening at the sediment surface, the other either opening within the

Plate 18. (A) Kiefferulus opalensis: larval tubes on rush stem.

(B) Corynocera sp.: Preferred sediment type - and openings to larval tubes.

A

B

sediment layer or at its surface. As the larvae age, the tubes are lengthened by the addition of detritus, the openings sometimes being raised up to two centimetres above the sediment by the arrangement of algae, detritus and faecal pellets. These projections are particularly prominent at emergence and are possibly an adaptation to aid the pupa leave the case. Tracing the tube is difficult as it branches at various points. Most of the short side passages do not seem to be in use.

Within these cases the larvae irrigate in the normal manner. This results in a strong water current being created along the case. In addition to the benefit of bringing fresh oxygenated water to the larvae as it burrows into the sediment, food may also be obtained by this method. Although not observed, it is possible that this species also builds a web or a net within its case and feeds on the collected material.

When larvae were placed in a shallow dish, another mode of feeding was observed. Like Calopsectra funebris, Corynocera are able to move up to four fifths of their body length out of the case, to reach out and collect lumps of algal/detrital material which they pull towards the entrance of the tube using mouth parts and prolegs. The larvae then eat the gathered lump of material in its entirety, using labrum and mandible to "shovel" it in. Large diatom frustules are not a hindrance to the larvae and if gathered, are efficiently crunched by the mouth parts. While the animals gather food and building materials, the long antennae constantly touch the substrate and presumably help in the selection of material.

Like many other chironomid species, Corynocera sp. is able to change its mode of feeding if required. Apart from the two feeding methods described, a larva was seen eating one of its live neighbours

which it eventually consumed completely.

Detailed gut content analyses were not carried out, but stomachs of animals collected from a water trough in the grounds of the Ruakura Research Station (Hamilton) were full of algae, particularly the diatom Cymbella ventricosa var. pareistrata. Examination of the sediment from which the larvae were collected revealed the same distribution of algal species. Similarly, the guts of larvae from Lake Rotomanuka had the same mixture of detritus and algal species as the sediment.

From the restricted habitat of the species, it seems that a high algal content of the sediment (particularly diatoms) is a prerequisite for the presence of the larvae.

Paratanytarsus agameta

The larvae of this species inhabit long tubes on the surface of plants, sediments etc. The animal grazes from the end of its tube on the surface of large particles such as fragments of reeds, but also amongst its own faecal material. P. agameta was also seen to ingest whole clumps of particles.

Only a cursory examination of the gut contents was made. This revealed that most of the gut was filled with a brown substance of unknown origin (fungal/ bacterial?). Algal filaments and diatoms made up three fifths of the measurable particle content. The rest was detritus of 10 µm to 40 µm in size, this being coarse compared to material found in the guts of other species examined.

3.4 SEASONAL AND DEPTH DISTRIBUTION OF CHIRONOMIDS IN LAKE MARATOTO

Chironomids form an important part of the benthic fauna in most lakes, and in Lake Maratoto constitute the second most numerous group, representing a considerable proportion of the benthic biomass (Chapter 2). Although the importance of chironomids in nutrient cycling in lakes, and their potential as biological indicators have long been recognised (Oliver 1971; Saether 1975; Wiederholm 1976), there are few New Zealand studies which have been directed at the phenology of the chironomid taxa within one lake. This section is devoted to the analysis of seasonal changes in age structure, population density and depth distribution of the chironomids found in Lake Maratoto.

3.4.1 Methods

Methods of collection and treatment of benthic samples from Lake Maratoto are described in Chapter 2. The density of the benthic chironomids and the variations in instar frequency distribution were determined to obtain information on their distribution, life cycles and life span. Simultaneously with these investigations, notes were made on flight periods, reproductive cycles and emergence (presence/absence of egg masses and floating exuviae).

3.4.2 Results

Thirteen chironomid taxa were recorded from Lake Maratoto (Table 2.1). Some of the rarer forms could be identified to family level only (see section 3.1).

The occurrence of the chironomid species collected, their abundance, and age structure at the different sampling dates and sites are given in Appendix 2. Relatively low numbers of first instar larvae were collected, while pupae were trapped only occasionally. The low recovery of the young larvae is thought to have been due to the use of a 225 µm mesh sieve opening which was greater than the head capsule width of most first instar larvae. There is also evidence to suggest that newly hatched larvae are photopositive and remain planktonic until a suitable habitat is found (Oliver 1971). In addition, the time spent in a particular stage will have some bearing on the likelihood of its being collected. This would apply particularly to pupae.

Larvae were most common on the edges of the lake (max. 43,000 per sq. m at 0.5 m on 17/12/79) and became progressively less abundant with increasing depth (Figure 3.3). The annual mean standing crop of chironomid larvae between 5/3/79 and 12/3/80 was 2,970 per square metre. This was composed of 40% Calopsectra funebris, 37% Chironomus zealandicus, 12% Cladopelma curtivalva, 5% Kiefferulus opalensis and 5% Tanypodinae, with Podonominae and Orthocladiinae making up the remaining 1%.

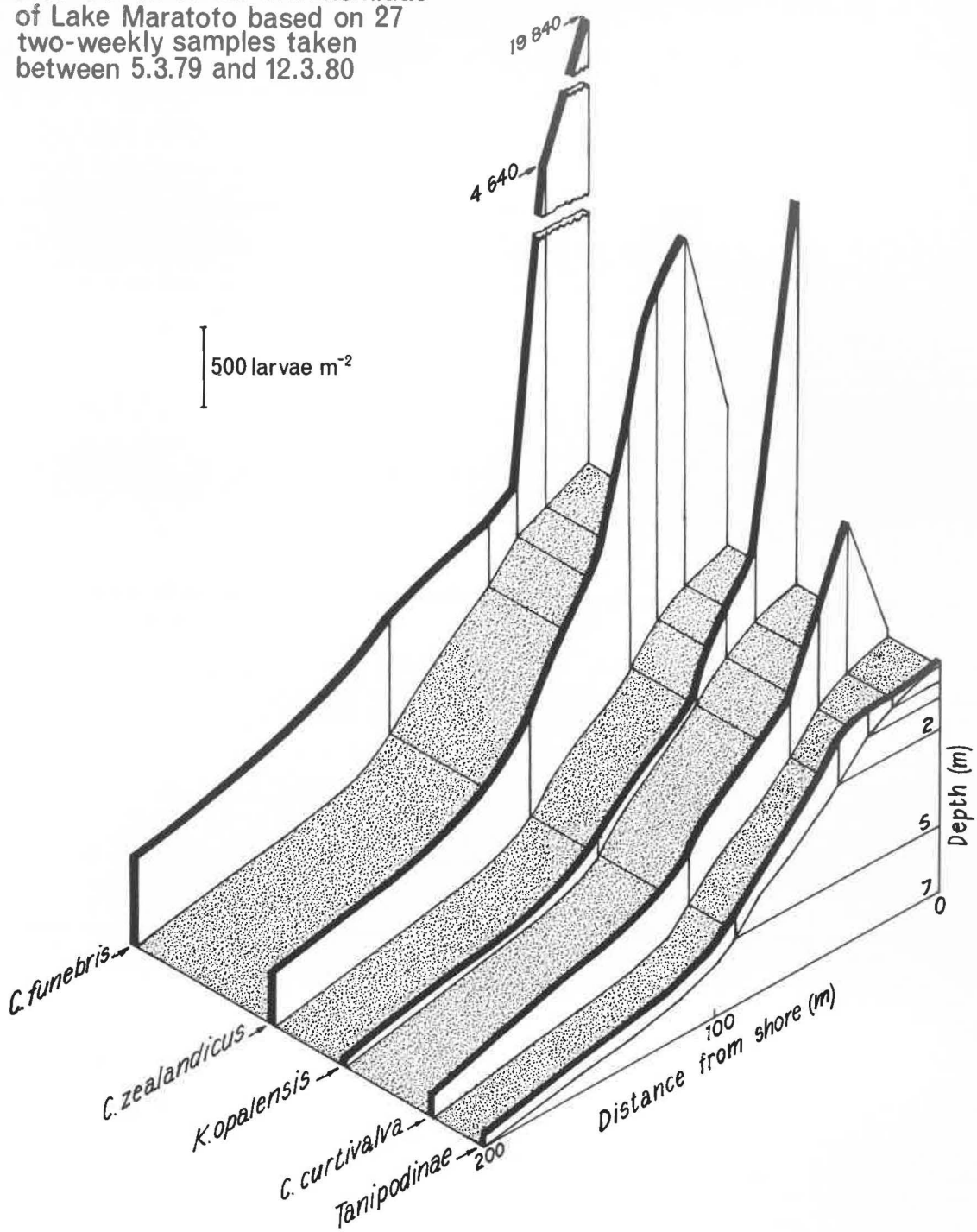
As both annual and seasonal fluctuation in the lake's mean standing crop and in the species composition were large (Figures 3.4 and 3.5), each chironomid taxa is analysed in detail below.

TANYPODINAE

The annual mean standing crop for this group was 160 per sq. m. The larvae were evenly distributed both spatially and temporally, such that density fluctuation, age structure, depth distribution and seasonal trends are difficult to discern. However, all stages of tanypods were most common in early winter (Figures 3.6A, 3.7A). Adults were found

Figure 3.3. Mean depth distribution of the major chironomid larvae in Lake Maratoto.

Distribution of the Chironomidae of Lake Maratoto based on 27 two-weekly samples taken between 5.3.79 and 12.3.80



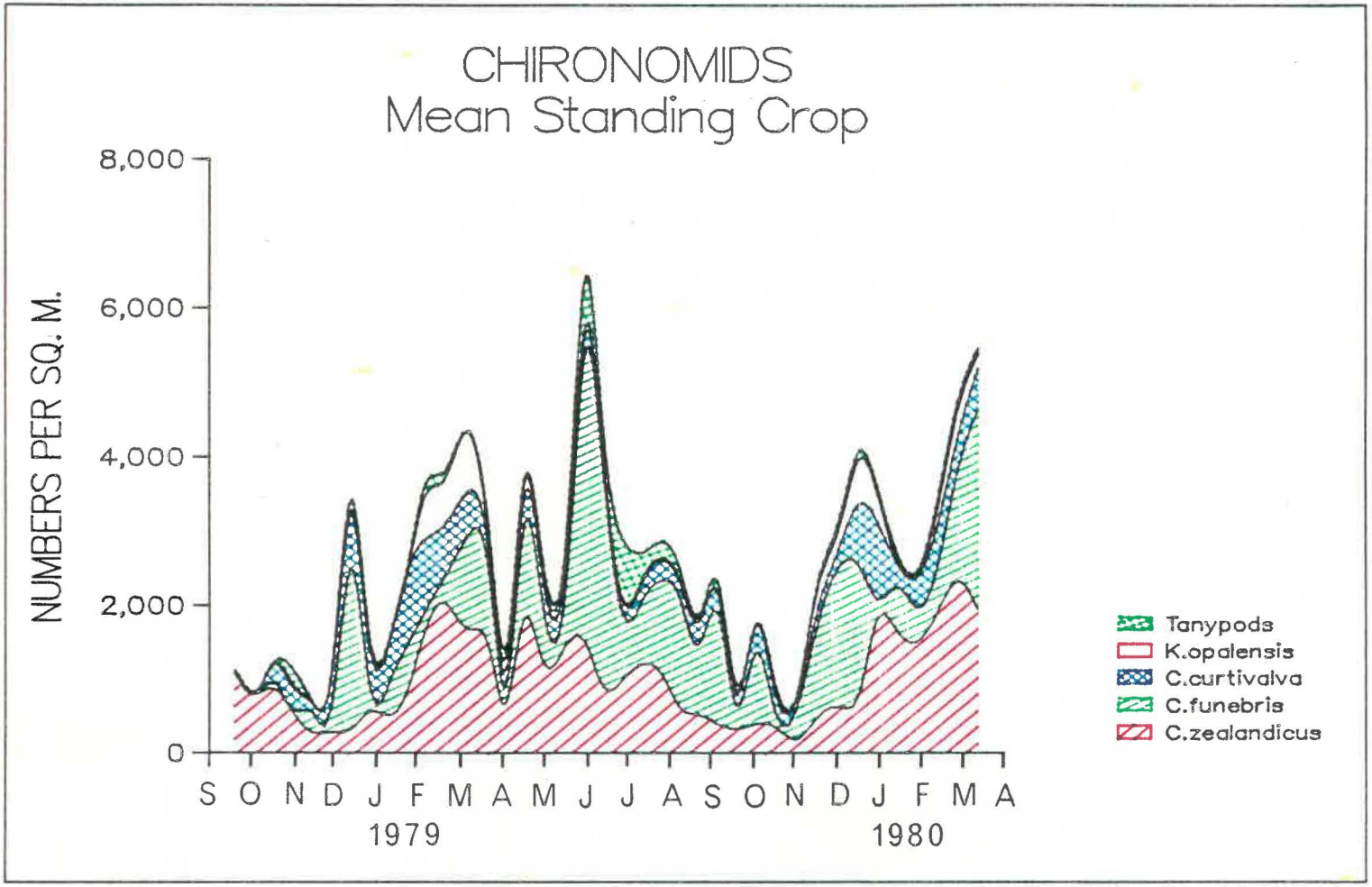


FIGURE 3.4. Mean standing crop of the major chironomids in Lake Maratoto.

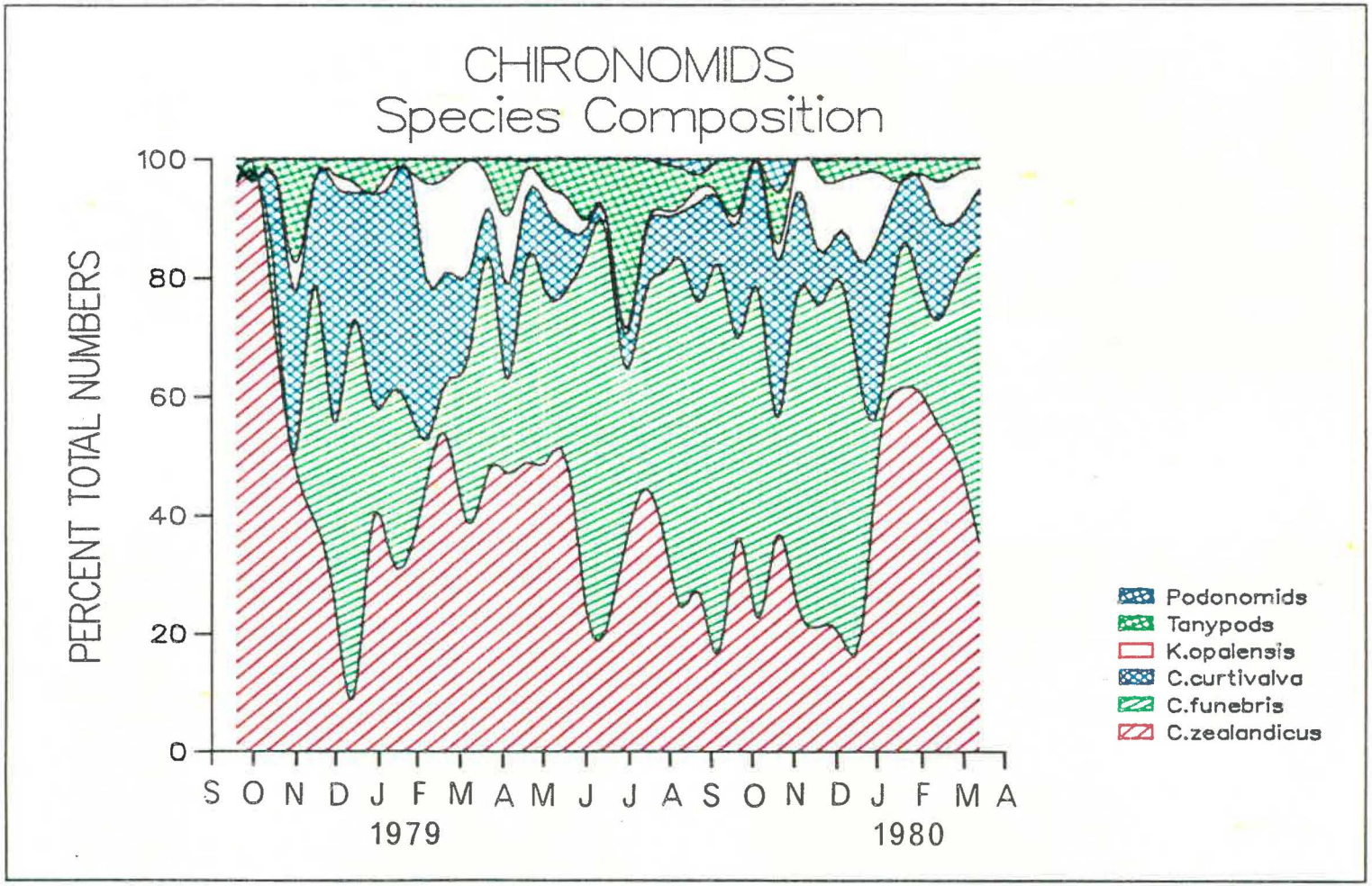


FIGURE 3.5. Species composition of the major chironomids in Lake Maratoto.

Figure 3.6A-F. Seasonal variation in chironomid mean larval numbers per sq. m at six stations in Lake Maratoto. Mean total larval density is also given. Horizontal black bars indicate periods when the oxygen concentration above the sediment was below 3 g per cubic metre.

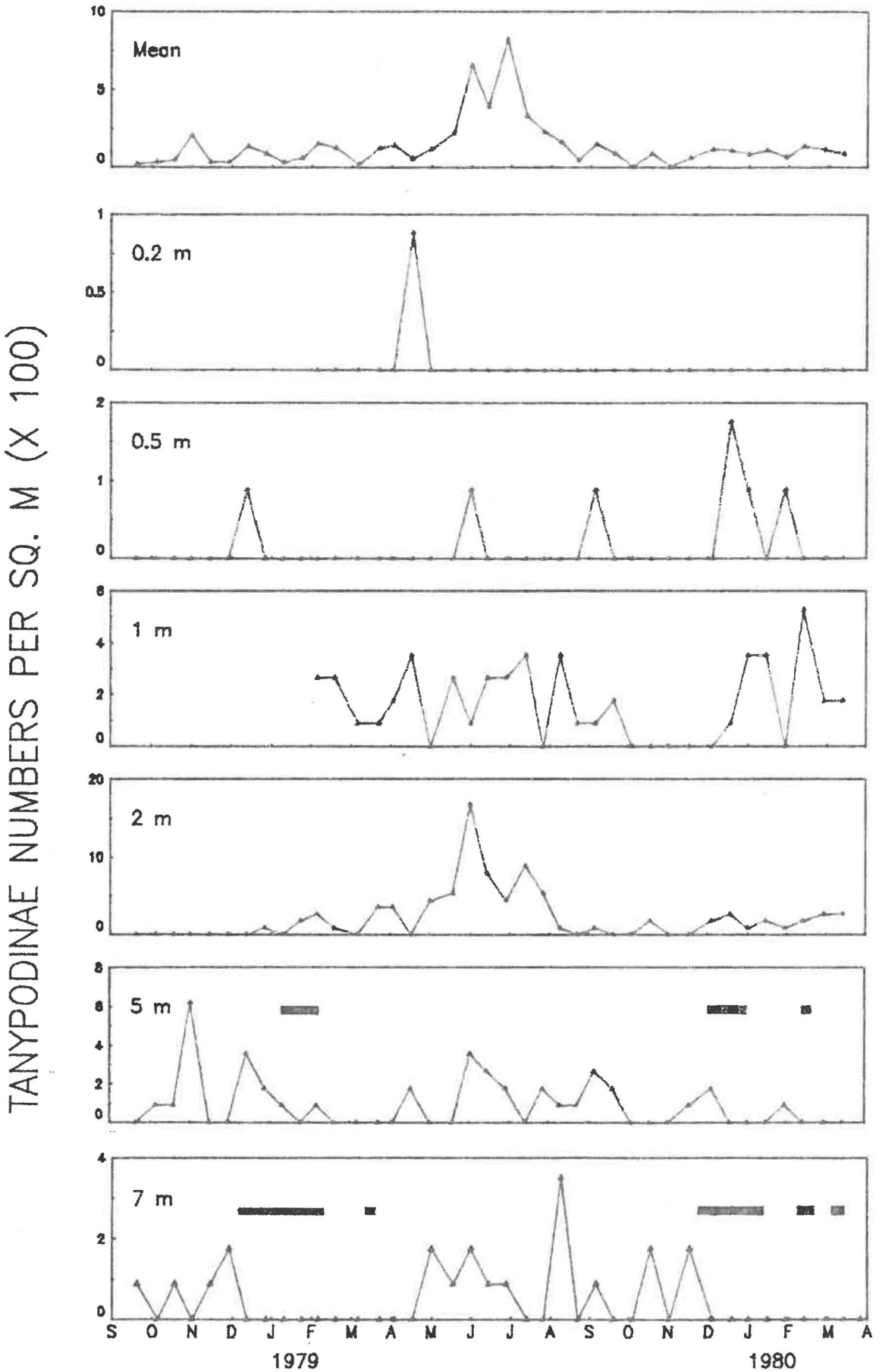

TANYPODINAE NUMBERS PER SQ. M (X 100)
Mean
0.2 m
0.5 m
1 m
2 m
5 m
7 m
S O N D J F M A M J J A S O N D J F M A
1979
1980

Figure 3.6A

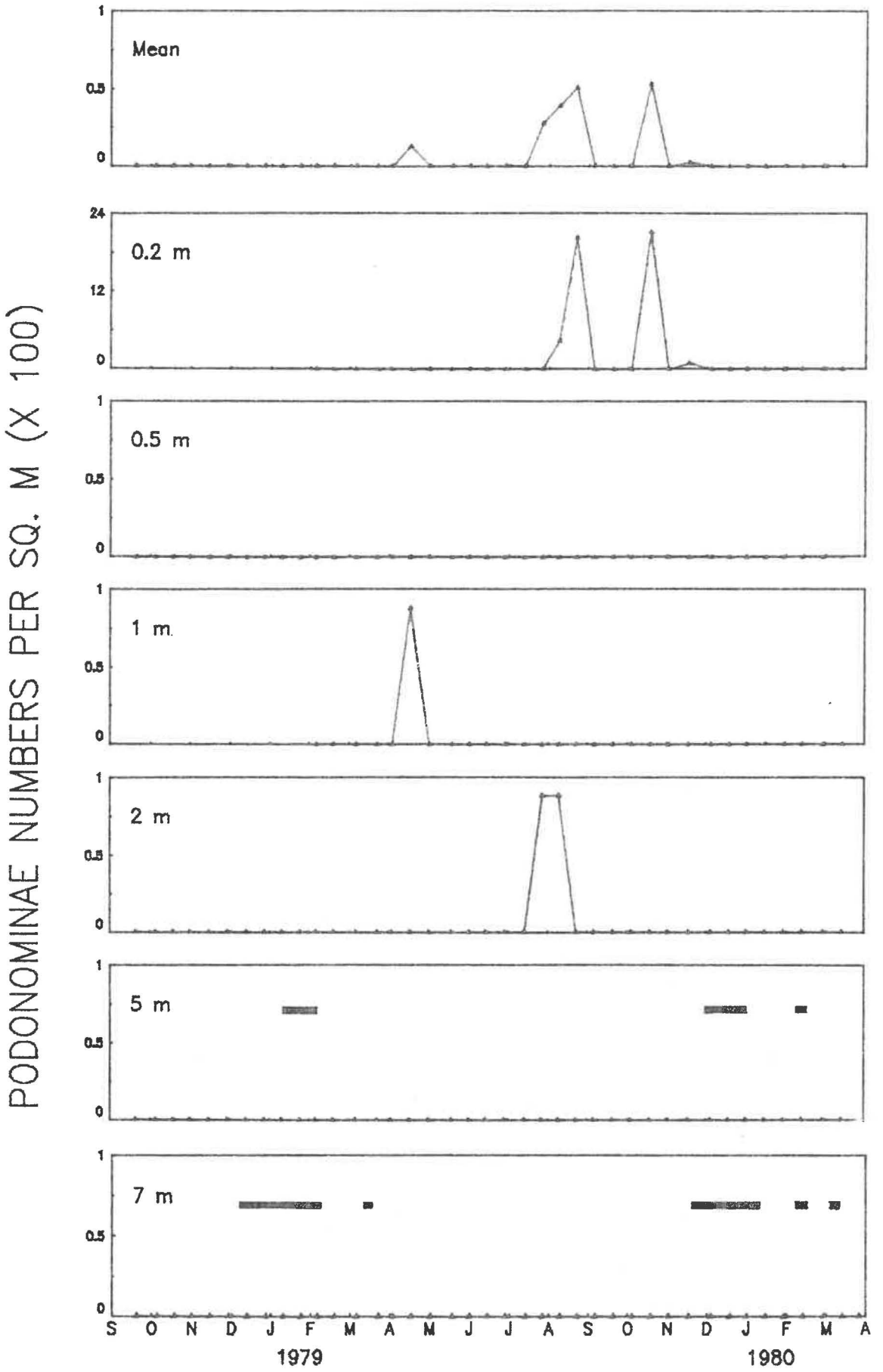

PODONOMINAE NUMBERS PER SQ. M (X 100)
Mean
0.2 m
0.5 m
1 m
2 m
5 m
7 m
1
0.5
0
24
12
S O N D J F M A M J J A S O N D J F M A
1979
1980

Figure 3.6B

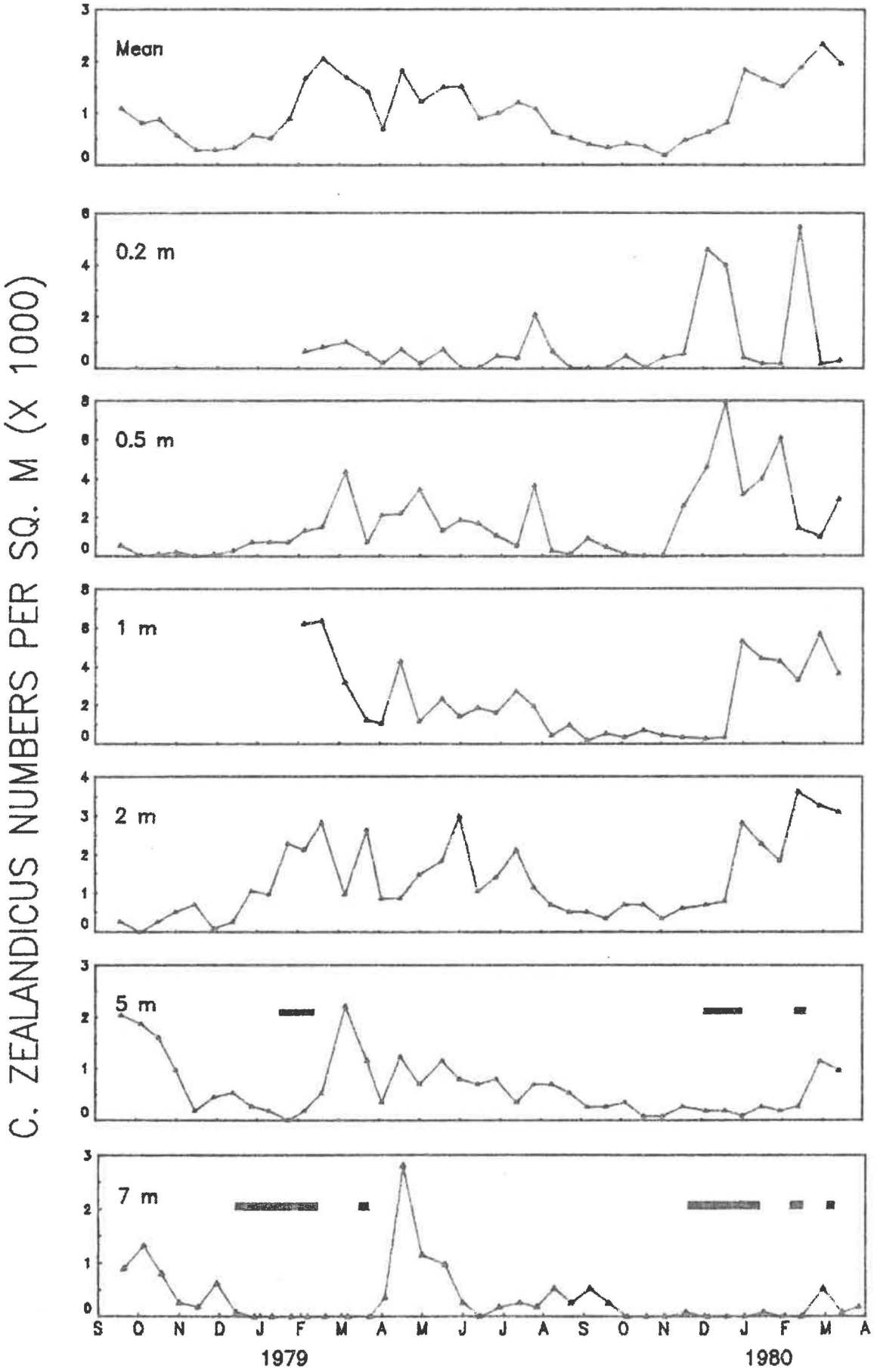

C. ZEALANDICUS NUMBERS PER SQ. M (X 1000)
Mean
0.2 m
0.5 m
1 m
2 m
5 m
7 m
S O N D J F M A M J J A S O N D J F M A
1979
1980

Figure 3.6C

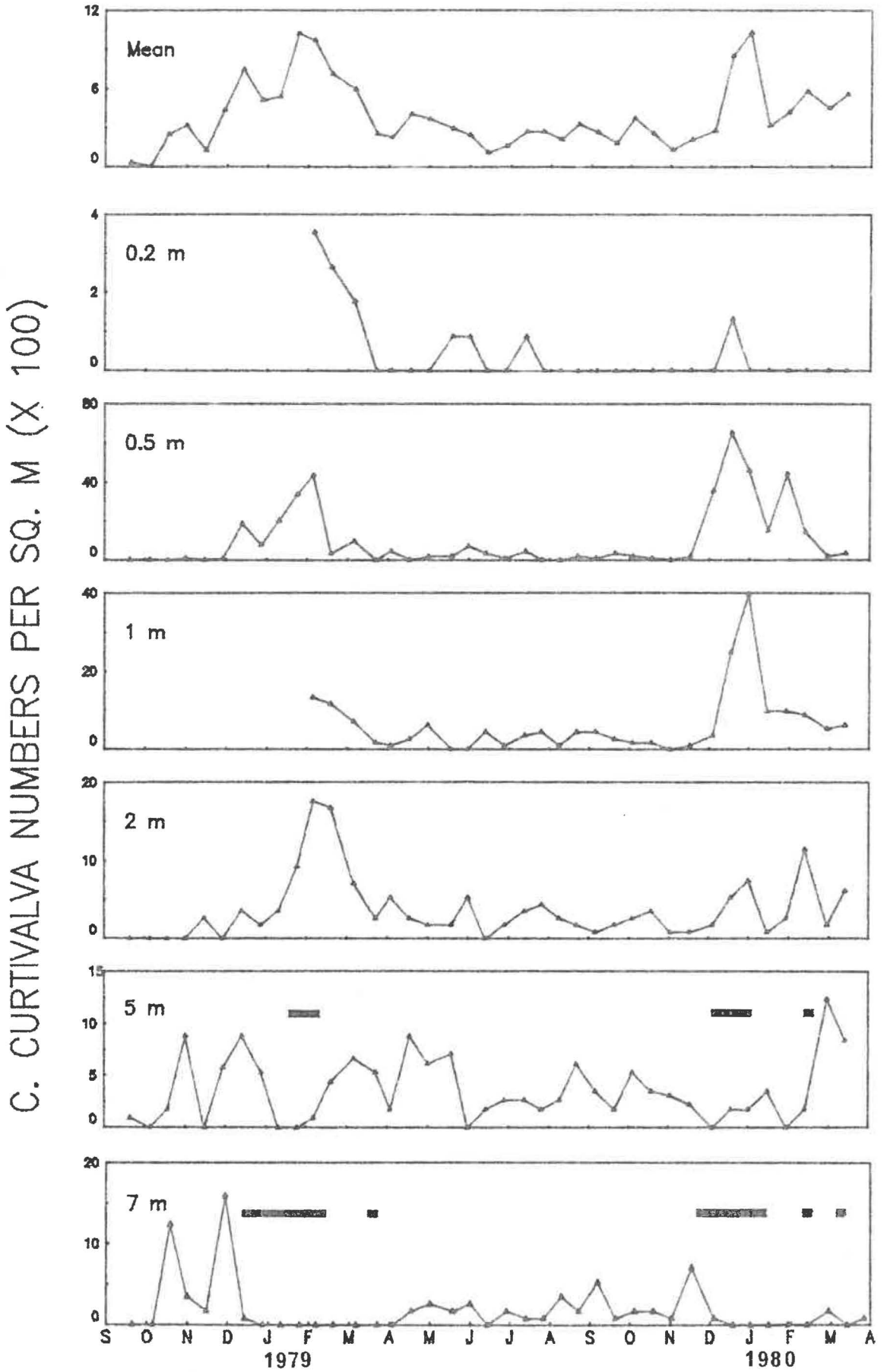

C. CURTIVALVA NUMBERS PER SQ. M (X 100)
Mean
0.2 m
0.5 m
1 m
2 m
5 m
7 m
S O N D J F M A M J J A S O N D J F M A
1979
1980

Figure 3.6D

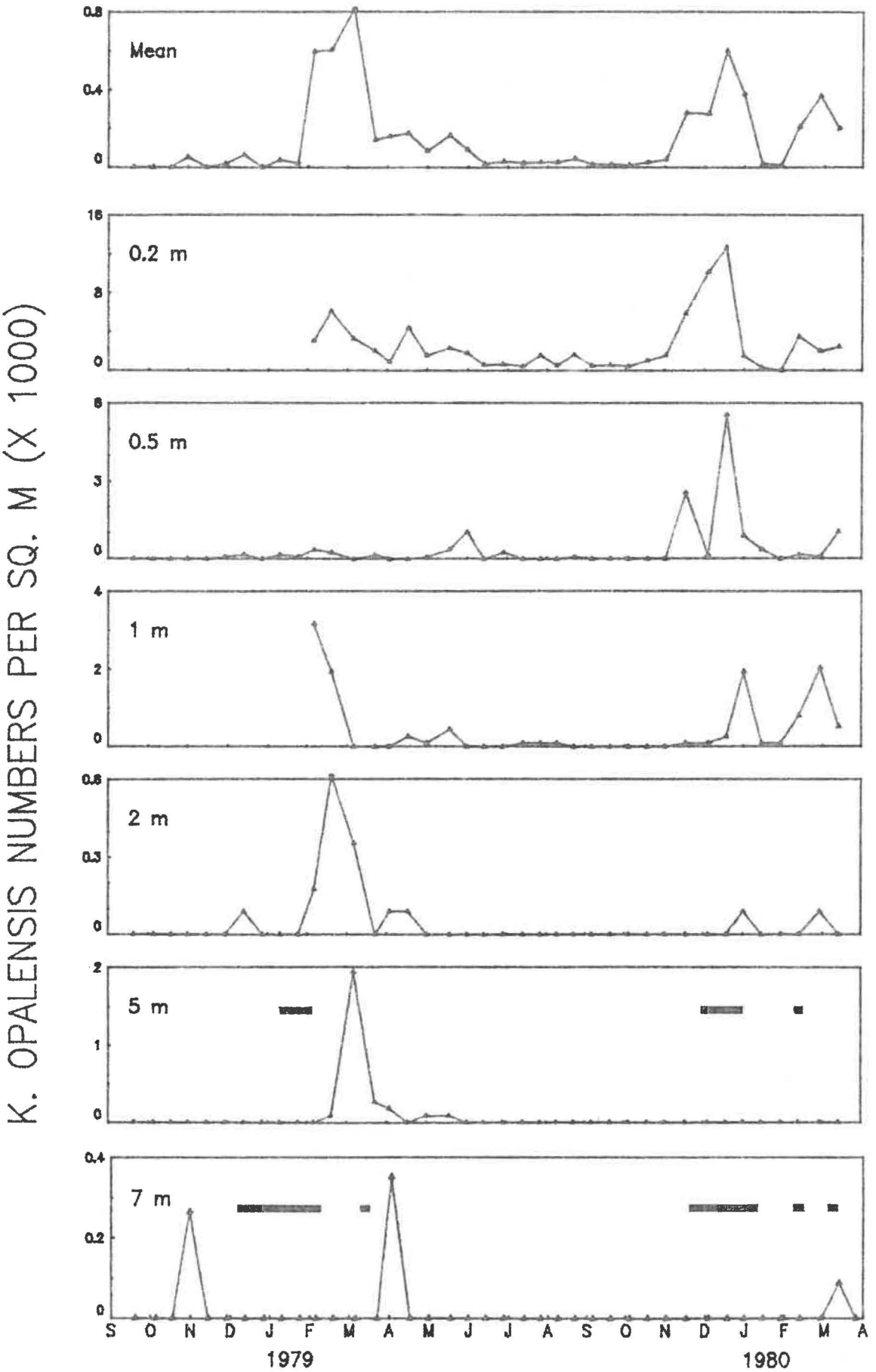

K. OPALENSIS NUMBERS PER SQ. M (X 1000)
Mean
0.2 m
0.5 m
1 m
2 m
5 m
7 m
S O N D J F M A M J J A S O N D J F M A
1979
1980

Figure 3.6E

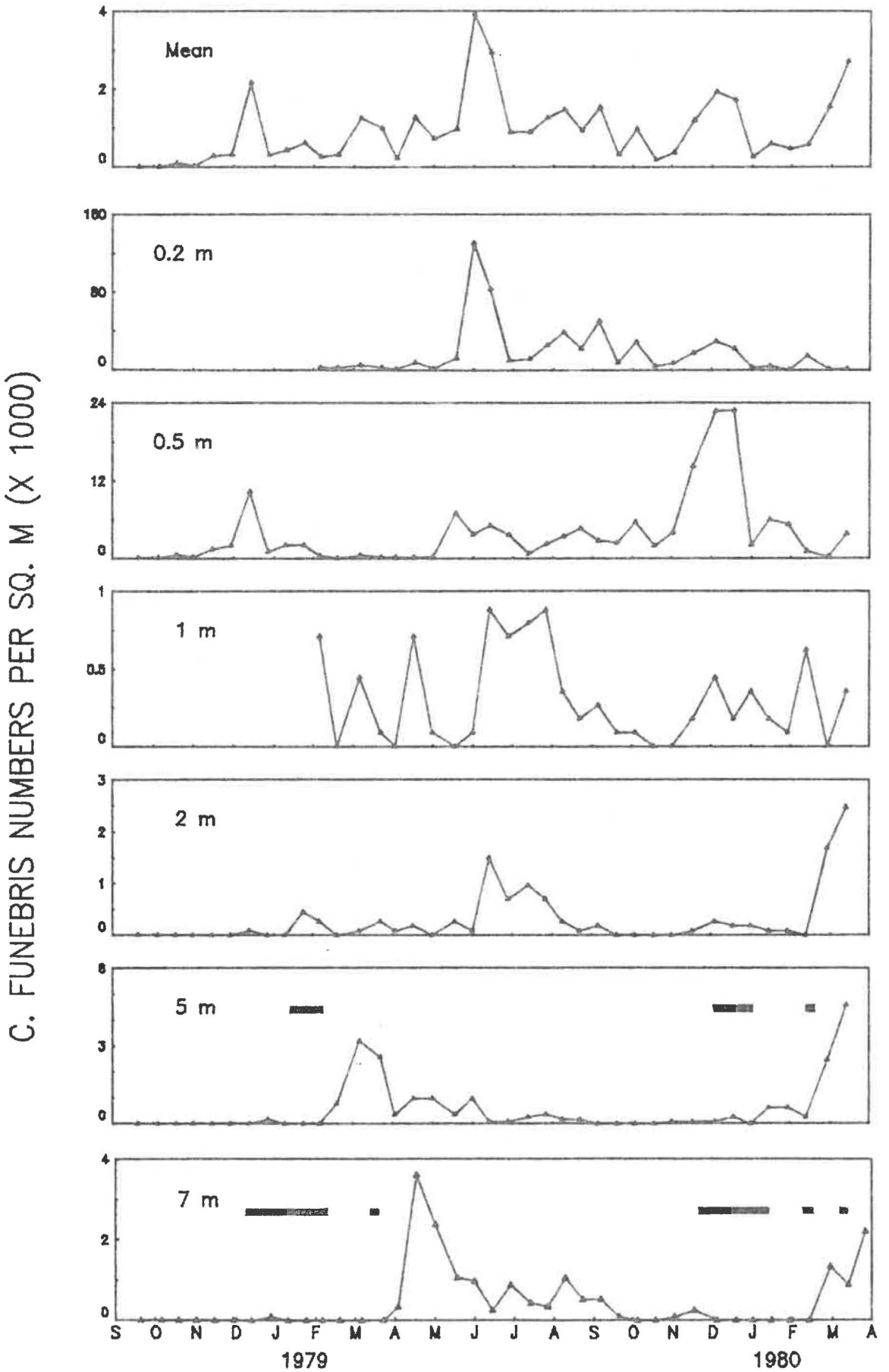

C. FUNEBRIS NUMBERS PER SQ. M (X 1000)
Mean
0.2 m
0.5 m
1 m
2 m
5 m
7 m
S O N D J F M A M J J A S O N D J F M A
1979
1980

Figure 3.6F

Figure 3.7A-F. Seasonal variation in age structure of the major chironomids from Lake Maratoto. Horizontal open bars indicate periods of maximum emergence and black bars periods of maximum egg laying.

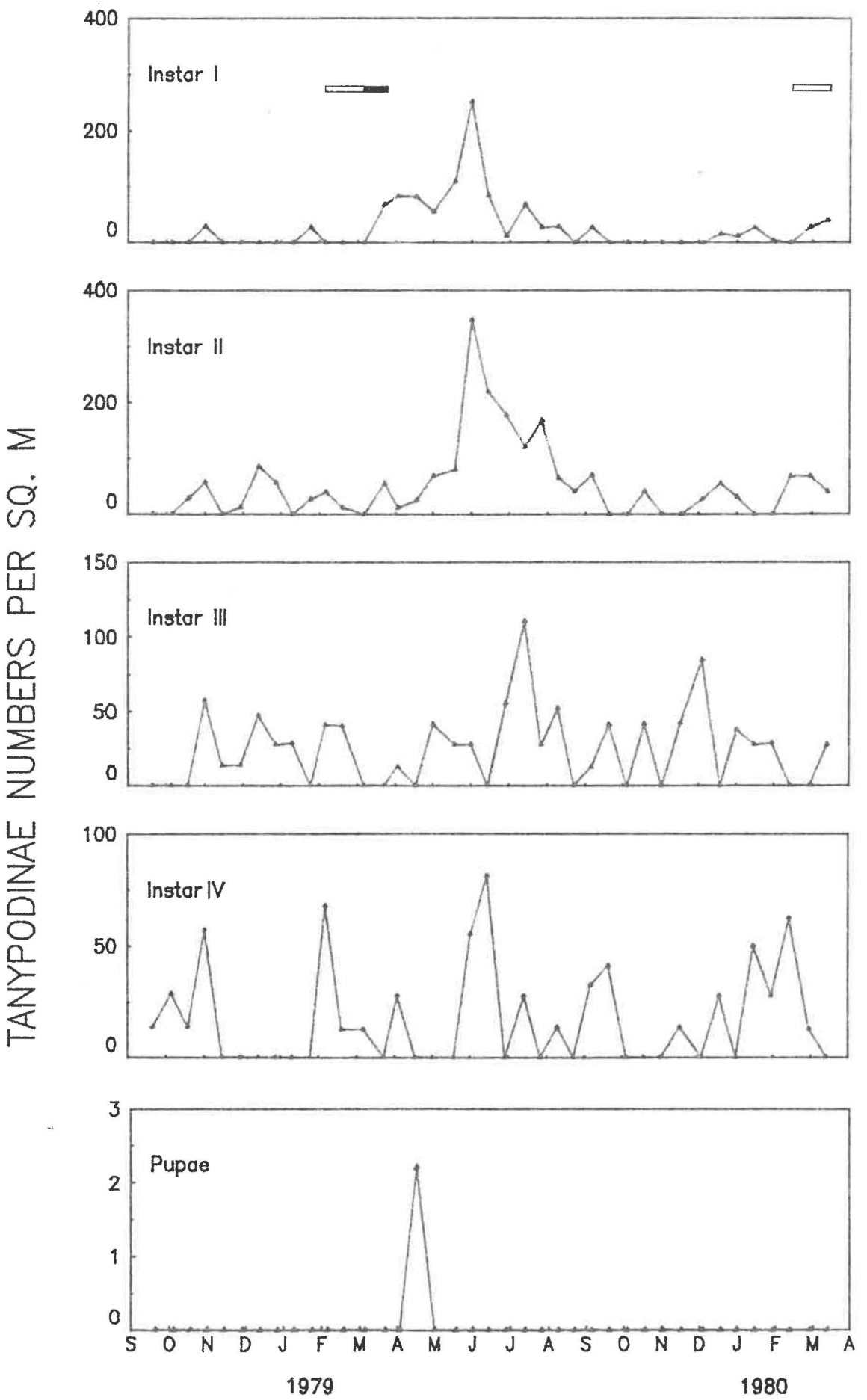

TANYPODINAE NUMBERS PER SQ. M
Instar I
400
200
0
Instar II
400
200
0
Instar III
150
100
50
0
Instar IV
100
50
0
Pupae
3
2
1
0
S O N D J F M A M J J A S O N D J F M A
1979
1980

Figure 3.7A

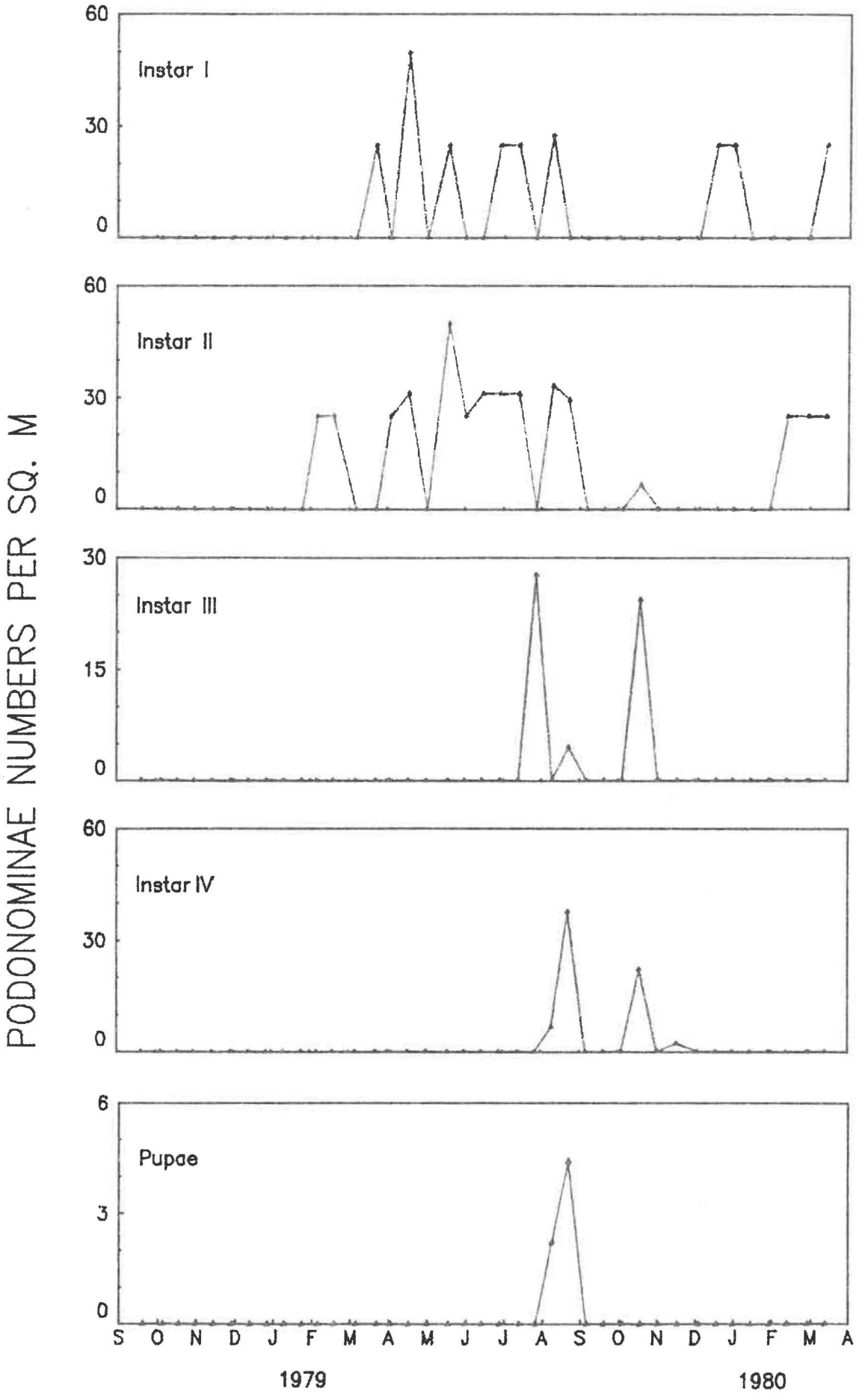

PODONOMINAE NUMBERS PER SQ. M
Instar I
Instar II
Instar III
Instar IV
Pupae
60
30
0
15
6
3
S O N D J F M A M J J A S O N D J F M A
1979
1980

Figure 3.7B

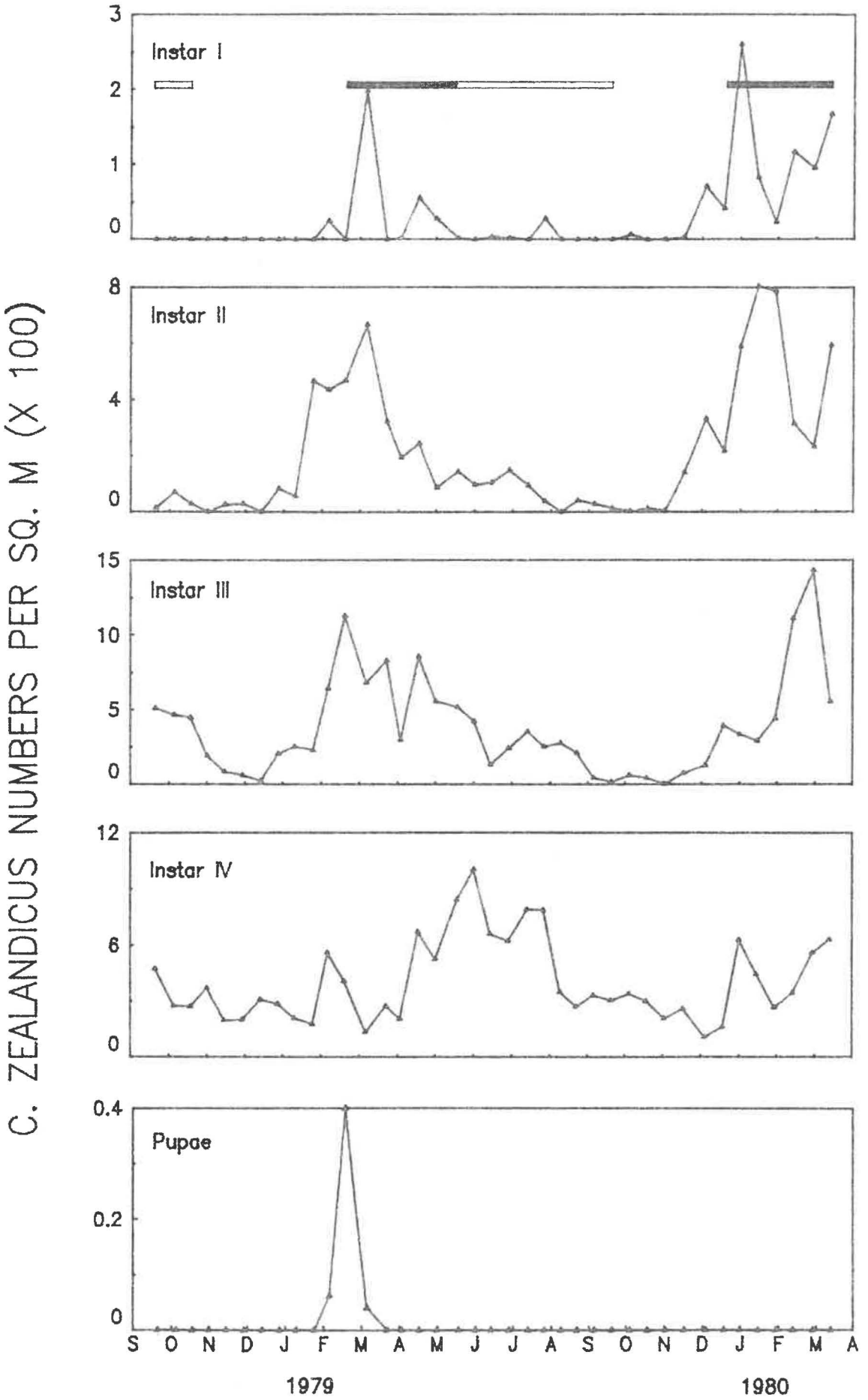

C. ZEALANDICUS NUMBERS PER SQ. M (X 100)
Instar I
Instar II
Instar III
Instar IV
Pupae
S O N D J F M A M J J A S O N D J F M A
1979
1980

Figure 3.7C

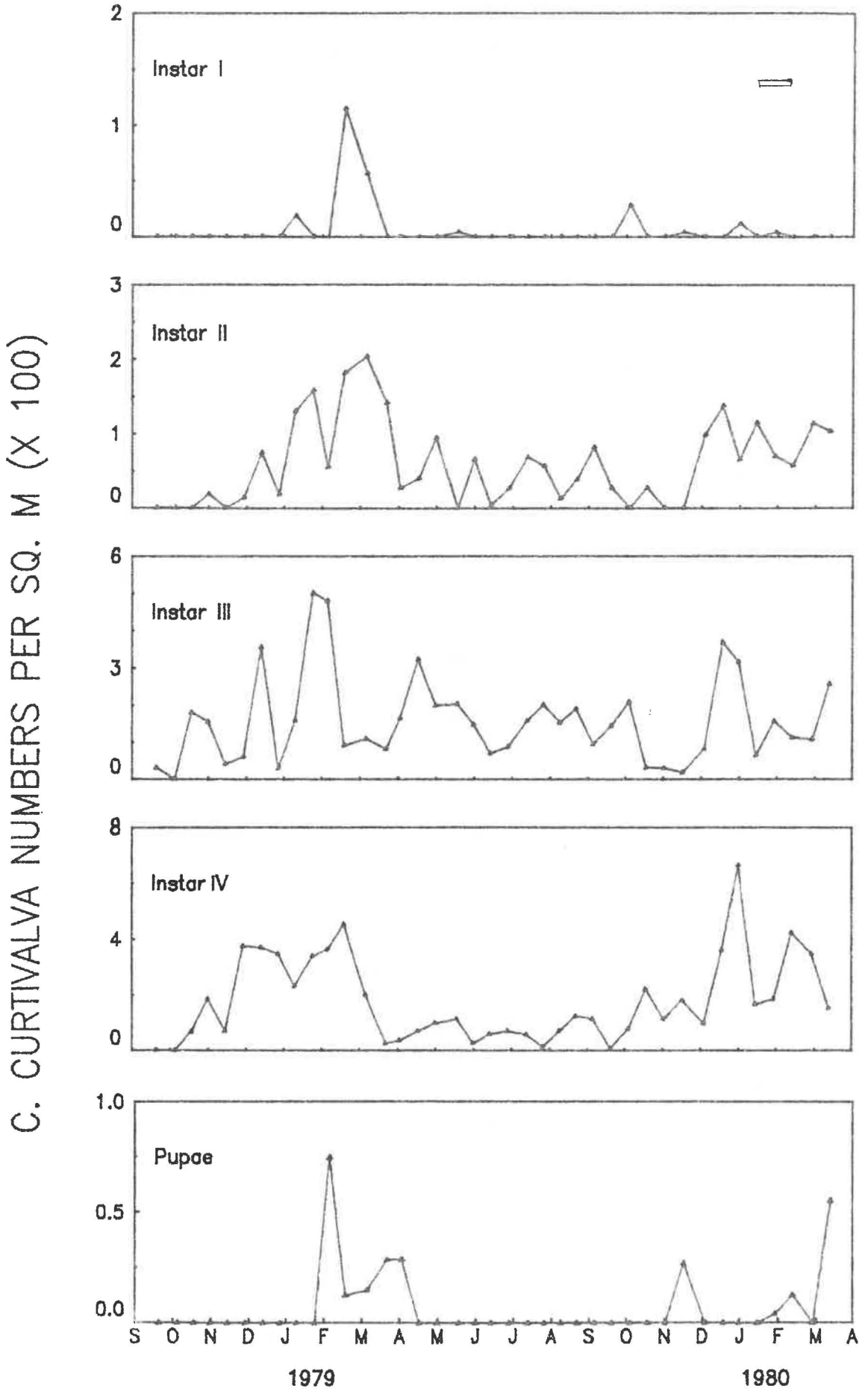

C. CURTIVALVA NUMBERS PER SQ. M (X 100)
Instar I
Instar II
Instar III
Instar IV
Pupae
S O N D J F M A M J J A S O N D J F M A
1979
1980

Figure 3.7D

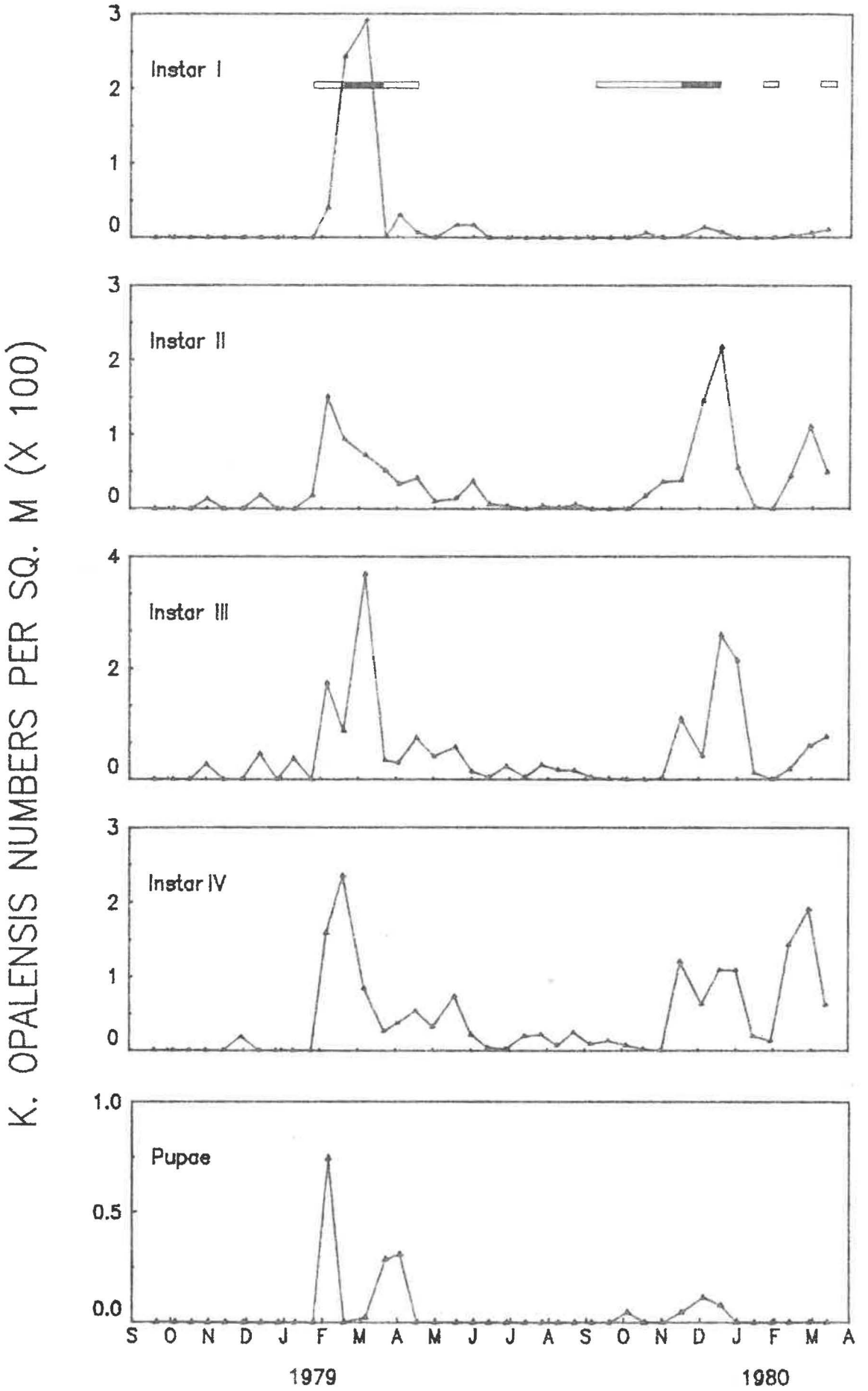

K. OPALENSIS NUMBERS PER SQ. M (X 100)
Instar I
Instar II
Instar III
Instar IV
Pupae
S O N D J F M A M J J A S O N D J F M A
1979
1980

Figure 3.7E

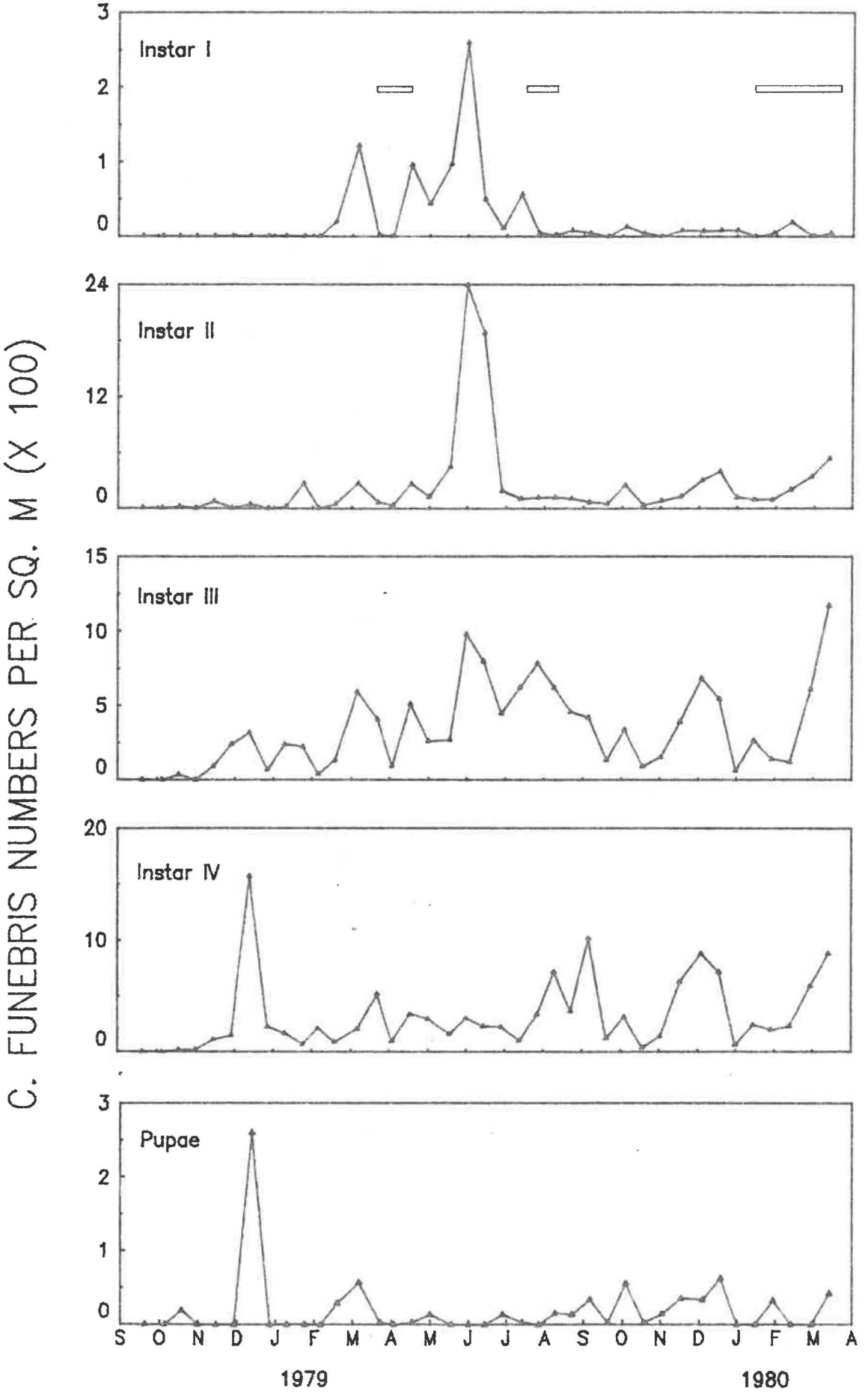

C. FUNEBRIS NUMBERS PER SQ. M (X 100)
Instar I
Instar II
Instar III
Instar IV
Pupae
S O N D J F M A M J J A S O N D J F M A
1979
1980

Figure 3.7F

from February to April each year when breeding is presumed to take place. Early stages of the larvae were most common at the 2 m station while the fourth instars were most dense at 1 m (Figure 3.8).

In Lake Tikitapu, Forsyth (1975a) found the maximum density of Gressittius antarcticus to be at 20 m in the winter while Forsyth and McCallum (1981) found them down to 20 m in Lake Taupo with their distribution inversely correlated with water depth.

The larvae, which have little or no blood pigmentation, are probably unable to survive low oxygen concentrations and the timing of reproduction in winter is likely to be a reflection of this. In Lake Maratoto, the period of maximum numbers also coincides with the maximum concentration of stage I Calopsectra funebris, upon which this carnivorous group is known to feed (Section 3.3). During the winter months also, many benthic animals are disturbed from their tubes and hides by wind and wave action, making them easy prey.

PODONOMINAE

Only about 60 larvae of Parochlus sp. were ever collected by core sampling in Lake Maratoto. Largest numbers were found on the edge of the lake from June to October (Figure 3.6B). The larvae are free living and have no blood pigment, hence presumably require highly oxygenated waters. First instars began to appear in December and the fourth instars and pupae in August (Figure 3.7B). Numbers were too low for further description of seasonal patterns.

ORTHOCLADIINAE

Larvae of orthoclads were only collected in large numbers by sweep netting along the shore of the lake, therefore no seasonal or age pattern is given. Larvae of Syncricotopus sp. were most common amongst

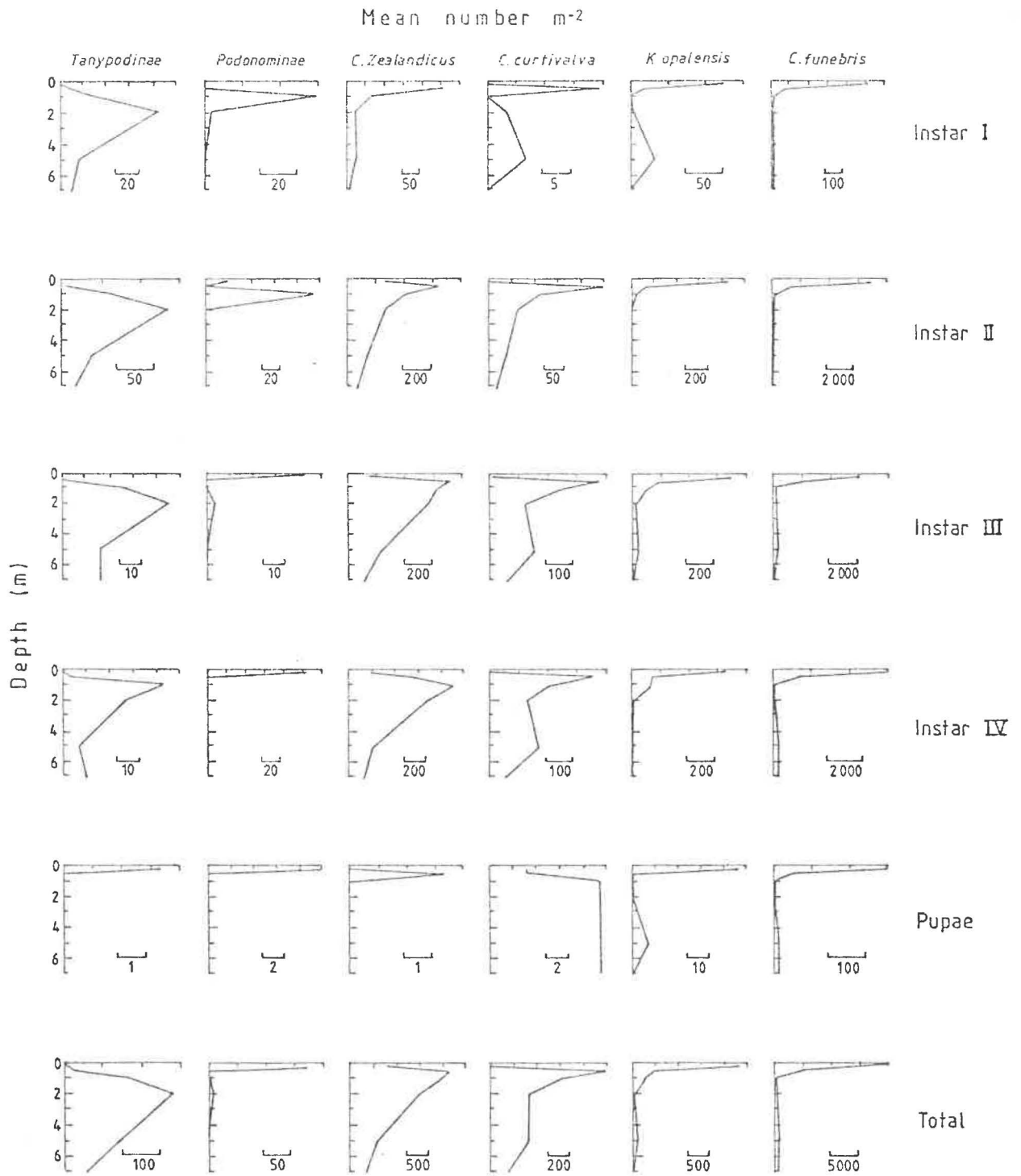


Figure 3.8. Depth distribution of the most common chironomids in Lake Maratoto. Values given are the annual mean numbers per sq. m.

moss and plants growing or submerged on the edges of the lake, particularly in March and April 1980. As these larvae feed by grazing filamentous algae (Section 3.3), no doubt there exists a correlation between density of the algae and larval numbers.

In other lakes in the Waikato, orthoclad larvae are most common in winter and swarms of adults can be seen in sheltered areas from August to December. The family is usually restricted spatially and temporally to relatively oxygen-rich cool waters (Iovino and Miner 1970). The rareness of this group in Lake Maratoto is probably a result of the high oxygen demand of the sediment and of the lack of suitable habitat.

CHIRONOMINAE

Chironomus zealandicus

This species complex was the second most common chironomid in Lake Maratoto. Their annual mean standing crop was 1,100 per sq. m, but marked fluctuations in population density were recorded, both seasonally and spatially (Figures 3.6C and 3.7C). Lowest numbers were found in October 1978 and September 1979. The population size then increased rapidly to a peak in January of both years, after which numbers slowly decreased. This pattern was repeated at each depth sampled, except that at the 7 m and 5 m stations no larvae were present during the period of deoxygenation. After high winds in mid February 1979, larvae were found once again at the 5 m station, but it was not until March, when stratification was completely broken down, that they returned in significant numbers at the 7 m station.

In 1979 the highest numbers of pupae and stage I larvae were collected in February and March. This also coincided with a peak in the numbers of stages II and III larvae, while stage IV larvae were most

numerous in June of the same year. No pupae were collected in the summer of 1979-80, but numbers of stage I larvae peaked in December, stage II in January and stage III in February. It is probable that the highest concentration of stage IV larvae for 1980 occurred in early winter as in the previous year. Pupal exuviae and adults were found in high numbers in September 1978, and from March to August 1979. Eggs were most common from February to April 1979, and from December 1979 to the end of the sampling period. During these periods, the largest numbers of stage I larvae were also found.

Egg development times and duration of larval instars of C. zealandicus at various temperatures are given by Robb (1966). He found that the period from egg laying until first emergence was 41 days at 15 'C and reduced to about 20 days at 22 'C and above. At 20 'C, emergence was spread over 30 days and was expected to be of longer duration at lower temperatures. Minimum temperatures for successful larval development lay between 8 'C and 12 'C. Robb also concluded that large scale pupation began when the temperature exceeded 13 'C.

In Lake Maratoto, temperatures are below 13 'C only for a brief period between June and August (Figure 1.6A). Accordingly, if Robb's observations apply in Lake Maratoto, egg hatching and emergence could take place for most of the year, except for a brief winter period. Furthermore, given suitable conditions, egg hatch to emergence could take place between successive sampling dates which, I postulate, occurs as soon as temperatures rise in the spring. This rapid succession of generations appears to continue until the turnover, when temperatures start to decrease and larval development and emergence slows down. This results in a build-up of stage IV larvae which reach a maximum in June. From August 1979, the temperature rose once again, and emergence continued at an increasing rate. Judging from the low rate of

recruitment, reproduction and survival of young larvae remain extremely low, at least until the spring when the population rapidly builds up once more.

A study of seasonal changes in population size by Graham (1976) suggests that in Lake Hayes C. zealandicus can develop rapidly during spring and summer, and may go through a series of generations before the autumn. Over the winter months, development rates slow down and numbers of stage IV larvae increase, to peak just before a mass emergence in the spring.

Forsyth (1978), who essentially collected only late instar larvae in his study of seven Rotorua lakes, also found a build up of larvae over the winter, and a large decline in the spring, due to mass emergence. Although Forsyth and McCallum (1981) could find a significant seasonal variation in C. zealandicus numbers at only one of three profundal sites they investigated in Lake Taupo, Stephens (pers. comm.) noticed a winter maximum, with mass emergence in the early spring at Waihaha Bay.

These patterns differ little from those observed in Lake Maratoto except that in this lake, higher water temperatures allows emergence to occur much earlier.

Depth distributions of the larvae found by Forsyth and McColl (1975), Graham (1976), and Forsyth (1978), suggest that C. zealandicus is a profundal species whose maximum number of larvae occurs below the metalimnion. However, in Lake Maratoto, larvae of all stages were most common at the 0.5 m station where a maximum of 7,930 larvae per square metre was recorded on 17/12/79. As the larvae aged, they gradually shifted to deeper waters (Figure 3.8).

Chironomus larvae are well known for their resistance to anoxia (e.g. Brundin 1950). This ability to survive low oxygen concentrations has been attributed to the presence of the pigment erythrocruorin in the blood of the larvae (Walshe 1950). The anal gills have also been shown to have some respiratory functions (Nagell and Orrhage 1981). In addition, the larvae are able to break down glycogen to lactic acid to help them survive anaerobic conditions (Czeczuga 1963; Augenfeld 1967). Both the concentration of blood pigments and glycogen are higher in the fourth instar larvae than in the younger larvae, and so may explain the ability of the older instars to inhabit the deeper parts of the lake. All these attributes, however, are insufficient to prevent the displacement of the larvae during periods of stratification and low oxygen concentrations. Toxic conditions associated with the stratification may also have been of importance here.

Cladopelma curtivalva

These bright red chironomid larvae were most dense at the 0.5 m station, but the majority of the total population was dispersed over the deeper sections of the lake. In these bottom waters there were mostly late instar larvae (Figure 3.8). Maximum densities of the larvae were recorded from December to February, while lowest numbers were found from May to October. This pattern was repeated at all depths and with all age groups (Figures 3.6D and 3.7D). No larvae were found at the 7 m station during periods of low oxygen tension. Adult and pupal skins were most abundant during the summer period. It would appear therefore, that there is but one development group during the summer period. It is probable that the larvae feed on epiphytic diatoms (see Section 3.3) and their growth in Lake Maratoto may be restricted to the periods of greatest abundance of these algae.

In Lake Tikitapu, Forsyth (1978) found the highest numbers in June and August, but failed to record them in October, while in Ngahewa a maximum of 266 per sq. m was recorded in July with a minimum again in early summer (Forsyth and McColl 1975).

Kiefferulus opalensis

This species is almost entirely restricted to the extreme edge of Lake Maratoto (Figure 3.8) and in the summer colonises almost every submerged object. Large numbers were found on reed stalks (Plate 18A). In the winter months larvae were found in the sediments, possibly due to the reed stem environment becoming inhospitable through temperature and wave action. Some larvae were found at the 7 m and 5 m stations immediately after the turnover, which suggests passive settlement following wind disturbance of the shoreline.

The annual mean standing crop was 157 per sq. m and the highest density of 13,900 larvae per sq. m was recorded on 17/12/79 at the 0.2 m station. The adults and eggs were numerous amongst the reed stems from September to May each year, when the larval population was also at its highest (Figure 3.6E). During the summer of 1978/79 all larval stages increased in number from early February to reach a maximum on 5/3/79 (Figure 3.7E). After this, numbers first decreased rapidly, then more slowly, until only a few larvae remained in the winter. These few larvae were apparently sufficient to start another population buildup in the following summer.

Possibly because of an earlier rise in the water temperature in the summer of 1979/80, numbers started to increase from mid November. Maximum population size that summer was recorded in December. Following a decline in numbers of all instars in January, numbers rose again. It is of interest to note that this short population decline corresponds to

a period of high water temperature (Figure 1.6A). Furthermore, it would appear that the increase and decrease of the K. opalensis population is closely linked to surface water temperature, 20 'C being roughly the minimum temperature at which population growth occurs. The time of maximum larval numbers also corresponds to a period when planktonic algae are most abundant (Figure 1.9). Since K. opalensis is a planktonic feeder, the availability of this nutritious food is likely to stimulate growth and development in the larvae.

TANYTARSINAE

Calopsectra funebris

Calopsectra funebris was the most abundant species of chironomid in Lake Maratoto, with a mean standing crop of 1,190 per sq. m. The larval population showed slight increases in numbers from October to December in both 1978 and 1979, but the highest numbers of larvae were collected in the winter of 1979 (Figure 3.6F). At the end of the sampling programme in March 1980, the population was increasing rapidly. Lowest numbers of larvae were found from September to October and when the lake was stratified (January and February). Larvae were most abundant on the very edge of the lake (Figure 3.8), and up to a maximum of 130,000 per sq. m was recorded at the 0.2 m station. They were also particularly common in the temporary pools and seepage water behind the shoreline. Larvae were absent from the deeper stations for a large part of the year, but appeared at the 7 m station in March 1979 and a little earlier at 5 m. In 1980, the same sudden increase occurred, but this time simultaneously at the 5 m and 7 m stations. The appearance of larvae at these depths coincides with reoxygenation of the bottom waters, following the break up of stratification by strong wind. These larvae, which were nearly all fourth instars, remained in the deeper water for

the duration of the winter.

Earlier stages of C. funebris were most common in May 1979, stage III in July, and stage IV during July and August. A few pupae were collected throughout the year. Adults were noted from April to August 1979, but were particularly common from February 1980 to the end of the sampling period (Figure 3.7F).

In the laboratory, an average development time of 30 days was noted between egg hatch and emergence, but this rate was noticeably altered by lighting and temperature. It is probable that the mid winter maximum of stage IV larvae is the result of a slow down of emergence rate. Generally, increase in the total population coincided with increase in temperature, but as the larvae appear to be particularly sensitive to low oxygen tension, overall numbers in the lake decreased during periods of stratification. Following the turnover, a rapid succession of generations resulted in large increases in the population, which was only halted by the return of cooler temperatures.

3.5 PLANKTONIC CHIRONOMIDS

3.5.1 Introduction

Benthic animals, including chironomids, are usually considered static in their distribution, yet there is much evidence showing that migration of chironomid larvae occurs both within and between water bodies (e.g. Deevey 1941; Bay et al. 1966; McLachlan 1970). Most species and stages migrate (Davies 1974, 1976a; Mundie 1959), thus ensuring extensive and continual distribution of the larvae. This is important as egg laying occurs, for the most part, on the edges of lakes and rivers and in areas sheltered from the wind.

On hatching, the young larvae show marked positive phototaxis which allows them to remain in the surface waters (Lellak 1968; Cantrell and McLachlan 1977). With age, the larvae usually become less responsive to light, and they can then settle on the bottom, where some species build tubes. The light response may be reactivated in these older larvae after expulsion by some noxious stimuli, such as rough water (Paterson and Walker 1974), light (Luferov 1971), low oxygen tension (Bay et al. 1966; Jonasson 1972) and intraspecific competition (Thut 1969).

Progress through the water is achieved by thrashing about in a figure of eight motion. With larvulae and stage II larvae, the presence of long setae projecting from the body help with flotation and passive dispersal.

Energy for swimming in the larvulae is probably derived from the remains of the egg yolk. Some young Chironomus larvae also collect and feed on suspended particles that adhere to a sticky viscous material on the anal brush and claws of the posterior prolegs (Oliver 1971). This method of feeding is possibly available to all planktonic larvulae which

may also feed directly on larger particles in suspension in the water. Feeding could also occur during brief visits to the sediment.

In the benthic data from Lake Maratoto (Section 3.4) no instances of upward migration during the early summer could be detected, as the pronounced sublittoral maximum coincided with the hatching of young larvae. The evidence for a downward migration at the end of the summer is more convincing and this is attributable to the re-aeration of the lower waters by water circulation.

3.5.2 Methods

Plankton samples were taken at varying intervals during the sampling period with a 20 cm diameter, 120 µm mesh plankton net, two hauls being made over the area of maximum depth. On three occasions, when chironomid planktonic activity was high, samples were also collected at metre intervals with a 10 litre Schindler - Patalas plankton trap.

3.5.3 Results and Discussion

The results of the planktonic counts are given in Tables 3.4 and 3.5. On an areal basis, the trap sampler collected at least three times as many larvae as the net haul. Whether the larvae avoided the net or the latter was not as efficient (e.g. as a result of a bow wave developing in front of the net) is not known.

From the three sets of samples taken with the trap sampler, it would appear that the planktonic larvae were concentrated at depths of four to six metres. This depth distribution, however, may alter, depending on the time of day, as diurnal cycles of planktonic activity have been observed (Mundie 1959; Thut 1969; Luferov 1971; Davies

Date	ZEA					CUR					KIE					FUN					TPO					
	1	2	3	4	P	1	2	3	4	P	1	2	3	4	P	1	2	3	4	P	1	2	3	4	P	Total
5 12 78																										0
17 12 78																	1					1				2
28 12 78		1																								1
10 1 79																										0
19 1 79																										0
1 2 79																										0
9 2 79																										0
19 2 79										1																1
7 3 79																										0
22 3 79																					1					1
5 4 79	1																									1
17 5 79		2									2							1	1							6
31 5 79																		2								2
27 6 79																	1									1
26 7 79																	4	1								5
23 8 79				1												2	1	2	1							7
19 9 79																1										1
27 9 79																	1									1
12 10 79																2										2
25 10 79																										0
8 11 79																										0
22 11 79																										0
6 12 79																										0
20 12 79																	1									1
3 1 80	1	1																								2
14 2 80																		1						1		2
13 3 80	1	4	5	2				1									12	4	9	1						48
26 3 80			3	3		1	2	4	1							2	2	1	6	5						102
27 3 80																										? 0
10 4 80				1				2								3	3	5	5							19
3 5 80	1		2													1	2	3								9

TABLE 3.4. Seasonal variations in the number of planktonic chironomid larvae in L. Maratoto. Samples obtained by taking two hauls with a 20 cm plankton net over the area of maximum depth. To convert to numbers per sq. m multiply by 15.9. ZEA = Chironomus zealandicus, CUR = Cladopelma curtivalva, KIE = Kiefferulus opalensis, FUN = Calopsectra funebris, TPO = Tanypodinae, 1 = stage I, 2 = stage II, 3 = stage III, 4 = stage IV, P = pupae.

Date	Depth (m)	ZEA 1	ZEA 2	ZEA 3	ZEA 4	CUR 1	CUR 2	CUR 3	CUR 4	FUN 1	FUN 2	FUN 3	FUN 4	Total
19 4 79	0													0
	1													0
	2										1			1
	3										1			1
	4				1									1
	5	1			1									2
	6										2	1		3
	7							1						1
13 3 80	0													0
	1													0
	2													0
	3													0
	4	1			1						1			3
	5		3	1	1						2	3	4	12
	6		1	1							1	3		6
	7			1							1	1		3
27 3 80	0									1				1
	1													0
	2													0
	3										1			1
	4										1	2	3	6
	5									1	1			2
	6											1	1	2
	7												1	1

TABLE 3.5. Depth distribution of planktonic chironomids in L. Maratoto. Samples taken with a 10 l Schindler-Patalas plankton trap at varying depths as shown. ZEA = *Chironomus zealandicus*, CUR = *Cladopelma curtivalva*, FUN = *Calopsectra funebris*, 1 = stage I, 2 = stage II, 3 = stage III, 4 = stage IV.

1974). No doubt weather conditions also greatly affect this distribution, since increases in water turbulence would tend to redistribute the larvae more evenly.

The number of larvae in the plankton increased markedly during windy periods, notably following the overturn. Thus, high numbers were recorded in April/May 1979 and in March/April 1980. Highest numbers (estimated at 1,620 per sq. m) were collected on 26/3/80 when strong winds on that day had just mixed the lake. Benthic larval numbers estimated on the same day at 7 m were 2,467 per sq. m, so that on that occasion at least, planktonic chironomids made up a significant proportion of the total larval population.

Plankton samples taken on 27/3/80 contained fewer animals than the previous day, presumably because most larvae had by then settled on the bottom mud. The time of collection is probably important in determining the planktonic activity of chironomid larvae. The lower numbers found at the end of the summer of 1979, as opposed to 1980, may simply have been a matter of timing. Nevertheless, wind turbulence at the end of summer 1980 was much greater and more prolonged than in 1979, and would have increased the chance of disturbing the benthic larvae. That year as well, deoxygenation and re-oxygenation took place repetitively over a matter of days and chironomid larvae may also have been evicted from the bottom muds by low oxygen concentrations. In addition, the number of benthic chironomids in 1980 was higher than in 1979, and the chance of larvae being disturbed and entering the water would have been higher. This effect of benthic population size on the limnetic activity of the larvae was also apparent in the winter of 1979, when high populations of Calopsectra funebris were recorded both in the sediment and in the water.

Most species and all stages were recorded in the water, but the percentage composition of species in the water and on the bottom of the lake were not always the same. This probably results from varying degrees of stimuli required to evict the various species and stages, and in differing light responses and settling rates.

No evidence was found of late fourth instar Chironomus larvae being more common than any other stage in the water, which was suggested by Forsyth (1971). Mass limnetic activity by older instars of C. zealandicus has been observed in Lake Rotorua (D. Rowe pers. comm.), but these animals were probably the last of a winter cohort being evicted from the bottom muds by low oxygen concentrations.

Chironomid larvae therefore can become planktonic at most times, but their numbers increase considerably during periods of water turbulence - especially at the turnover. This limnetic activity is usually of short duration. Larvae may also enter the water in response to toxic conditions, notably low oxygen tension, and remain planktonic until they can resettle in a more favourable habitat.

3.6 GENERAL DISCUSSION

3.6.1 Feeding

The principal diets and feeding methods of chironomids found in the Waikato region are given in Table 3.6. Most of the species could also adopt the feeding habits and behaviour of other groups. The chironomid community of Lake Maratoto is dominated by detritus feeders, but the nutritional requirements of the taxa overlap considerably.

Food sources in Lake Maratoto are primarily autochthonous. There are no major streams flowing into the lake and little particulate organic matter enters via the farm drains. As the lake is fringed by manuka (*Leptospermum scoparium*) and gorse (*Ulex europaeus*) which are both evergreen and woody, input of allochthonous plant material will be slight and of low nutritional value. Since there are no macrophytes in the lake and the area of emergent reeds is small and slow growing, these usually important sources of organic matter are also largely absent. Eroded peat particles however may be a major food source. These particles, once colonised by obligate and facultative aerobic micro-organisms, become palatable to many invertebrates and have a high calorific and protein content (McLachlan and Dickinson 1977; McLachlan et *al*. 1979). In Lake Maratoto the highest concentration of these particles occurs in winter (see section 1.2.11). This period corresponds to the highest population of detritus feeders, notably *Calopsectra funebris* which grazes the surface sediments.

The other major food source of Lake Maratoto is algae. Numbers of these are highest in the summer (Figure 1.9), and chironomid species that make use of this food source (e.g. *Kiefferulus opalensis*) have their highest numbers also at this time. Detritus feeders will also benefit from these algae as they settle and accumulate in the sediments.

Taxa	Principal diet	Preferred feeding method
TANYPODINAE	Chironomid larvae	Carnivorous
PODONOMINAE	Algae/detritus	Scraping
Eukiefferiella sp.	Algae/detritus	Scraping
Syncricotopus sp.	Filamentous algae	Grazing
Metriocnemus sp.	Algae	Scraping
Chironomus zealandicus	Detritus	Direct ingestion
Cladopelma curtivalva	Diatoms ?	?
Polypedilum pavidus	Planktonic material	Filtering (net)
Kiefferulus opalensis sp.	Planktonic material	Filtering (net)
Calopsectra funebris	Detritus/algae	Sediment surface Scraping
Corynocera sp.	Algae/detritus	Collection and ingestion of lumps
Paratanytarsus agameta	Detritus/algae	Surface scraping

Table 3.6. Postulated feeding for some lake dwelling chironomid larvae of the Waikato region.

3.6.2 Seasonal Variation

In cool, temperate habitats, variations in temperature and food greatly affect breeding and growth, and impose marked seasonal periodicity on the development of chironomids. In consequence, it is possible to make reasonably complete analyses of population turnover (e.g. Jonasson 1965; Hilsenhoff 1966; Thut 1969). In New Zealand the warm oceanic climate results in reproduction being more continuous rather than resulting in distinct cohorts. (e.g. Winterbourn *et al.* 1981) and as a result adults are present for much of the year. Such long flight periods, which spread the risk of emergence, would be selectively advantageous as they offset the effects of New Zealand's variable weather patterns. However, they make it difficult to determine population turnover rates.

Recruitment in Lake Maratoto probably takes place throughout the year, but there are periods of increased rates. The importance of success in mating and oviposition in determining the size of a chironomid population has been stressed by Davies (1976b), although Kajak *et al.* (1968) maintained that the abundance of benthos is determined more by biocenotic and environmental conditions than by the number of eggs coming into the environment.

In Lake Maratoto, both these sets of factors influence the population. Although emergence generally coincided with periods of calm sunny days when swarming and egg-laying were favoured, it would be erroneous to suggest that increases in the larval population were solely due to higher numbers of eggs being deposited. Survival of the young larvae is just as significant, this being dependent on the quantity and quality of the food as well as on oxygen concentration and temperature (Jonasson 1972; Ward and Cumming 1979). Since it was only with the

return of warm conditions in the early summer that algal numbers increased markedly (Figure 1.9), it is likely that the survival of young larvae is linked to the presence of this amino acid-rich food (Mason and Bryant 1975) which enables them to grow and metamorphose more quickly. The decrease in spring to the annual minimum shown by the larvae of all species may be a result of food depletion after the winter period of low algal abundance. Thus the abundance of chironomids in Lake Maratoto may be strongly influenced by the magnitude of summer algal growth and its contribution to the sediments.

The oxygen concentration of the water also places restrictions on the success of some species. In summer, the dominant species were those with large amounts of blood pigment (e.g. Cladopelma curtivalva and Chironomus zealandicus). In the winter months when oxygen levels remain high species with no blood pigment were more common (e.g. Tanypodinae and Calopsectra funebris).

3.6.3 Depth Distribution

On the edges of the lake, all stages of chironomids, especially stage I larvae, were found in greater numbers. Reasons for this were the deposition of egg cases near the shore, the higher concentration of food, notably algae, in the littoral, and the reduced oxygen concentrations existing in summer in the deeper water. In the centre of the lake, the few larvae collected were predominantly species with erythrocruorin. They were mainly stage IV larvae which have a higher concentration of this blood pigment (pers. obs.) and are presumably better equipped to tolerate the low oxygen conditions of the profundal for a longer time. Yet, even these were excluded from the deeper region of the lake during periods of low oxygen tension, and only reappeared in the profundal following the turnover.

3.6.4 Population Size

A comparison of larval densities recorded in Lake Maratoto with those noted in other lakes by different authors is hindered by the many differing methods of collection and treatment of samples. Generally, numbers of animals found in acid lakes are lower than in other water bodies, and both the number of individuals and the number of taxa decrease with depth. Wiederholm and Eriksson (1977) for example, found a chironomid population mean of 1,500 per sq. m (made up of 12 taxa) on the edges of a Scandinavian lake, but only 40 per sq. m (three taxa) in the centre. Similarly, Berg (1955), in a study of Lake Gribsø, found a maximum of around 2,000 per sq. m at the shallowest station, and no animals at the deeper end of the lake. Such low numbers however, are not always the rule, and McLachlan (1975) reported up to 22,000 individuals per metre square in an acid lake in North East England. Similar data for New Zealand acid or bog lakes are sparse. Two South Island dystrophic lakes were studied by Timms (1982) who found a mean number of 296 chironomids per sq. m (nine species) in Lake Gault and 263 per sq. m (five species) in Lake Matheson. In the North Island, the only published data on such types are for Lake Ngahewa (Forsyth and McColl 1975), which is humic stained, but no longer acid. Here, chironomid larvae of five species varied from 1,260 per sq. m in early summer to 31 per sq. m in late summer. In Lake Maratoto the mean standing crop of chironomids was 2,970 per sq. m. This is five times that of Lake Ngapouri, the most productive of seven meso-eutrophic lakes of the Rotorua area studied by Forsyth (1978) and comparable to those recorded by Timms (1982) for some of the shallower and more productive South Island lakes. The value for Lake Maratoto is about 0.3 times that of Lake Rotowhero (Forsyth and McColl 1974) and 0.5 times that of Opal Lake (Forsyth and MacKenzie 1981), two highly eutrophic lakes of the

central North Island. On this basis, Lake Maratoto may be classified among the more productive New Zealand lakes.

CHAPTER 4

LIVING AND FOSSIL LARVAL CHIRONOMID LARVAE AND THEIR REPRESENTATIVENESS IN SURFICIAL SEDIMENTS

"Le soir montre ce qu'a été le jour."

Anon.

4.1 INTRODUCTION

Relationships between the abundance of indicator species and various physical and chemical parameters have increasingly been used to make inferences about the history, status and quality of fresh water habitats. Chironomids, which often form a high proportion of benthic macroinvertebrates, are particularly useful indicators, as the different groups usually have varying feeding requirements and tolerance to oxygen depletion. The abundance of the indicator organisms is normally obtained from surveys designed to describe the spatial distribution and actual or relative abundance of the organism This requires representative collections from all available habitats and at all seasons.

Examination of benthic sediments usually reveals considerable numbers of identifiable remains of larval and pupal chironomids, and since Deevey (1942), many workers have successfully used these remains for interpreting lake ontogeny (see review by Stahl 1969). A study of the remains from surficial layers of sediments can also provide an easy means for the comparative study of present day chironomid faunas in different benthic environments (e.g. Iovino 1975; Henrikson et al. 1982).

The distribution of these animal remains is governed by two sets of processes.

1. Environmental factors that determine where the animals live in the lake and how abundant they are.

2. Physical processes such as resuspension and redeposition.

Redeposition probably has little effect on the distribution of remains of larger lakes (Iovino 1975) but in smaller lakes it is likely to help homogenise the remains from the surrounding micro-habitats. Although resuspension may help even out the variations in accumulation of remains, where sedimentation rates are low it will cause mixing of older with more recent sediments. Thus, where the habitat has undergone major changes in recent years, the fossilised remains may show little affinity with the present conditions. In most lakes, however, it is expected that any mixing by storms probably only affects the extreme superficial layer of sediment, producing a certain amount of homogeneity. A small sample of sediment may therefore be expected to reflect the constitution of the 'average' chironomid fauna of the period of deposition.

In summarising data on the abundance of benthic fauna, whether derived from a detailed sampling programme or from remains found in surficial sediments, much use has been made of computed indices such as the Shannon-Weiner diversity index, Jaccard Similarity index, Spearman correlation coefficient (Hellawell 1978) and the benthic quality index (Wiederholm 1976). The value of these indices however, depends largely on seasonal timing, procedures of sampling and the degree of taxonomic penetration. Most of these indices, particularly the benthic quality index, greatly oversimplify the ecological state under study. Indices of this type are not entirely satisfactory as they do not utilise all of the available information amassed by a biological survey. Data from this type of survey may include abundance of several species for each of several habitats or points in time, and require the use of multivariate statistical techniques such as cluster analysis (e.g. Hellawell 1978, Carter 1979, Rossaro and Ferrarese 1979) and principal component analysis (Sprules 1977, Bindford 1982).

Cluster analysis, on its own, provides valuable information on similarities between sites, but none on underlying causes. Principal component analysis on the other hand, summarises the information in terms of new components, a small number of which account for most of the variation.

The variation summarised by each of the principal components is the variation in abundance of those species having high positive and negative correlations with the respective component. One significant feature of principal component analysis is that it is the variation in species abundance which is important and not simply the magnitude of the abundance. Rare and common species alike can have high correlation with a component so long as their abundances vary greatly over the habitats sampled.

From the simplification achieved by the above techniques, one can then formulate hypotheses about the cause of the variation in the system. Thus, correlations between limnological variables and principal component scores can relate the variation along a component to those limnological characteristics having high positive and negative correlation with that component. Furthermore, using the result of this analysis as a simple model, an independently selected lake could be categorised limnologically by its principal component scores and the environmental interpretation given to the components.

This section of the study therefore aims to: 1/ Determine what limnological factors affect the distribution of chironomid larvae. 2/ Ascertain whether chironomid community structure can be used to make predictions about the limnological characteristics of habitats.

4.2 MATERIAL AND METHODS

Over the duration of this study, semi-quantitative samples of the chironomid fauna were obtained from 24 localities in the lower Waikato and volcanic plateau regions. Location and some characteristics of these lakes are given in Table 4.1. Where more than one habitat was recognised in a lake, separate samples were taken using dredges, cores or sweep nets - as appropriate for the particular site. Chironomid larval numbers were recorded as dominant, subdominant and present. Some of the habitats were sampled on more than one occasion, in which case an average record is reported.

Samples of the surficial sediment were obtained by slowly lowering a 25 sq. cm Ekman grab to the mud surface to ensure minimal disturbance. The dredge and contents were then brought to the surface and the overlying water slowly decanted. Subsamples of the mud surface were obtained by carefully skimming the undisturbed mud surface.

In Lake Maratoto, five samples were taken at sites equi-distant from the shore and from each other along the main axis of the lake, starting from the northern end of the lake. In Lake Waahi, five samples were also taken in a similar manner along a transect starting on the south west shore and ending on the eastern shore. For Lakes Rangiriri, Rotoroa, Kimihia, Mangahia, Rotomanuka, South Serpentine, Mangakaware, Ngaroto, Arapuni, and Awaatua crater, samples were taken in the area of maximum depth (usually the lake centre).

Each sample of surficial sediment was then stirred up and several 1 ml subsamples obtained with an open ended 5 ml plastic syringe. For each set of samples, the water content of duplicate subsamples was obtained by determining the weight loss on drying at 80 'C. Carbon content was calculated from the weight loss of the dry sediment on

Location	Code	NZMS1 Sheet	Grid Ref.	Max. Depth (m)	Area (ha)	pH	Secchi (m)	Chl. a (g/m3)	Total P (mg/m3)	Abs. 270nm	Sediment		Ref.
											%C	%H20	
Waikato R.	Wr	N52	560083										
L. Waikare	Wk	N52	750856	2	3440	7.8	0.3	35	189				i
L. Rotokawau	Rw	N52	695840	1			0.6						ii
L. Rangiriri	Ri	N52	650910	2	52	8.5	0.2	292	383		15	61	i,v
L. Kimihia	Ki	N56	705782	1	54	7.0	0.1		30		34	69	i,v
L. Hakanoa	Ha	N56	680755	3		7.5	0.5						i
L. Pikopiko	Pk	N56	703620										
L. Waahi	Wh	N56	643740	5	500	8.0	0.6	28	105	0.15	13	81	i,iii,v
L. D	D	N56	743603	7		6.8	0.6						i
L. B	B	N56	756600										
L. Rotoroa	Ra	N65	785455	6	55	7.6	2.0	11	21		26	76	i,v
L. Mangahia	Mh	N65	738358	2	10	5.4	0.3	34	108	2.12	56	76	i,iv,v
L. Maratoto	Mo	N65	812350	7	17	4.6	0.5	26	47	1.60	67	90	iv,v
L. Ruatuna	Ru	N65	798300	2	13	6.8	0.5	29	54	1.04			i,iv
L. Mangakaware	Mk	N65	731292	4	10	7.2	1.3	33	71	0.47	28	78	i,iv,v
L. Rotomanuka	Ro	N65	822303	9	12	7.5	4.0	8	16	0.19	41	84	i,iv,v
L. Rotomanuka (South)	Gn	N65	828298	3	5	7.5	0.4			0.74			iv
L. Serpentine (North)	SN	N65	825283	4		6.7	1.8			0.76			iv
L. Serpentine (South)	SS	N65	825274	3	8	6.4	1.3	40	40	0.62	37	82	iv,v
L. Ngaroto	Ng	N65	798268	4	96	7.6	1.2	43	84	0.56	18	82	i,iv,v
L. Rotopataka	Rp	N65	834254	1	2	4.8	0.5	19		0.92			iv
L. Arapuni	Ar	N75	128090	50	1370	7.5	2.0	5	26		17	88	i,v
L. Tarawera	Tw	N76	842958										
Awaatua Crater	Aw	N86	945858	31	13	7.5	3.9	10	16		13	75	vi,v
Waihaha lagoon	Wa	N93	230334										
L. Kiriopukae	Kr	N105	533220										

Ref.

i WVA and MWD Records (R. Pridmore pers. comm.)
ii J. Edwards pers. comm.
iii Chapman (1980)
iv Chapman and Boubée (1977)
v This study
vi Chapman et al. (1981)

Table 4.1. Location and limnological characteristics of some central North Island lakes sampled in this study.

ashing at 550 'C in a muffle furnace. Further subsamples were placed separately in 20 ml P.V.C. containers, sealed and stored at -15 'C until required.

For the determination of microfossil remains, a 1 ml subsample of wet sediment was soaked in water and a 10% hydrofluoric acid solution added to make up to a final concentration of 5%. This solution was placed in a boiling water bath until all gas emission ceased (about 10 minutes) and rinsed in a 70 µm sieve using copious amounts of tap water. The remains were then transferred to a 50 ml glass beaker using minimal amounts of water. Hot 20% KOH was added to make the solution to about 10% strength. This was sonicated for 45 seconds using a 'Kontes' micro-ultrasonic cell disrupter set at maximum strength. The solution was next heated at just below boiling point for 5 minutes, re-sonicated for 30 seconds and rinsed in a 70 µm sieve with copious amounts of water. The sediment was transferred back to the beaker and 1 drop of chlorazol black solution added, together with a few mls of 50% ethanol. The solution was covered and allowed to stand overnight, after which it was rinsed with water in a 70 µm sieve. The remains were then transferred to a graduated container with 0.5 or 1 ml of water depending on the amount of material remaining. This solution was well stirred and 50 µl of it was transferred to a glass slide, together with 50 µl of warm glycerine jelly (see below). The material was mixed uniformly with fine needles and a square cover glass was finally placed over the preparation. These last steps were repeated until all the material was mounted. The recognisable microfossils on the quantitative slides were systematically counted by examination at 100X with a microscope equipped with a mechanical stage. The microfossil density governed the number of mounts examined.

This technique ignores accumulation of remains shed by the same individual over several instars. Although the dilution effect of sedimentation rate can markedly effect the interpretation of results (Smol 1981), this was an unknown quantity in some of the lakes sampled and could not be taken into account. Because numbers were usually low, each identifiable chironomid fragment was counted as a whole animal. Microfossil densities were reported in a taxa by lake matrix as the number of remains per ml of surface sediment.

The glycerine jelly used as mounting medium was made by dissolving 10 g of gelatine in 60 ml of distilled water. This solution was heated gently while stirring until all the gelatine dissolved, at which point 70 ml of glycerol and 0.25 g of phenol crystals were added. This solution sets at normal room temperature but can be remelted in a boiling water bath.

After log transformation to normalise error variances (Elliott 1971), the data was standardised to Z scores (where x' = (x - mean)/standard deviation) and a BMDP4M (Dixon and Brown 1981) principal component analysis used to distinguish statistically between the lakes.

To help identify lake groupings, a BMDP2M (Dixon and Brown 1981) cluster analysis of cases was carried out. This uses the centroid linkage method for linking cases (= lakes) into clusters with Euclidean distances (sum of square) as a measure of interlake similarity.

To test the suitability of the method for classifying independently selected lakes and/or habitats within these lakes, a further two samples of surface sediments were obtained in about one metre of water, near the edges of four of the previously sampled lakes. These sites were chosen to provide maximum contrast of habitats. In Lake Maratoto, one sample

(MoN) was taken near the outlet. This part of the lake's catchment is in pasture. The second sample (MoSW) was taken on the south west edge where the peat is deepest. The surrounding land here is covered in scrub. For Lake Ngaroto, sample NgN was taken near the outlet drain. Some of the shoreline at this end of the lake consists of sand and clay. The second sample (NgS) was taken on the opposite shore where there are extensive beds of exotic macrophytes. Some nearby swampy grounds, although now partly drained, also affect this habitat. In Lake Rotoroa, the bay where sample RaNE was taken is infested with exotic macrophytes and most of the shoreland is sandy clay. This side is bordered by low hills. The opposite shore (sample RaW) adjoins the once encroaching Rukuhia peat swamp and has fewer submerged macrophytes. Lake Waahi has, until recently, been entirely covered by exotic macrophytes. Although massive die off of the weed has occurred recently, the bottom sediment is still expected to reflect this ecological dominance by macrophytes. Samples were taken on the east (WhE) and south west (WhSW) edges of the lake. In addition to this brief description of the sites, a summary of some pertinent characteristics of each habitat is given in Table 4.2.

The resulting counts from these edge samples were normalised by taking the log + 1 of each value, and standardised to Z scores using mean number of each taxa per ml, and the standard deviation calculated from the lake centre data. The principal component scores equal the sum of the standardised abundance of each taxa times the principal component coefficient for that taxa (determined by the BMDP4M principal component analysis of the lake centre samples).

i.e. $$\sum_i ((\log (n_i + 1) - \bar{X}_i) / SD_i)(PCC_i)$$

Where : n_i = number of taxa i per ml of edge sediment.

Lake	Sample code	NZMS1 sheet	Grid ref.	Sediments %C	Sediments %H20	Exotic weeds	Reeds	Sand/Clay shoreline	Bordering land Swamp	Bordering land Clay	Bordering land Grass
Maratoto	MoN	N65	814354	81	87				+		+
	MoSW	N65	799347	70	84		+		++		
Ngaroto	NgN	N65	793276	18	82	+	+	+		+	+
	NgS	N65	804259	20	82	+	+		+		+
Rotoroa	RaNE	N65	784462	17	66	++		+		+	+
	RaW	N65	778456	22	72	+	+		+		+
Waahi	WhSW	N56	633728	20	72	+		+		+	+
	WhE	N56	650744	9	47	+		+		+	+

Table 4.2. Position and pertinent physical/chemical characteristics of the lake edge sampling sites used in this study. + = Present, ++ = Dominant.

$\overline{X}_i$ = mean number (log) of taxa i per ml of sediment from the centre of the 12 lakes sampled in this study.

SD_i = standard deviation of $\overline{X}_i$.

PCC_i = principal component coefficient for taxa i as determined in the BMDP4M multivariate analysis of the centre samples.

4.3 RESULTS AND DISCUSSION

4.3.1 Living Chironomid Fauna

The chironomid fauna recorded from the 24 localities visited is summarised in Table 4.3, although this species list is not intended to be exhaustive. The dominance of the taxa may vary considerably both seasonally and from year to year. For example, in Lake Rotomanuka, the weed bed fauna was dominated by orthoclads in the winter but by tanytarsines in summer. In the profundal regions of many lakes also, oxygen depletion displaced most species during the summer months.

Although no attempts were made to determine quantitatively the total chironomid population in the lakes sampled, it was noted that larvae were most numerous on the edges of dystrophic lakes (Mangahia, Maratoto) while low populations were recorded in both oligotrophic lakes (e.g. Awaatua Crater of lake Rerewhakaaitu) and eutrophic lakes (e.g Rangiriri). Forsyth (1978) in his study of seven Rotorua lakes did not find a strong relationship between the mean annual standing crop of chironomids and lake water quality. In the present study some of the lakes were more eutrophic than the Rotorua ones and it is likely that their small chironomid population is related to low oxygen concentrations to which chironomids are susceptible, while high

Location	Habitat	TANYPODINAE	PODONOMINAE	*Symaricotopus* sp.	*Eukiefferiella* sp.	*Metriocnemus* sp.	ORTHOCLADIINAE (indet.)	*Chironomus zealandicus* (gilled)	*Chironomus zealandicus* (ungilled)	*Cladopelma curtivalva*	*Kiefferulus opalensis*	*Polypedilum* spp.	*Calopsectra funebris*	*Calospectra* sp.	*Corynocera* sp.	*Paratanytarsus agameta*
Waikato R.	Weeds			P	P	P	D		P			P	P			P+
L. Waikare	Edges			D								P				P
L. Rotokawau	Edges							D	P							P+
L. Rangiriri	Edges						P		P			D	P			
L. Kimihia	Centre							D								
	Edges	P					P+									D
L. Hakanoa	Reeds							D	P	P	P+		P			
	Edges						P	D	P	P	P		P+			P
L. Pikopiko	Weeds			P				P+					P			D
	Edges			P				D					P			P+
L. Waahi	Centre						P	P+				P				D
	Edges			P	P+		P	P	P			P		P		D
	Beach			P	P		P					D				P
L. D	Reeds						P	D			P+	P				
	Edges						P+	D								
L. B	Weeds							P+			P		P			D
	Reeds							D								
L. Rotoroa	Centre							P+		D			P			P
	Reeds	P		P		P		D		P			P+			P
	Edges											P+	P			D
L. Mangahia	Centre							D								
	Edges	P		P	P		P	D		P	P		P+			P
L. Maratoto	Centre	P						D		P			P+			
	Edges	P	P	P	P	P		P		P	P+		D			
L. Ruatuna	Centre							D		P+						
	Reeds			P				P		P+						D
L. Mangakaware	Centre							P+		D						
	Reeds						P	D	P							P+
	Edges			P			P+	D								P
L. Rotomanuka	Centre				P			D	P	P			P			
	Weeds			P+	P+			P					D			P
	Edges												P			D
	Lagoon							P+	P		P				D	P
	Inflow	P		P	P		P+	D				P	P		P	P
L. Rotomanuka South	Reeds			P		P		D	P				P			P+
	Edges			P	P											D
L. Serpentine North	Edges			P	P		P	P					D			
L. Serpentine South	Centre							P+		D			P			
	Edges	P		D	P+			P			P		P	P		P
	Lagoon			P	P			P					P+		D	P
L. Ngaroto	Centre							P	D	P+						
	Weeds							P		P+						D
	Beach							D		P	P	P				
	Lagoon			P				P		P			P		P+	D
L. Rotopataka	Edges						P									D
L. Tarawera	Edges					D	P	P+								
Awaatua Crater	Centre							P								
	Edges							P		D						
Waihaha lagoon	Edges	P+					D						P			
L. Kiriopukae	Edges	D					P+			P		P	P			

Table 4.3. Chironomid fauna recorded in some central North Island lakes. Location of sampling sites are given in Table 4.2. P = Present, P+ = Sub-dominant, D = Dominant.

population densities in dystrophic lakes may be due to a higher food supply and to a lack of fish predation.

Species richness in all the lakes sampled was low and most chironomid species were found in a wide range of habitats, regardless of the water's trophic state. These findings are in accordance with those of Forsyth (1978) and Timms (1982) for other New Zealand lakes. Unlike these authors however, I found that most species exhibit definite micro-habitat preferences. These are summarised in Table 4.4 and discussed below.

TANYPODINAE

The distribution pattern of tanypods is difficult to discern, possibly because they are a varied carnivorous group. Numerous larvae were collected amongst weed in streams and at the edges of many lakes. It is interesting to note also that tanypods were the dominant taxa in some of the tarns of the Urewera National Park in central North Island (pers. obs.). This distribution pattern deserves more work, as these tarns with their forested catchment, harsher climate and morphometry may well represent modern analogues of developing Lake Maratoto (see Chapter 5).

ORTHOCLADIINAE

Orthoclads are usually restricted to oxygen rich environments and are particularly common amongst exotic weeds or the vegetation on the edges of lakes. Further habitat segregation occurs within the family, due in part to a definite food preference. For example, Syncricotopus sp. which feed predominantly on filiform algae will be most common where these algae grow profusely while Eukiefferiella sp., which is a detritus feeder, will be found mainly towards the base of plant stems

Taxa	Preferred Habitat	Oxygen requirement	Case
TANYPODINAE	Any surfaces	Med.	No
PODONOMINAE	Plant surfaces	High	No
Eukiefferiella sp.	Any surfaces	High	Yes
Syncricotopus sp.	Plant surfaces	High	No
Metriocnemus sp.	Plant surfaces	High	No
Chironomus zealandicus	Fine mud	Low	Yes
Cladopelma curtivalva	Sediments and plants notably Characeae	Med	Yes
Polypedilum pavidus	Inorganic sediments high phytoplankton	Med	Yes
Kiefferulus opalensis sp.	Edges acid lake	Med	Yes
Calopsectra funebris	Sediments/edges dystrophic waters	Med	Yes
Corynocera sp.	Algal high sediments clear shallow water	High	Yes
Paratanytarsus agameta	Sediments and plants	High	Yes

Table 4.4. Habitat requirements for some lake dwelling chironomids of the Waikato region.

where its preferred food accumulates (see also Section 3.3).

CHIRONOMINAE

Chironomus zealandicus (complex)

Chironomus zealandicus occurs in most habitats with the highest numbers of the gilled larvae being found in rich organic ooze.

Polypedilum spp.

These species are found in highest numbers on the sandy edges of lakes having enriched, but still moderately clear water (Rotoroa, Waahi, Rangiriri, Ngaroto).

Cladopelma curtivalva

Cladopelma curtivalva is most dense among beds of Characeae (Rotoroa, Mangakaware, Serpentine). Distribution data presented by Forsyth (1976, 1978) and Forsyth and McCallum (1981), as well as my own observations, suggest that C. curtivalva is a species whose maximum depth distribution is linked to high light penetration and perhaps indirectly to the presence of characean meadows.

Kiefferulus opalensis

In the Waikato, Kiefferulus opalensis is restricted to the edges of the more dystrophic lakes (Maratoto, D, Hakanoa), occurring in large numbers on reed stems and submerged branches. Forsyth and MacKenzie (1981) recorded it in Opal lake (pH 4.0 to 4.6), but in no other lakes of the Volcanic Plateau, although it has been reported in stock ponds in Northland (Forsyth 1975b). Seasonal distribution of the larvae in Lake Maratoto suggests that development of the larvae is directly or indirectly dependent on temperature. Their distribution in the central

North Island lakes also suggests that they prefer acid waters.

TANYTARSINAE

The Tanytarsini are a significant group because of their extensive typological use (Brundin 1958). In New Zealand this subfamily does not appear to occur widely (Forsyth 1976, 1978; Timms 1982), but nevertheless it dominates much of the chironomid fauna in the Waikato basin.

Calopsectra funebris

This species occurs in a wide range of habitats, but is most abundant on the edges of dystrophic lakes and in temporary pools.

Corynocera sp.

Of all chironomid species found, the distribution of Corynocera sp. appears to be the most localised. It occurs principally in clear, shallow pools (often temporary) formed behind the main reed margin of some lakes (Rotomanuka and Serpentine South notably) (Plate 19B).

Paratanytarsus agameta

P. agameta is common among exotic macrophytes. It is also abundant on the vegetation and detritus of most temporary ponds.

Plate 19. (A) Aerial view of Waikato basin taken above Te Awamutu township and looking north. Lakes, from left to right: Ng = Ngaroto, Ru = Ruatuna, Ng = Ngarotoiti, Mo = Maratoto, Ro = Rotomanuka (North and South) and Si = Serpentine (North and South).

(B) Lake Rotomanuka, showing area of flooding which is densely populated with chironomids, notably Corynocera sp.. Note native bush stand in background, once more extensive.

A

B

4.3.2 Surficial Sediment Fossil Remains

4.3.2.1 General Description -

Remains of various developmental stages of many arthropods, including those of several species of chironomids, ceratopogonids, mites, beetles and caddis were recovered from the surface sediments of the lakes investigated. Results of the counts are presented in Appendix 2.

Numerous other remains were encountered but not recorded, including cladocerans, copepods, ostracods, tardigrades and rotifers, as well as some of unknown origin. Although a few entire bodies were found, the bulk of the material consisted of body fragments, notably mouth parts. As a result of poor preservation and/or orientation on the slide, and of the limited taxonomic knowledge available, many of the remains could only be identified to some of the higher taxonomic levels. With the chironomids, although mandibles and pupal spurs can, in some instances be identified to genus and species, the labial plate is the most useful taxonomically. The numbers of these feeding appendages varied from 6 per ml of sediments in Lake Arapuni to over 600 in Lake Mangahia. From the five samples taken in transects in both in Lake Maratoto and Lake Waahi, it was calculated that the 95% confidence limit of the mean number of total chironomid fossils estimated from a single surficial sediment sample was x $X \div 1.47$ for Lake Maratoto and $X \div 1.41$ for Lake Waahi. Since not all the head capsule remains could be identified accurately, some degree of 'lumping' was required and only ten of the more common and more easily identified chironomid groups were used in statistical analyses. No doubt some of the finer details were lost in the condensing of the data but the present state of New Zealand chironomid taxonomy allowed little choice.

The taxa retained were: Tanypodinae and Orthocladiinae in which were grouped all remains identifiable to these families; the Chironomus zealandicus complex; Cladopelma curtivalva; Kiefferulus opalensis; Polypedilum spp.; Paucispinigera spp. (both P. approximata and Paucispinigera sp.); Paratanytarsus agameta; Corynocera sp. and Calopsectra spp. which included both C. funebris and Calopsectra sp..

A summary of the results is given in Tables 4.5 and 4.6.

Of the species found, Kiefferulus opalensis and Polypedilum spp. are considered lake edge dwellers, hence off-shore redeposition of larval remains is important in most of the lakes investigated. Analysis of surface sediment from the centre of a small lake therefore must be considered as reflecting the lake's entire fauna.

The remains in surficial sediments were also found to describe both past and present fauna. Thus, while no living larvae, pupae or adults of Polypedilum spp., Corynocera sp. and Paucispinigera spp. were ever collected from Lake Maratoto, these taxa made up a significant proportion of the remains recognised in the sediments. In addition, the species composition of the chironomid fossils found in the sediments shows little similarity to the present population (Table 4.7). Orthoclads and tanypods form a high proportion of the fossils, yet, in the living fauna anoxia, resistant species (Chironomus zealandicus and C. curtivalva) are more important. One can conclude that although Lake Maratoto is one of the least disturbed lakes in the Waipa County, it has undergone marked enrichment over recent years. The existence of Corynocera sp. in the past also suggests that there were then swampy areas of the shore which flooded and remained covered with about half a metre of water for substantial periods of time. These areas would have been destroyed when the present outlet drain was dug through the low

Sample Code	Taxa									
	TPO	ORT	ZEA	CUR	KIE	POL	PAU	AGA	COR	CAL
Ar	0.	4.	0.	0.	0.	0.	0.	1.	0.	0.
Hl	3.	6.	13.	30.	5.	0.	3.	5.	18.	15.
Kh	0.	8.	0.	0.	0.	0.	0.	20.	0.	9.
Re	0.	2.	4.	1.	0.	0.	0.	0.	0.	2.
Mh	34.	111.	71.	4.	13.	6.	26.	6.	1.	107.
Mo1	42.	24.	22.	4.	14.	10.	10.	4.	10.	34.
Mo2	36.	46.	55.	3.	40.	13.	8.	3.	20.	105.
Mo3	35.	53.	44.	7.	22.	7.	6.	0.	13.	67.
Mo4	19.	41.	36.	7.	40.	13.	7.	0.	20.	99.
Mo5	24.	56.	26.	4.	24.	4.	11.	0.	18.	46.
Mk	4.	12.	37.	9.	0.	1.	1.	1.	1.	35.
Ng	1.	2.	1.	0.	0.	1.	3.	1.	2.	1.
Ra	13.	23.	13.	0.	10.	28.	0.	10.	13.	30.
Ro	3.	12.	18.	0.	2.	3.	1.	2.	9.	61.
SS	1.	1.	7.	6.	1.	0.	0.	0.	16.	3.
Wh1	0.	36.	5.	0.	0.	3.	0.	48.	0.	0.
Wh2	0.	41.	5.	0.	0.	3.	0.	48.	0.	0.
Wh3	2.	16.	5.	0.	0.	3.	0.	30.	0.	0.
Wh4	0.	20.	1.	0.	0.	3.	0.	27.	0.	1.
Wh5	2.	30.	6.	0.	0.	0.	0.	24.	0.	6.

Table 4.5. Numbers of larval remains of the 10 most common chironomids recovered from surficial sediments collected in some Waikato lakes. Values given are numbers per ml of sediments. Sample codes and location of lakes as in Table 4.1. See text for details of sampling sites. TPO = Tanypodinae, ORT = Orthocladiinae, ZEA = Chironomus zealandicus, CUR = Cladopelma curtivalva, KIE = Kiefferulus opalensis, POL = Polypedilum spp., PAU = Paucispinigera spp., AGA = Paratanytarsus agameta, COR = Corynocera sp., CAL = Calopsectra spp..

Sample Code	Taxa									
	TPO	ORT	ZEA	CUR	KIE	POL	PAU	AGA	COR	CAL
MoN	8.	14.	18.	0.	24.	2.	0.	0.	2.	32.
MoSW	15.	67.	63.	15.	55.	43.	0.	3.	58.	113.
NgN	0.	8.	8.	2.	1.	2.	2.	6.	0.	5.
NgS	9.	18.	19.	4.	1.	2.	2.	19.	10.	15.
RaNE	16.	73.	17.	0.	13.	7.	20.	7.	27.	27.
RaW	3.	20.	3.	0.	0.	0.	0.	8.	0.	13.
WhSW	3.	46.	13.	0.	0.	0.	0.	35.	0.	25.
WhE	0.	12.	2.	0.	0.	10.	0.	16.	0.	2.

Table 4.6. Numbers of larval remains of the 10 most common chironomids recovered from surficial sediments collected on the edges of some Waikato lakes. Values given are numbers per ml of sediments. Sample codes and location of sampling site as per Table 4.2 . TPO = Tanypodinae, ORT = Orthocladiinae, ZEA = *Chironomus zealandicus*, CUR = *Cladopelma curtivalva*, KIE = *Kiefferulus opalensis*, POL = *Polypedilum* spp., PAU = *Paucispinigera* spp., AGA = *Paratanytarsus agameta*, COR = *Corynocera* sp., CAL = *Calopsectra* spp..

Taxa	% Composition	
	Living fauna	Surficial sediment remains
Tanypodinae	5	12
Orthocladiinae	1	18
C. zealandicus	37	15
C. curtivalva	12	2
K. opalensis	5	11
Polypedilum spp.	0	4
Paucispinigera spp.	0	3
P. agameta	0	1
Corynocera sp.	0	6
Calopsectra spp.	40	28

Table 4.7. Percentage composition of chironomid larvae in Lake Maratoto as determined by analysis of remains in surficial sediments, and by sampling the living fauna during 1979 and 1980.

hills to the north east of the lake.

4.3.2.2 Multivariate Analyses of Lake Centre Samples -

The first three principal components of the analysis of chironomid remains in the centre of the lakes account for a total of 88% of the variance in the data. Except for Paratanytarsus agameta, which has a negative correlation with the first principal component (PC1), all other taxa have highly significant positive correlations with it (Table 4.8). As this first principal component accounts for 63% of the variance in the data, it can be concluded that there are major differences between the lakes in the density of the fauna.

A secondary source of variation in the data is summarised in the second principal component (PC2) which accounts for an additional 18% of the variance. Because both P. agameta and orthoclads have the highest correlation with this principal component (Table 4.8), they are the most important discriminator taxa along it, together with Cladopelma curtivalva and Corynocera sp. which are negatively correlated to it. Hence, lakes which have a relatively high abundance of P. agameta, orthoclads and Polypedilum spp. in comparison to C. curtivalva and Corynocera sp. have a high score on PC2.

The relations among the lakes can be established by comparing the lake scores on the first two principal components (Figure 4.1) and a cluster analysis of the data (Figure 4.2). The most appropriate interpretation is that the lakes fall into the five groups denoted A to E in Figures 4.1 and 4.2. The first group, which is characterised by high numbers of all taxa, includes Lake Maratoto samples. At the other extreme lie Group C (Waahi and Kimihia) and Group D (Ngaroto, Arapuni and Crater) which have low population size. Mid way between these

Taxa	Mean	Standard deviation	Coefficients	
			PC1	PC2
TANYPODINAE	0.68033	0.62775	0.15256	0.06309
ORTHOCLADIINAE	1.24140	0.48525	0.09032	0.40512
C. zealandicus	1.00772	0.56501	0.14293	0.03802
C. curtivalva	0.40713	0.46866	0.10577	-0.27923
K. opalensis	0.54526	0.63948	0.15184	0.02481
Polypedilum spp.	0.54278	0.45711	0.10823	0.30182
Paucispinigera spp.	0.40303	0.48100	0.13710	-0.01065
P. agameta	0.71925	0.61314	-0.07448	0.41139
Corynocera sp.	0.59226	0.57975	0.12693	-0.18055
Calopsectra spp.	1.03390	0.76744	0.14326	-0.02465

Table 4.8. Mean of the log number per ml, standard deviation and first two principal component coefficients of chironomid remains found in surficial sediments collected from the middle of 12 central North Island lakes.

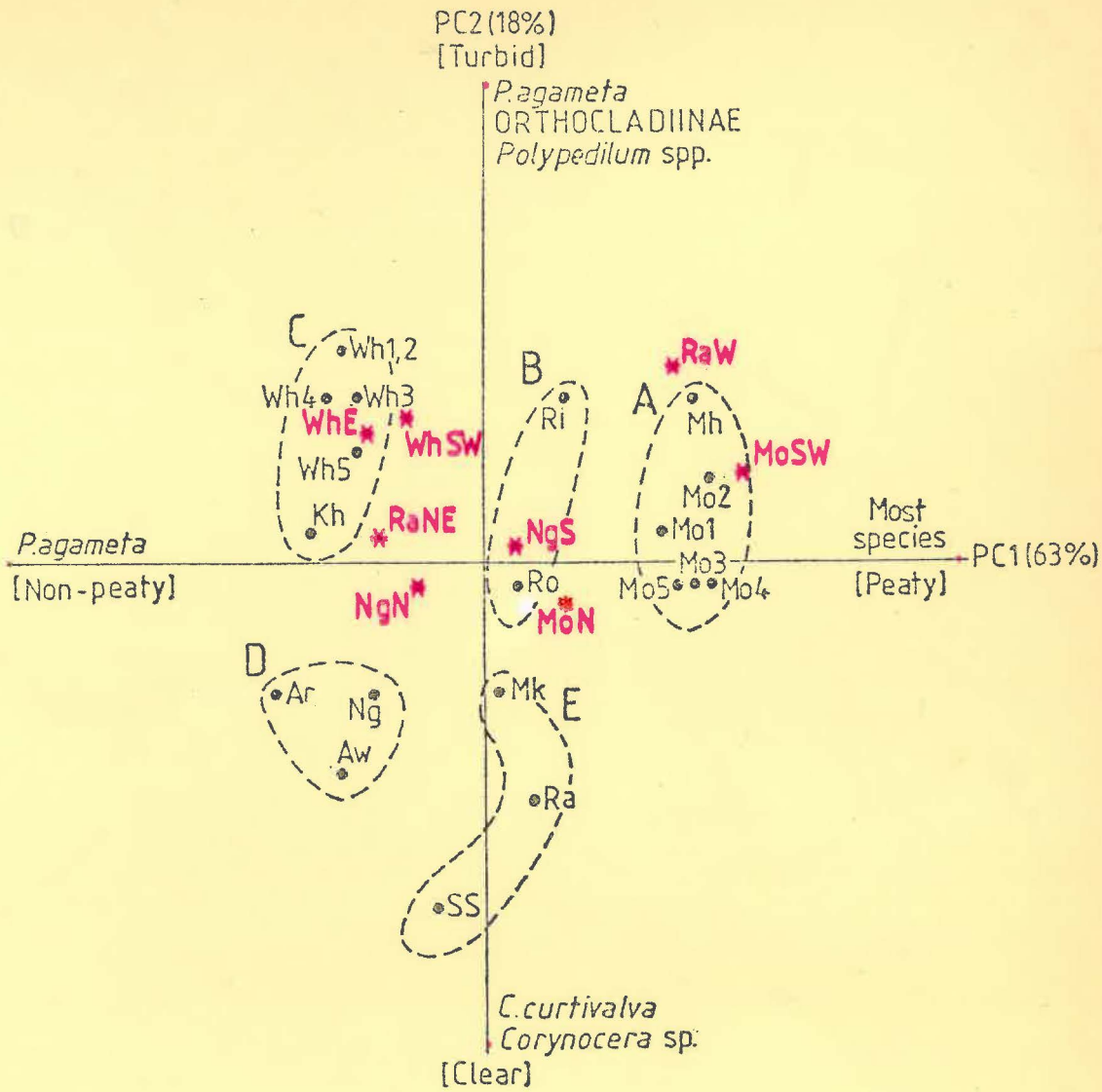


Figure 4.1. Principal component ordination of some central North Island lakes. Analysis based on the number of chironomid microfossils per ml of surficial sediment. Samples collected towards the centre of the lakes and in the littoral (overlay). Dashed line encircles lake groups determined from a cluster analysis. Lake codes as in Tables 4.1 and 4.2.

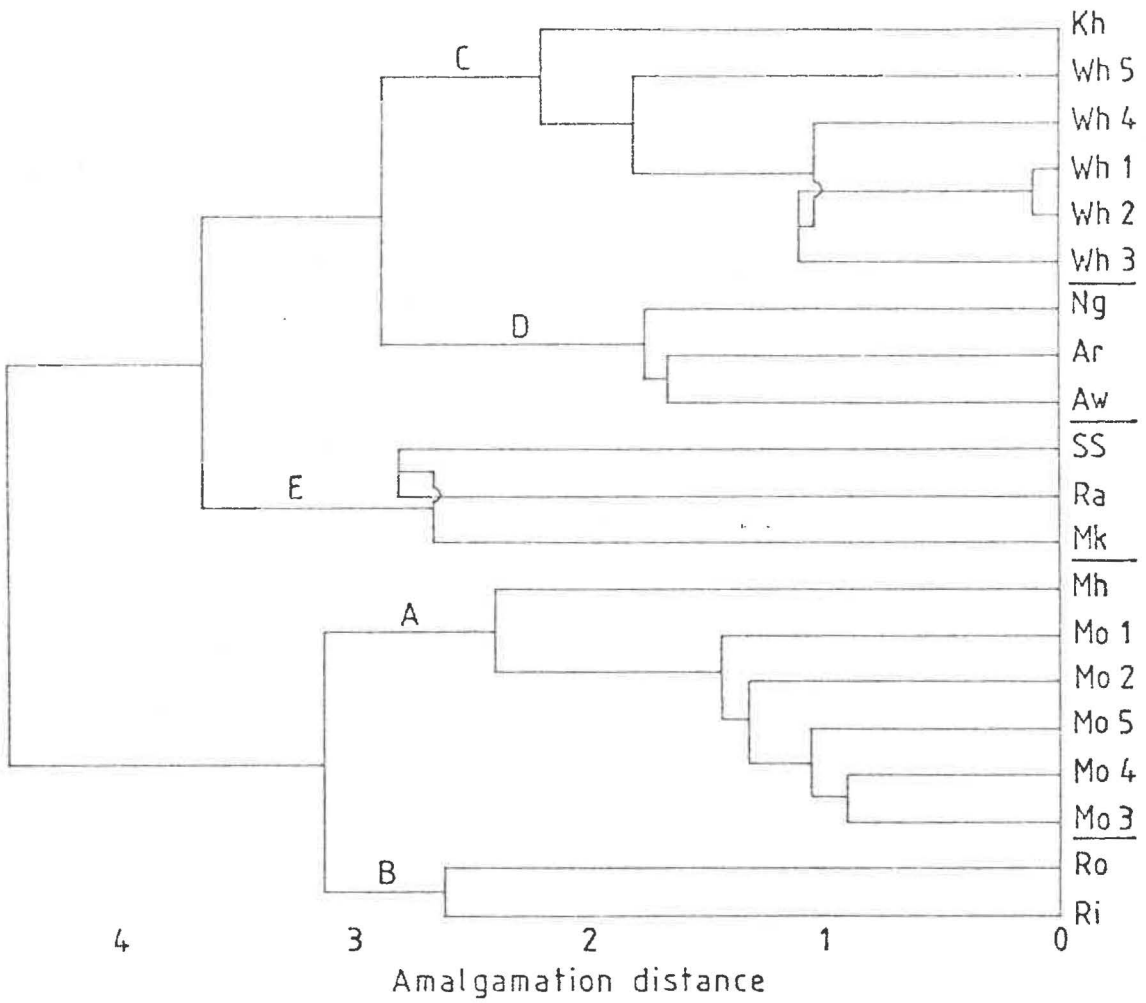


Figure 4.2. Cluster analysis of some central North Island lakes. Analysis based on the number of chironomid microfossils per ml of surficial sediment collected towards the centre of each lake. Similarity is measured by Euclidean distances. Lake codes as in Tables 4.1 and 4.2.

groups lie Rangiriri and Rotomanuka (Group B) and Mangakaware, Rotoroa and Serpentine South (Group E).

The second principal component makes a separation between Groups B and E, and Groups C and D. Groups B and C have a higher density of P. agameta, orthoclads and Polypedilum spp., while C. curtivalva and Corynocera sp. predominate in Groups D and E.

The limnological characteristics underlying these patterns emerge from an analysis of the rank correlation between principal component scores for samples collected at the centre of each lake and the physical/chemical characteristics of these lakes (Table 4.9).

The first principal component is related to the degree of 'peatiness' (i.e. high carbon content of the sediment, water strongly humic stained and with a high proportion of the watershed in swamps, but low amounts of sand/clay along the shoreline or as substrate). With increased dystrophy, a lake will score higher on the first principal component and will be characterised by large numbers of chironomid remains in the sediment.

The second principal component on the other hand differentiates between clear lakes that have proportionally high areas of the bottom covered by Characeae, and enriched lakes with high phosphate and algal content. In the clear lakes, both Corynocera sp. and Cladopelma curtivalva were found to predominate. As neither of these species feed directly on Characeae, this suggests that the distribution and abundance of both these species is dependent on the existence of some specific algal food growing on the substrate in these clear waters.

	Principal component			
	1		2	
Surface area (ha)	-0.43		0.10	
Maximum depth (m)	-0.20		-0.48	
% of catchment in swamp	0.73	***	0.02	
% of shoreline with sand/clay beach	-0.68	**	-0.19	
% of lake covered by exotic weeds	-0.50		-0.22	
% of lake bed covered by Characeae	-0.35		-0.85	***
Carbon content sediments (%)	0.54	*	0.16	
Water content sediments (%)	0.21		-0.06	
Suspended solids	0.15		-0.74	***
Secchi disc visibility (m)	-0.20		-0.72	**
Absorption at 270 ηm	0.83	***	0.29	
pH	-0.22		0.06	
Chlorophyll a (g/m^3)	0.10		0.53	*
Total phosphorus (mg/m^3)	0.18		0.63	*

Table 4.9. Rank correlation between limnological variables and the first and second principal component scores of chironomid larval remains recovered from surficial sediments collected from the middlle of 12 central North Island lakes. * = $P < 0.5$, ** = $P < 0.01$, *** = $P < 0.005$.

Of the taxa that I have found to be associated with enriched lakes, both Paratanytarsus agameta and the orthoclads require oxygen rich water, and are usually confined to the littoral, occurring often in high numbers amongst exotic aquatic macrophytes. Their apparent dominance of the chironomid fauna in this lake type is likely to be the result of the exclusion of other species from the deeper regions of these lakes.

Polypedilum spp., the third taxa having a positive loading on PC2, has mainly been found on the inorganic shores of the more eutrophic lakes, and Forsyth (1981) suggested that their presence is linked to the deposition of wind blown blue-green algae, a view reinforced by the above independently derived correlation.

The categorising of the lakes into the five groups described is primarily for comparison. As for all biological systems, it would be more realistic to think of the patterns in community composition and limnological characteristics as continua along the principal components.

4.3.2.3 Lake Edge Samples -

The principal component scores for the edge samples, are plotted on the overlay in Figure 4.2. Good concordance was found between the position of the scores on the axes and the nature of the sample sites. In Lake Maratoto, MoSW is more dystrophic than the central stations (which tend to describe the lake as a whole), while sample MoN, being closer to farm land and inorganic soil, shows the least dystrophy.

In Lake Rotoroa, the littoral habitat was no longer dominated by Cladopelma curtivalva and the species found were those that typically live in an exotic weed infested habitat. RaNE tends toward a fauna not unlike that found in Lake Waahi, - in part due to the high inorganic

content of the sediment - while RaW tends toward an enriched type of environment.

Similarly, in Lake Ngaroto the edge samples tend towards an exotic weed type of fauna, with NgS being the more dystrophic of the two sites. Lake Waahi shows little change between centre and edge, a reflection of the overall low chironomid population density and of the homogeneity of the habitat.

4.3.2.4 Conclusions -

Despite the problem of resuspension and the presence of relatively older remains within the surface sediment, the assemblage of animal remains within these sediments appears to be a useful tool in separating and describing habitats. Such analysis also provides a means of interpreting information from deeper layers of lake sediment. It is important to emphasise nonetheless, that the principal component loadings derived in this work are probably suitable only for lakes closely resembling those sampled here. Further refinement could be achieved by analysing a more diverse series of lakes (and/or concentrating on closely related lakes) and using a finer taxonomic classification. However, it will only be with increased knowledge of the taxonomy, autecology and geographical distribution of the chironomids that the full potential of the method can be assessed.

CHAPTER 5

PALAEOLIMNOLOGY OF LAKE MARATOTO

"Scribitur historia ad narrandum, non ad probandum"

Quintilien (90)

5.1 INTRODUCTION

The characteristics of a lake are largely dependent on the physical, chemical and biological events occurring in its catchment and any long term perturbations in this system will usually be reflected in the aquatic biota. If changes such as in water depth and quality of nutrients entering the lake alter the aquatic communities, then the organisms that leave recognizable fossils in the sediments can be used to reconstruct past conditions.

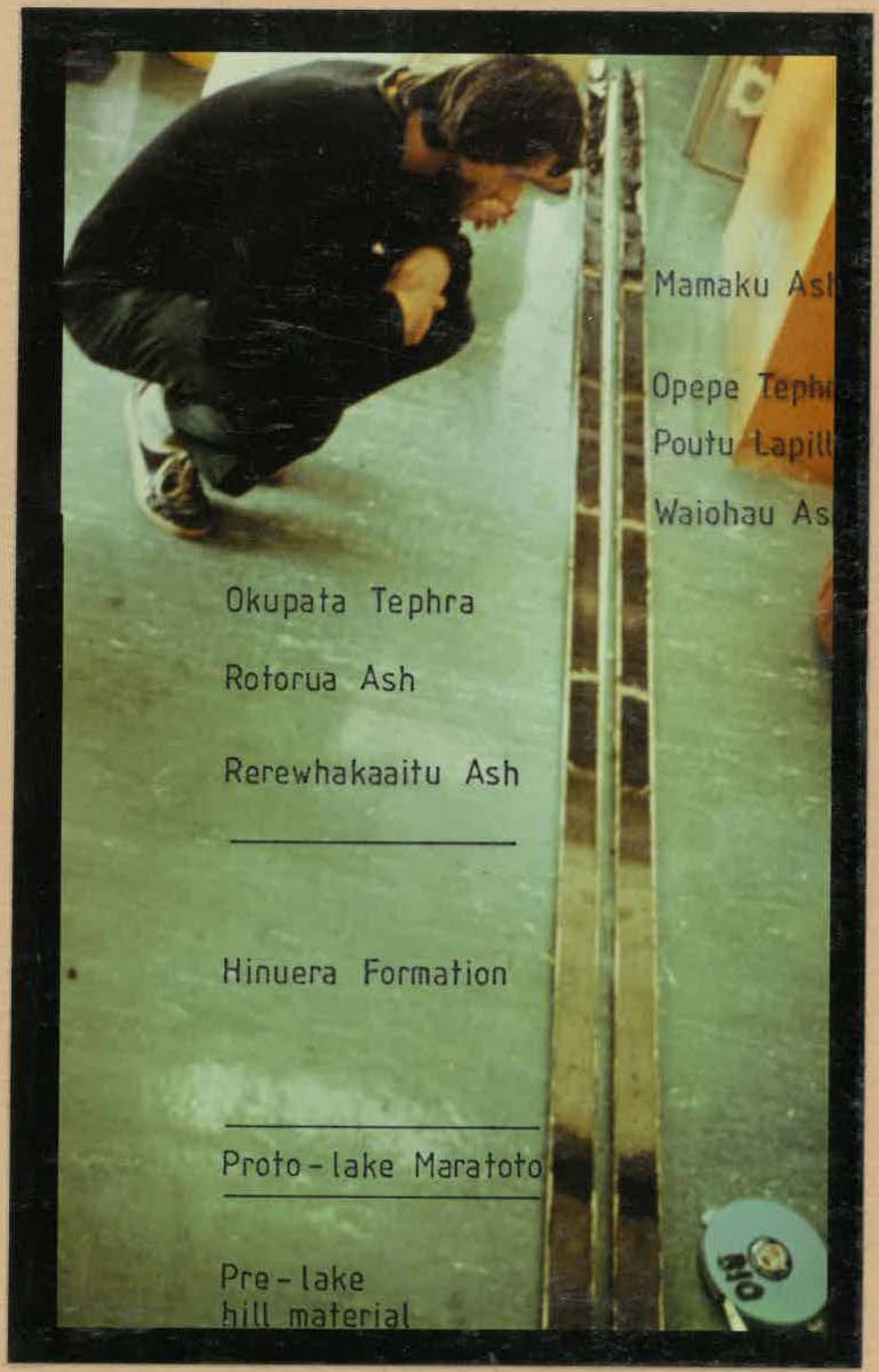
Palaeolimnological studies are common in North America and Europe. In New Zealand however, there has never been a comprehensive study of the history of a lake, although Deevey (1955) made a valuable description and analysis of a short core from the Pyramid Valley upper swamp deposit.

This chapter describes and evaluates the occurrence of aquatic insect remains, particularly chironomids, in the sediments of Lake Maratoto. It is part of an extensive study undertaken at the University of Waikato to define a comprehensive history of the lake and its drainage basin.

5.2 METHODS

A sediment core was taken in 4 m of water at the northern end of the lake, using a modified hand operated Livingstone piston corer (Green et al. in prep.) consisting of 4 m of 60 mm I.D. P.V.C. tubing. This tube had previously been sawn in half longitudinally and was held together by waterproof adhesive tape. In the laboratory, the core was split longitudinally and sampled usually at 5 cm intervals, although this interval was varied occasionally to avoid the volcanic ash layers (Plate 20). Towards the top of the core the sediment was sloppy, and

Plate 20. Lake Maratoto core showing lake sediments - Pleistocene hill interface and some of the tephras.


Mamaku As
Opepe Tephr
Poutu Lapill
Waiohau As
Okupata Tephra
Rotorua Ash
Rerewhakaaitu Ash
Hinuera Formation
Proto-lake Maratoto
Pre-lake
hill material

1 ml subsamples were obtained with an open ended 5 ml plastic syringe. Lower down, the sediment was firm enough for 1 cc cubes to be sectioned by means of razor blades. This subsampling was done only towards the centre of the core as a certain amount of smearing had occurred along the tube walls. Treatment of the samples thereafter was as described in Chapter 4 for the surface sediment samples.

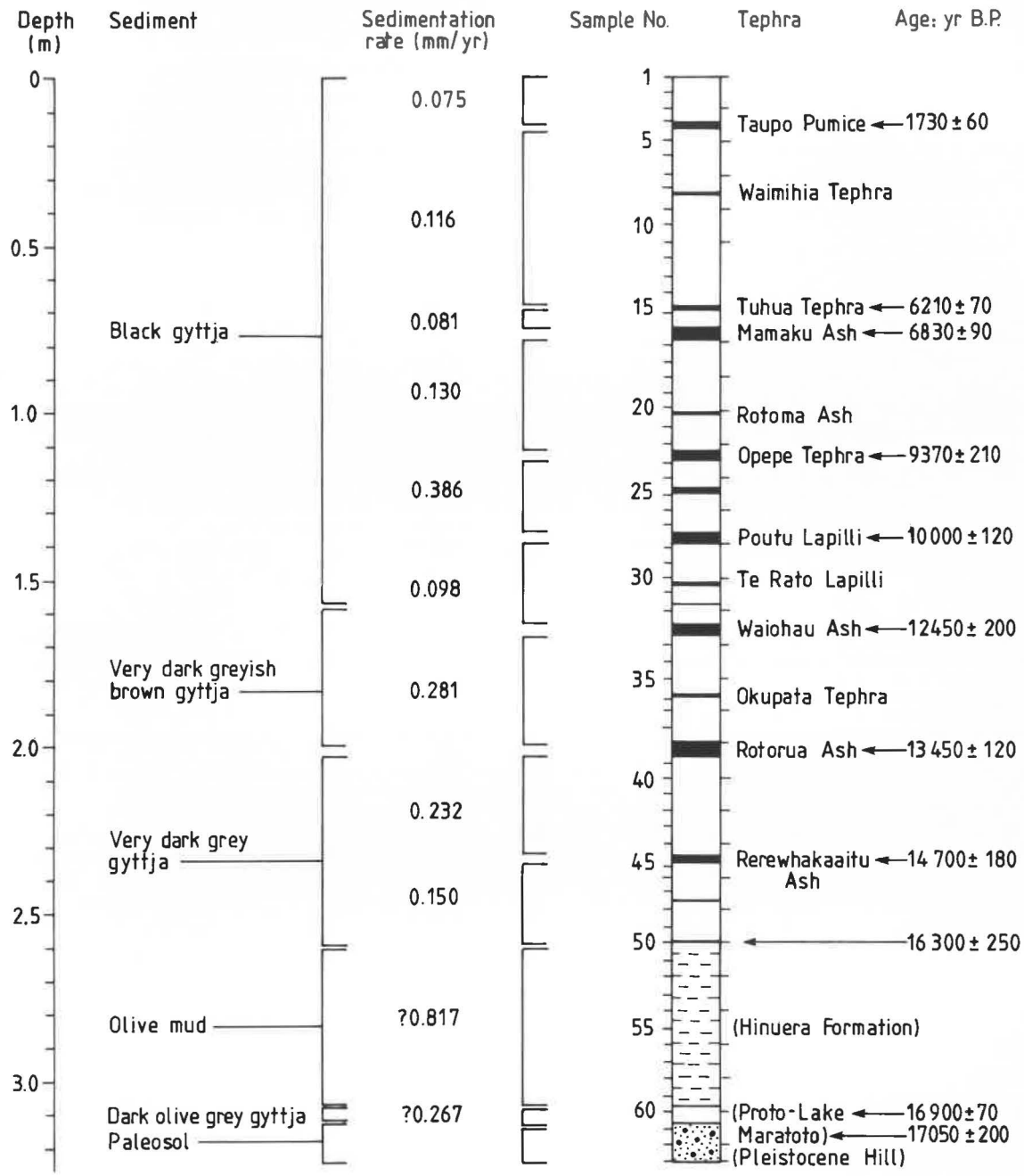
Counts were recorded in a taxa by depth matrix, as the number of remains per ml of sediment. To overcome problems of variations in sedimentation rate mentioned by Smol (1981), this raw data was multiplied by the sedimentation rate (Green and Lowe in prep.; see Figure 5.1) and discussed in terms of the number of remains per unit area of sediment per year.

All statistical analyses were done after transformation of the raw data to log(n + 1). Computation was undertaken on a Vax computer at the University of Waikato using BMDP (Dixon and Brown 1981) and MINITAB (Ryan et al. 1981) statistical packages.

5.3 STATISTICS OF SAMPLING

In Section 4.3.2.1 it was noted that within a lake, marked variations exist in the density and composition of chironomid remains in surface sediments obtained at different locations. Towards the centre and/or deepest region of small lakes however, the samples become less variable and usually give the best description of the entire lake's chironomid community. In addition to this inter-core variation, there is also an intra-core variation. To determine the extent of this, a separate short core was taken close to the original coring site. In this core, six replicate samples were taken just above the Waimihia tephra. The resulting counts of identified remains within these

Figure 5.1. Stratigraphy of the core from Lake Maratoto and position of subsamples analysed in this study. Dates given are based on the old 14C age.


Depth (m)
Sediment
Sedimentation rate (mm/yr)
Sample No.
Tephra
Age: yr B.P.
0
0.5
1.0
1.5
2.0
2.5
3.0
Black gyttja
Very dark greyish brown gyttja
Very dark grey gyttja
Olive mud
Dark olive grey gyttja
Paleosol
0.075
0.116
0.081
0.130
0.386
0.098
0.281
0.232
0.150
?0.817
?0.267
1
5
10
15
20
25
30
35
40
45
50
55
60
Taupo Pumice ← 1730 ± 60
Waimihia Tephra
Tuhua Tephra ← 6210 ± 70
Mamaku Ash ← 6830 ± 90
Rotoma Ash
Opepe Tephra ← 9370 ± 210
Poutu Lapilli ← 10000 ± 120
Te Rato Lapilli
Waiohau Ash ← 12450 ± 200
Okupata Tephra
Rotorua Ash ← 13450 ± 120
Rerewhakaaitu Ash ← 14700 ± 180
16300 ± 250
(Hinuera Formation)
(Proto-Lake Maratoto) ← 16900 ± 70
← 17050 ± 200
(Pleistocene Hill)

subsamples are given in Table 5.1. For the total chironomid remains, the 95% confidence limits of the density estimated from a single sample was calculated (Elliott 1971) as x X÷ 1.15.

5.4 RESULTS

5.4.1 Core Description

The core was not compressed during the sampling but a certain amount of smearing occurred near the tube surfaces. The sediment was composed of about 250 cm of dy-gyttya deposits intercalated with distinct volcanic ash layers. Most of these tephras have been identified (Lowe et al. 1980; Green and Lowe in prep.) and so provide valuable markers for intercore comparisons and dating of the sediment. Below the organic sediment there was 50 cm of clayey mud, thought to be part of the Hinuera formation, then a small 4 cm layer of organic sediment representing the oldest lake sediment. This overlaid the Pleistocene hill material where no fossilised aquatic invertebrates were found. A summary of the stratigraphy of the core is given in Figure 5.1.

5.4.2 Animal Microfossils

All remains recognised as parts of aquatic insects or mites were identified to the lowest taxonomic level possible and are enumerated in Appendix 2. The best preserved and by far the most common of these remains belonged to the Chironomidae. Although some mandibles and pupal appendages (e.g. respiratory horns and anal spurs) could be identified to species level, this was not the case for all the groups encountered. With the chironomids, near complete head capsules and labial plates were the most useful taxonomically and only the distribution of these fossils

	subsample					
	1	2	3	4	5	6
CHIRONOMIDAE (indet.)	100	88	108	170	140	172
TANYPODINAE	36	45	67	78	51	60
ORTHOCLADIINAE	46	128	78	53	63	58
C. zealandicus	38	23	33	35	74	25
K. opalensis	12	20	13	5	20	8
C. curtivalva	3	5	5	8	3	5
Polypedilum spp.	63	60	80	67	60	33
CHIRONOMINAE (indet.)	3	20	5	8	7	5
C. funebris	180	185	193	255	246	107
Calopsectra spp.	35	40	38	65	23	98
Corynocera sp.	30	50	70	68	43	45
P. agameta	3	3	8	3	0	0
TANYTARSINAE (indet.)	60	73	108	92	83	78
CERATOPOGONIDAE	20	8	18	18	3	13
Total Remains	629	748	824	925	816	707

Table 5.1. Number of fossilised larval remains per ml of sediment in six sediment subsamples obtained immediately above the Waimihia Tephra. Core taken in 4 m of water at the northern end of Lake Maratoto with a modified Livingstone corer.

will be discussed here.

5.4.2.1 Chironomidae -

TANYPODINAE

Although eight taxa of this subfamily were separated, their taxonomic placement and ecological requirements are uncertain. This subfamily is therefore discussed as a single group.

ORTHOCLADIINAE

Four taxa of this subfamily were recognised. Two of these are undescribed and photographs of their labial plates are given in Plate 8. The greatest proportion of remains were of Syncricotopus sp., Eukiefferiella sp. being the second most numerous. As little is known about the orthoclads generally, they will be discussed here as one group.

CHIRONOMINAE

Remains of Chironomus zealandicus complex, Cladopelma curtivalva, Kiefferulus opalensis, Polypedilum spp. and Paucispinigera spp. were common in the core and were easily identified. Only a few remains of Cryptochironomus sp. and of an unknown Chironominae (Plate 14) were recorded. In preliminary work on separate cores, a few fossils of Harrisius sp. and Parachironomus cylindricus were also recognised.

TANYTARSINAE

Calopsectra funebris, Corynocera sp., Paratanytarsus agameta and Calopsectra sp. were recognised in the core. In the analysis of the data, Calopsectra sp. and Calopsectra funebris were 'lumped' into one taxa.

5.4.2.1.1 Stratigraphy -

Variations in the total chironomid remains recorded along the core as well as that of the 10 major taxa are given in Figure 5.2. For convenience of description of the data, a BMDP2M cluster analysis (Figure 5.3) was used to divide the core into 12 zones and the variations summarised by a BMDP4M principal component analysis (see Chapter 4 for description).

The first principal component of the analysis accounted for 46% of the variance in the data. This first component was highly positively correlated with Calopsectra spp., Tanypodinae, Orthocladiinae, Chironomus zealandicus, Kiefferulus opalensis and Polypedilum spp.. As chironomid numbers tend to increase with eutrophy and as K. opalensis and Calopsectra funebris are most common in acid waters (see also Chapter 4), increases in this first principal component would suggest increases in both eutrophy and dystrophy.

A second principal component accounts for an additional 17% of the variation and has a high positive correlation with Corynocera sp. and Cladopelma curtivalva. Corynocera sp. is a littoral species while C. curtivalva is often found among Characeae. Both species require clear water and are possibly dependent on some specific algal food.

Finally, the third component that accounted for a further 12% of the variation was positively correlated with Paucispinigera spp. but negatively correlated with Polypedilum spp. Polypedilum is normally found on the edges of lakes that have a sandy bottom and high phytoplankton densities. Paucispinigera approximata can be found in most forested streams, and has been recorded among allocthonous organic debris of two South Island mesotrophic lakes (Timms 1980). Paucispinigera sp. on the other hand, has only been found in two South

Figure 5.2. Accumulation rate of chironomid remains in Lake Maratoto. Zones determined from a cluster analysis.

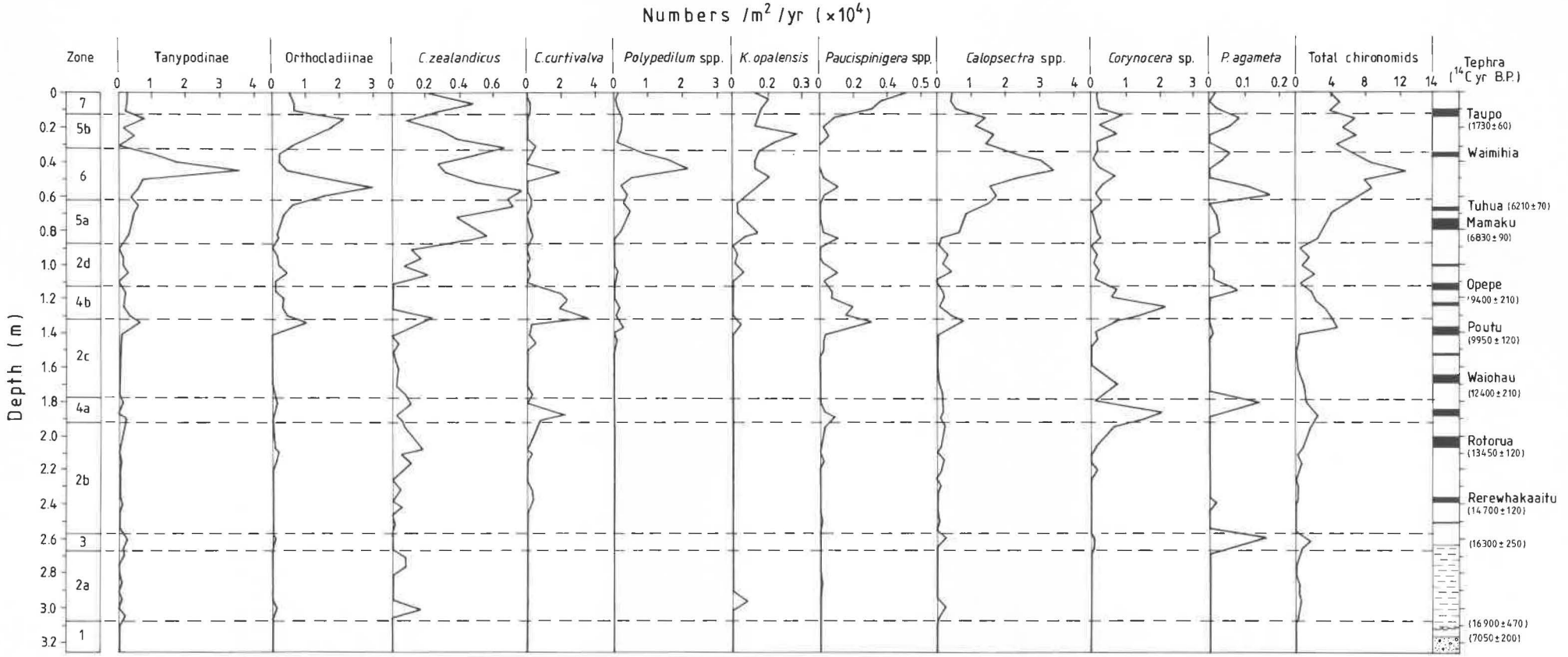

Numbers /m² /yr (×10⁴)
Zone
Tanypodinae
Orthocladiinae
C. zealandicus
C. curtivalva
Polypedilum spp.
K. opalensis
Paucispinigera spp.
Calopsectra spp.
Corynocera sp.
P. agameta
Total chironomids
Tephra (¹⁴C yr B.P.)
Depth (m)
7
5b
6
5a
2d
4b
2c
4a
2b
3
2a
1
Taupo (1730±60)
Waimihia
Tuhua (6210±70)
Mamaku (6830±90)
Opepe (9400±210)
Poutu (9950±120)
Waiohau (12400±210)
Rotorua (13450±120)
Rerewhakaaitu (14700±120)
(16300±250)
(16900±470)
(7050±200)

Figure 5.3. Cluster analysis of chironomid remains (No./m^2/yr) recovered from Lake Maratoto sediment. Similarity is measured by Euclidean distances. Sample numbers as in Figure 5.I.

Island dystrophic lakes (Timms 1982).

The temporal variations in loadings along these three principal components are given in Figure 5.4.

5.4.2.1.2 Description and Interpretation of the Chironomid Zones -

The greatest change in the lake's development occurred about 7,300 years ago when its productivity greatly increased. This change, which is largely described by the first principal component, separates the lower section of the core - where the total chironomid populations are low - from the top 90 cm, where the populations are much higher. The lower section of the core is divided into eight zones that are largely accounted for by the second principal component. The third principal component summarises the variation in the upper third of the core which is divided into four zones.

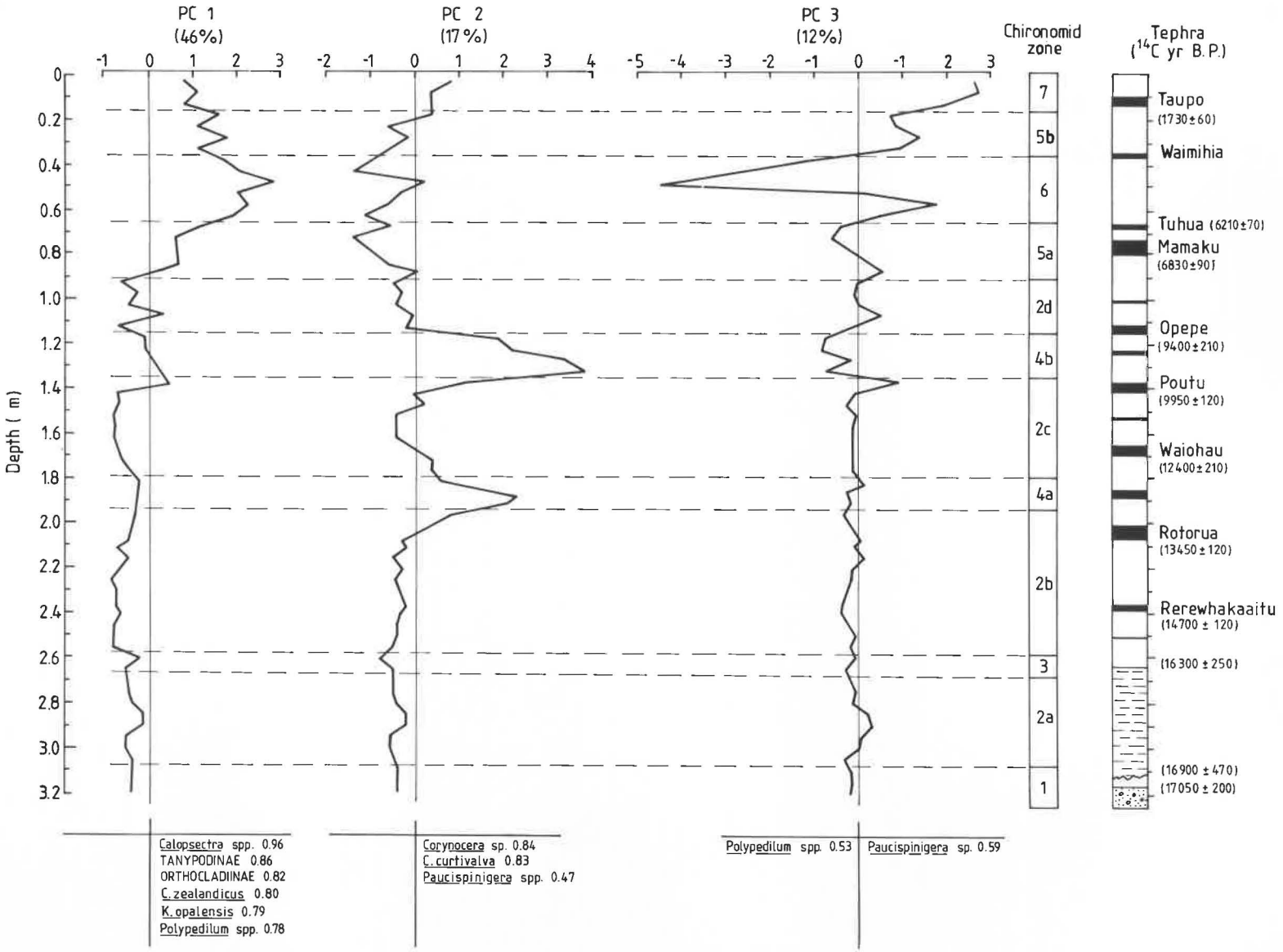
Zone 1 - 16,900 yr B.P. and older.

This lower section of the core includes Pleistocene hill material on which the lake was formed. Few chironomid remains were found in these sediments.

Zone 2a - 16,900 to 16,300 yr B.P.
2b - 16,100 to 13,100 yr B.P.
2c - 9,300 to 7,300 yr B.P.

The chironomid population in these zones is low compared to the others in the core. The taxa present are dominated by C. zealandicus and tanypods, which suggests open water with a muddy bottom and narrow littoral area.

Figure 5.4. Principal component analysis of chironomid remains in Lake Maratoto sediment (No./sq. m/yr). Depth variation in the scores on the first three principal components and weightings of each taxa on the components. Zones determined from a cluster analysis.


PC 1
(46%)
PC 2
(17%)
PC 3
(12%)
Chironomid zone
Tephra
(^{14}C yr B.P.)
Depth (m)
7
5b
6
5a
2d
4b
2c
4a
2b
3
2a
1
Taupo
(1730±60)
Waimihia
Tuhua (6210±70)
Mamaku
(6830±90)
Opepe
(9400±210)
Poutu
(9950±120)
Waiohau
(12400±210)
Rotorua
(13450±120)
Rerewhakaaitu
(14700±120)
(16300±250)
(16900±470)
(17050±200)
Calopsectra spp. 0.96
TANYPODINAE 0.86
ORTHOCLADIINAE 0.82
C. zealandicus 0.80
K. opalensis 0.79
Polypedilum spp. 0.78
Corynocera sp. 0.84
C. curtivalva 0.83
Paucispinigera spp. 0.47
Polypedilum spp. 0.53
Paucispinigera sp. 0.59

Zone 3 - 16,300 to 16,100 yr B.P.

There was a slight increase in the chironomid fossil numbers during this period which is situated between Zones 2a and 2b.

Zone 4a - 13,100 to 12,600 yr B.P.

4b - 9,800 to 9,300 yr B.P.

Both Corynocera sp. and Cladopelma curtivalva increased markedly in these zones. This suggests clear water, an increase in the area of the littoral, and large amounts of flocculated algae on the sediments.

Zone 5a - 7,300 to 5,900 yr B.P.

This was a period of increased chironomid numbers, particularly of Calopsectra spp. Kiefferulus opalensis and Chironomus zealandicus. It is envisaged that the lake became more dystrophic during this zone.

Zone 6 - 5,900 to 3,100 yr B.P.

The chironomid population peaked during this period. In the earlier part of the zone, Chironomus zealandicus and orthoclads predominated. Chironomus zealandicus can sustain quite low oxygen concentrations, while in eutrophic lakes orthoclads are normally restricted to the littoral. It is likely therefore that the lake was deoxygenated for at least part of each year. In the later part of the zone, C. zealandicus and the orthoclads decreased in numbers but there were large increases in Polypedilum spp., Calopsectra spp. and Tanypodinae. It is likely that this may have been the result of further increases in productivity, and so to sustained deoxygenation excluding profundal species. Since Polypedilum is normally found on the sandy bottoms of eutrophic lakes, it is postulated that the 5 cm thick Mamaku ash (6,800 yr B.P.) was exposed in large areas of the shoreline.

Zone 5b - 3,100 to 1,700 yr B.P.

The numbers of most chironomid species had already dropped or were decreasing during this period, suggesting a lowering of the lake's productivity. Kiefferulus opalensis however, reached its greatest abundance during this zone, indicating increases in the water's acidity. The population of the orthoclad Syncricotopus sp. also increased during this time. This species feeds on filamentous algae which Hendrey et al. (1976) suggest can be particularly common in acid waters. The decline in the total chironomid population could also have been caused by increased dystrophy.

Zone 7 - 17,000 yr B.P. to present

Except for Paucispinigera sp. which increased in numbers, most species had stable populations during this period. The increase in Paucispinigera sp. is difficult to explain without a better knowledge of its ecology but I have never found it in Waikato lakes. This may be because agricultural development of the catchments has caused major alterations in their pH and nutrient levels, resulting in very recent profound changes within them.

5.4.2.2 Other Animal Remains -

Ceratopogonid head capsules were present in most samples in the top 1 m of the core. They were particularly common in the upper half of Chironomid Zone 6 and above the Taupo ash (Chironomid Zone 7). Andersen (1938) (quoted by Stahl 1969) has concluded that ceratopogonids are favoured by a warm climate. In New Zealand they are common in streams and in shallow water at the edges of lakes.

A number of caddis mandibles, particularly those of Oecetis were recognised below the Waimihia Tephra. They were most numerous in the middle of Chironomid Zone 6 then decreased rapidly in numbers. Few, if any, were found between the Opepe and Okupata tephras and in the Hinuera muds at the bottom of the core. Cowley (1978) has found living larvae of Oecetis in shallow areas of many lakes with clear sandy areas of beach. They are common in Lake Maratoto where volcanic ash has been exposed.

Various mite remains were also recognised but could not be identified. They were particularly common below the Opape ash.

5.5 COMPARISON WITH SURFACE SEDIMENTS OF OTHER LAKES

In Chapter 4 a principal component analysis of chironomid remains in surface sediments was used to discriminate between lake types. This method was applied to the core data in an attempt to interpret its history in terms of modern lake type. The calculations involved (described in Section 4.2) use mean fossil number per ml of sediment, the standard deviation and principal component coefficients for each species, as determined for surficial sediments at the centre of 12 North Island lakes (Table 4.8). The resulting scores are plotted in the overlay in Figure 5.5. The general trend along the core is from an unproductive, clear lake at the bottom of the core to a productive, dystrophic lake in the surface sediments. There are two major concentrations of data points, Zones 5 and above showing signs of dystrophy, the rest of the core being clear and non peaty. The major change between the two types occurs in Zone 2d (9,300 - 7,300 yr B.P.).

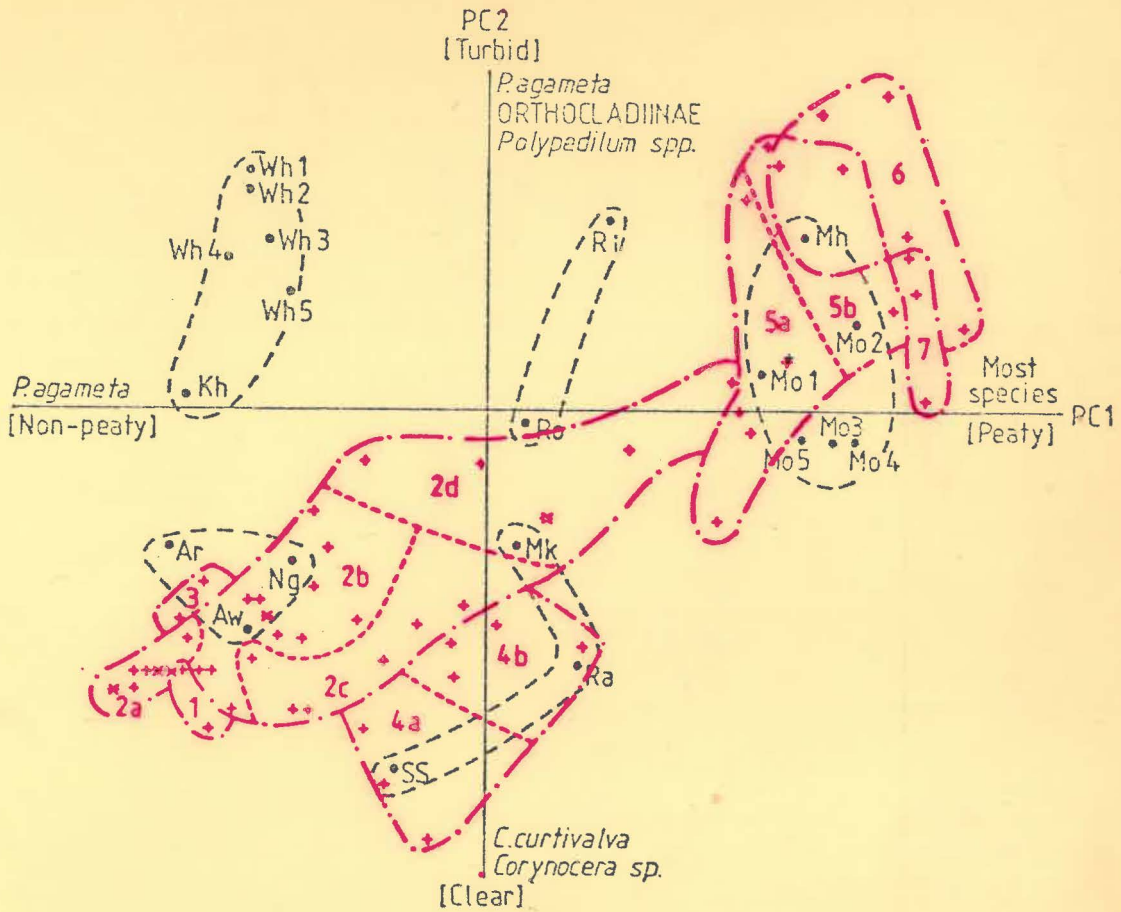


Figure 5.5. Principal component ordination of chironomid microfossils recovered from Lake Maratoto core (overlay) and from surficial sediments of 12 central North Island lakes. Analysis based on the number of remains per ml of surficial sediments collected towards the centre of the lakes. Dashed lines encircle groupings determined from cluster analyses. Ar = L. Arapuni, Aw = Awaatua Crater, Kh = L. Kimihia, Mh = L. Mangahia, Mk = L. Mangakaware, Mo = L. Maratoto, Ng = L. Ngaroto, Ra = L. Rotoroa, Ri = L. Rangiriri, Ro = L. Rotomanuka, SS = L. Serpentine South, Wh = L. Waahi. Numbers on overlay refer to chironomid zones determined by cluster analysis of the core.

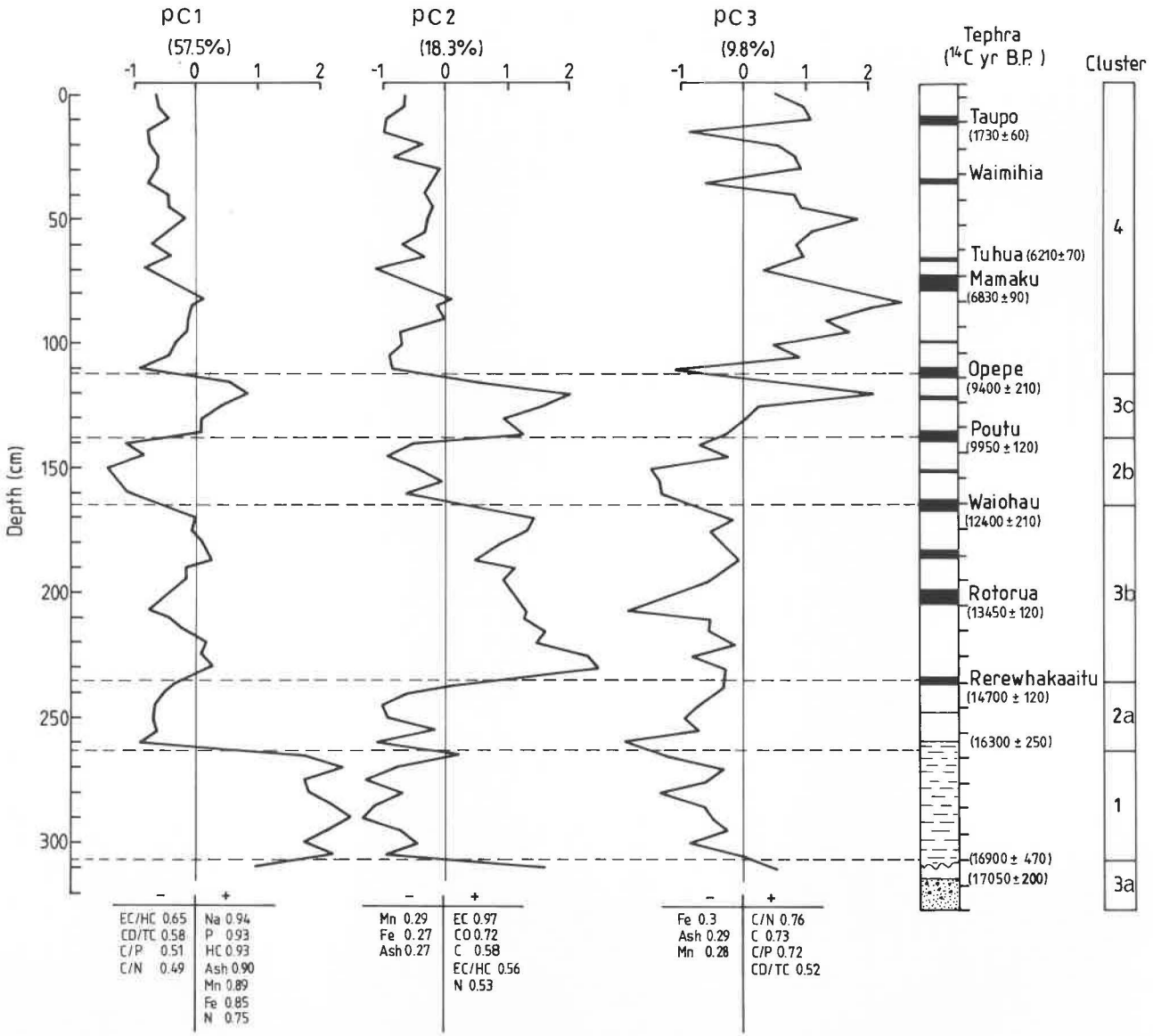
The lake began (Zones 1 and 2a) as an unproductive clear lake, much like the Awaatua Crater, but obviously much shallower and perhaps more like some modern shallow high country tarns. A slight change occurred in Zone 3 where there was a small increase in productivity. Zone 2b shows affinity with the centre of Lake Ngaroto but a major change occurred in the next phase of development (Zone 4a). The lake at this time resembled Lake Serpentine with its shallow water and important area of littoral and flooded areas. In Zone 2c, there was a return to an unproductive, mainly open water lake type. Zone 4c shows resemblances to Lake Rotoroa and Lake Mangakaware that have not only proportionally large areas of the total lake surface with shallow water, but also large amounts of Characeae on the lake bed. Up to this point in the core, all chironomid communities suggest clear water but increasing depth. Further deepening of the lake and an increase in the area of peaty shore probably took place in Zone 2d. This zone shows similarities to Lake Rotomanuka. The lake then went through a dystrophic period (Zone 5a) and increased markedly in productivity. In Zone 6, which closely resembles Lake Mangahia, the lake decreased in productivity; possibly as a result of a return to or increase in dystrophy. Above the Taupo ash (Zone 7), all samples were similar to modern surface sediments.

5.6 COMPARISON WITH OTHER DATA FROM LAKE MARATOTO

5.6.1 Chemical

Using chemical analyses of the sediment, Green (1979, and in prep.) divided the lake's history into 7 zones of events and was able to summarise the data by three principal components (Figure 5.6). The first principal component summarised the terrigenous input. Hence, an increase in the loading is probably the result of increased wetness. High rates of chlorophyll deposition gave a positive loading of the

Figure 5.6. Principal component analysis of chemical components of Lake Maratoto sediment (Units/sq. m/yr), showing depth variation in the scores on the first three principal components and weightings of each variable on the components. Zones determined from a cluster analysis. CD = chlorophyll derivatives, TC = total carotenoids, EC = epiphasic carotenoids, HC = hypophasic carotenoids. (From Green in prep.).


PC1
(57.5%)
PC2
(18.3%)
PC3
(9.8%)
-1
0
1
2
Depth (cm)
0
50
100
150
200
250
300
Tephra
(14C yr B.P.)
Cluster
Taupo
(1730 ± 60)
Waimihia
Tuhua (6210±70)
Mamaku
(6830 ± 90)
Opepe
(9400 ± 210)
Poutu
(9950 ± 120)
Waiohau
(12400 ± 210)
Rotorua
(13450 ± 120)
Rerewhakaaitu
(14700 ± 120)
(16300 ± 250)
(16900 ± 470)
(17050 ± 200)
4
3c
2b
3b
2a
1
3a
EC/HC 0.65
CD/TC 0.58
C/P 0.51
C/N 0.49
Na 0.94
P 0.93
HC 0.93
Ash 0.90
Mn 0.89
Fe 0.85
N 0.75
Mn 0.29
Fe 0.27
Ash 0.27
EC 0.97
CO 0.72
C 0.58
EC/HC 0.56
N 0.53
Fe 0.3
Ash 0.29
Mn 0.28
C/N 0.76
C 0.73
C/P 0.72
CD/TC 0.52

second principal component while positive loading on the third principal component was related to increases in dystrophy.

Green suggests that from about 14,700 yr B.P. there was a marked change in the climate from cold and dry to a warm and wet environment. Another major change in the chemical composition of the core occurred about 9,370 yr B.P. which Green attributes to the lake becoming dystrophic.

Three other chemical zones are also significant as they coincide with times of marked changes in the chironomid littoral fauna:

Chemical Zone 3b: This section of the core shows high concentrations of chlorophyll degradation products. It is possible that this was a time of increased effective rainfall (high PC1). The period ends with a decrease in PC1 and was probably drier.

Chemical Zone 2b: The climate is thought to have been drier since PC1 is low.

Chemical Zone 3c: The first principal component increases, therefore the climate is thought to have been wetter once again. The zone ends with a brief period of dryness. High concentrations of chlorophyll degradation products characterise this zone.

5.6.2 Pollen

5.6.2.1 Aquatic and Bog Vegetation -

In the lower portion of the core, particularly near tephras or in the tephras themselves, there are numerous charophyte remains (rhizomes and fruiting bodies). These remains show that when the lake was young, light penetrated to the bottom.

Pollen analysis (McGlone and Green in prep.) reveals the presence of aquatic plants such as Myriophyllum, and Potamogeton, with sedges and rushes on the margin of proto-Lake Maratoto (approx. 17,000 yr B.P.). Between 17,000 and 15,000 yr B.P. most aquatic plants present were typical of shallow water. The highest concentration of these plants occurred just before 16,300 yr B.P. From 15,000 yr B.P. the lake appeared to deepen as shallow water aquatic plants disappeared leaving only the bottom dwelling fern Isoetes. Between 11,000 and 12,000 yr B.P. there was an upsurge of Gleichenia, Empodisma, Sphagnum and Cyperaceae suggesting the establishment of a raised bog close to the lake.

5.6.2.2 Land Vegetation -

McGlone et al. (in prep.) have studied the pollen sequence of a separate core taken from Lake Maratoto and give the following account of the major vegetation changes and climatic implications that they discussed in terms of seven zones.

Zone 1. Before 17,000 yr B.P. Vegetation dominated by shrubland/grassland. Temperatures cold and summers dry.

Zone 2. 17,000 to 16,900 yr B.P. Proto-Lake Maratoto. Sediment of higher organic content. Vegetation dominated by grassland/shrubland. Climate harsh.

Zone 3. 16,900 to 16,300 yr B.P. Population of Libocedrus increased, possibly as a result of a moistening climate.

Zone 4. 16,300 to 11,000 yr B.P. A sharp increase in Podocarps was recorded. Significant moistening and warming of climate.

Zone 5. 11,000 to 8,000 yr B.P.

Peak in dominance of D. cupressinum and Metrosideros, Ascarina lucida, and tree ferns also abundant. Climate wet and mild without severe frosts in winter and no significant droughts in summer.

Zone 6. 8,000 to 5,000 yr B.P. D. cupressinum maintained its position but Metrosideros and Ascarina were declining. Hardwood species expanding. Dense podocarp forest probably opening out. Climate worsening once again.

Zone 7. 5,000 to 2,000 yr B.P. Metrosideros forest continued to open up. Hardwood species still increasing. Agathis australis expanding. Climate similar to present with drought and frost again becoming significant.

5.6.3 Geomorphology

It is now well established that most lakes in the Waikato basin were formed when valleys were dammed by the deposition of sediments from an ancestral braided Waikato River system. This material, which originates from volcanic activity in the central North Island, is known as the Hinuera formation and was deposited at the end of the last Otiran glaciation (Schofield 1965; McGraw 1967; Hume et al. 1975; McGlone et al. 1978). A rise in sea level at this time is thought to have contributed to a decrease in volcanic activity (Schofield 1965) which, together with the re-establishment of forest in upland sites due to a warming of the climate, resulted in less erosion. The lack of sediment material caused the river to abandon its former braided course and flow in the present bed. The next stage in the development of the Hamilton basin saw the formation and expansion of peat bogs, which not only marrkedly altered the landscape, but also greatly affected some of the

lakes, including Lake Maratoto.

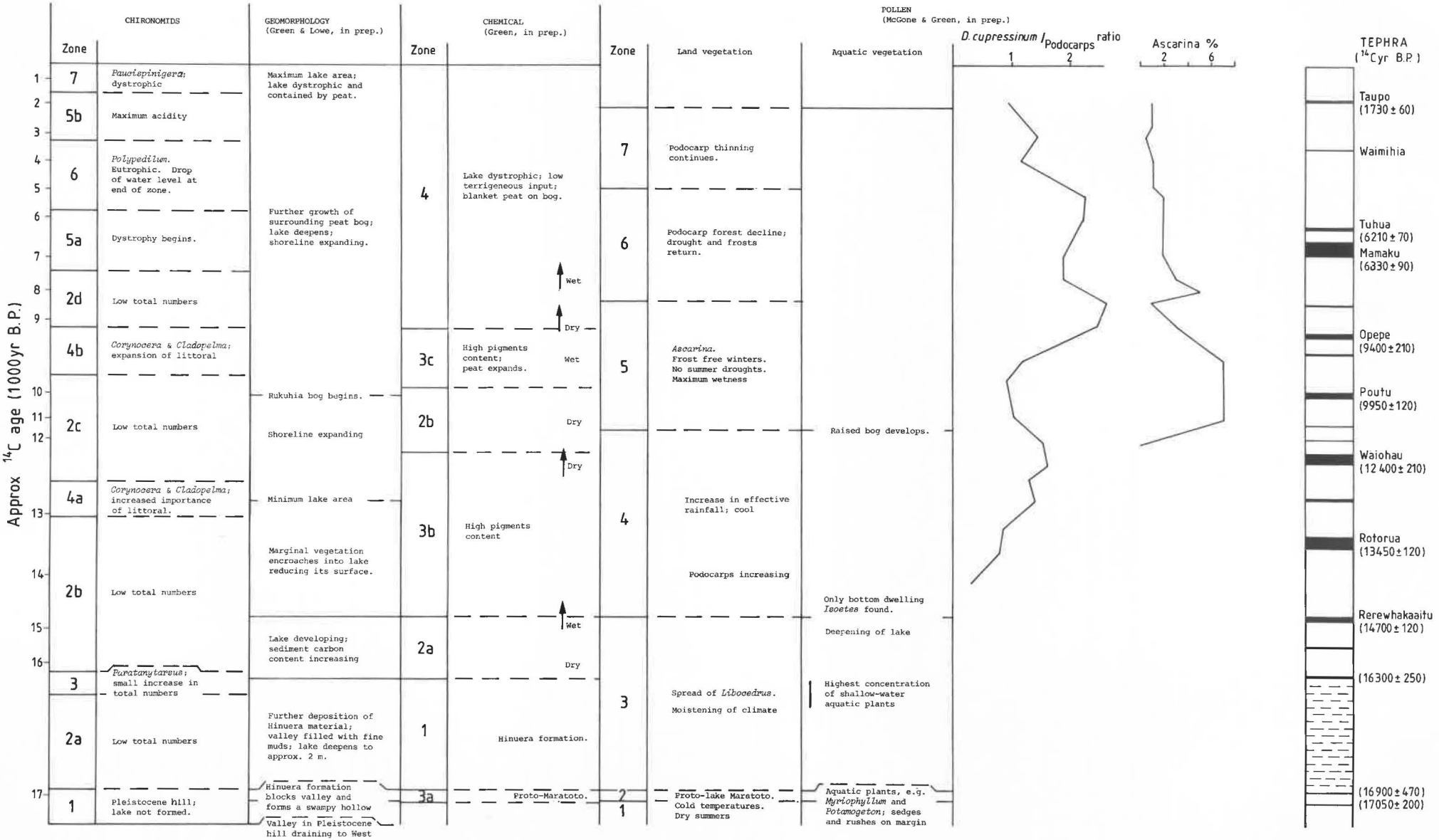
From a detailed geomorphological survey of the lake basin, Lowe and Green (in prep.) give essentially the following account of its historical development.

17,000 years ago on the site of the present lake, there was a valley in the Pleistocene hill that drained to the west. About 17,000 yr B.P. a first phase of the Hinuera formation deposited some coarse, sandy material at the mouth of the valley. This damming formed proto-Lake Maratoto, which was then shallow and possibly only a swampy hollow. A second phase of the Hinuera formation took place between 16,900 and 16,300 yr B.P. when more coarse material was deposited at the valley mouth. Finer muds were also deposited further up the valley. The lake thus formed was perhaps 2 m deep. From 16,300 to 14,700 yr B.P. the lake became more productive, the sediments showing increasing amounts of organic material. The next stage of development saw marginal swamps encroaching into the lake, reducing its surface area to a minimum about 13,000 yr B.P. After this, the shoreline expanded again, possibly because of decomposition and mechanical erosion of the swampy shoreline. From 10,000 yr B.P. the Rukuhia peat bog expanded and embraced the lake. The water depth increased since peat growth was greater than the sedimentation rate of the lake. The lake increased in size but at no stage was it larger than at present.

5.7 LAKE DEVELOPMENT AND CLIMATIC CHANGES

A summary of the information presented above is given in Figure 5.7. The lake began about 17,000 yr B.P. as a swampy hollow containing aquatic plants but few chironomids. Pollen analysis suggests a cold climate with dry summers. From 16,900 to 16,300 yr B.P., fine Hinuera

Figure 5.7. Comparison of chironomid zones of Lake Maratoto with other phases in the lake history deduced from geomorphology, chemical and pollen analysis of the sediment.


Approx ^{14}C age (1000yr B.P.)
CHIRONOMIDS
Zone
7
Pauciepinigera; dystrophic
5b
Maximum acidity
6
Polypedilum. Eutrophic. Drop of water level at end of zone.
5a
Dystrophy begins.
2d
Low total numbers
4b
Corynocera & Cladopelma; expansion of littoral
2c
Low total numbers
4a
Corynocera & Cladopelma; increased importance of littoral.
2b
Low total numbers
3
Puratanytarsus; small increase in total numbers
2a
Low total numbers
1
Pleistocene hill; lake not formed.
GEOMORPHOLOGY (Green & Lowe, in prep.)
Maximum lake area; lake dystrophic and contained by peat.
Further growth of surrounding peat bog; lake deepens; shoreline expanding.
Rukuhia bog begins.
Shoreline expanding
Minimum lake area
Marginal vegetation encroaches into lake reducing its surface.
Lake developing; sediment carbon content increasing
Further deposition of Hinuera material; valley filled with fine muds; lake deepens to approx. 2 m.
Hinuera formation blocks valley and forms a swampy hollow
Valley in Pleistocene hill draining to West
CHEMICAL (Green, in prep.)
Zone
4
Lake dystrophic; low terrigeneous input; blanket peat on bog.
Wet
Dry
3c
High pigments content; peat expands.
Wet
2b
Dry
Dry
3b
High pigments content
Wet
2a
Dry
1
Hinuera formation.
3a
Proto-Maratoto.
POLLEN (McGone & Green, in prep.)
Zone
Land vegetation
Aquatic vegetation
7
Podocarp thinning continues.
6
Podocarp forest decline; drought and frosts return.
5
Ascarina. Frost free winters. No summer droughts. Maximum wetness
Raised bog develops.
4
Increase in effective rainfall; cool
Podocarps increasing
Only bottom dwelling Isoetes found.
Deepening of lake
3
Spread of Libocedrus.
Moistening of climate
Highest concentration of shallow-water aquatic plants
2
Proto-lake Maratoto.
Cold temperatures.
Dry summers
Aquatic plants, e.g. Myriophyllum and Potamogeton; sedges and rushes on margin
1
D. cupressinum / Podocarps ratio
1
2
Ascarina %
2
6
TEPHRA (^{14}Cyr B.P.)
Taupo (1730 ± 60)
Waimihia
Tuhua (6210 ± 70)
Mamaku (6330 ± 90)
Opepe (9400 ± 210)
Poutu (9950 ± 120)
Waiohau (12 400 ± 210)
Rotorua (13450 ± 120)
Rerewhakaaitu (14700 ± 120)
(16300 ± 250)
(16900 ± 470)
(17050 ± 200)

mud was deposited on the lake floor burying much plant material with it. The presence of plant remains and an upsurge in aquatic plant pollen show that the lake was probably densely colonised by aquatic weeds towards the end of this phase.

Between 16,300 and 13,400 yr B.P. the lake was possibly 2 m deep but clear. Apart from a brief increase in the chironomid population at the start of the zone, the lake remained unproductive. During this period, the climate of the southern hemisphere was getting wetter and warmer (e.g. Harris 1963; Burrows 1979; Heusser et al. 1981). Locally this was shown by a marked increase in Podocarp forests. Along the lake edge, marginal vegetation developed and encroached on the lake, reducing its surface area. The period from 13,400 to about 12,500 yr B.P. shows a marked rise in the littoral chironomid Corynocera sp. and in Cladopelma curtivalva. Pigment degradation products were also high and the lake shrank to its minimum size. This suggests that marginal swamps invaded the lake but that there were also areas much like those now present in Lake Serpentine (Plate 21) where there is about 50 cm of clear water and a high algal content in the sediment.

A marked decline in chironomid numbers occurred between 12,500 and 10,000 yr B.P. Chemical analyses of the sediment indicate a drying of the climate, although McGlone et al. (in prep.) postulate a wet and mild climate. During this period however, even though Ascarina pollen counts are high, there is a marked decline in the ratio between Dacrydium cupressinum pollen and pollen of other tree podocarps (Figure 5.7). A decrease in this ratio suggests an increase in the frequency and intensity of drought (McGlone and Topping 1977) while Ascarina is a cold sensitive species (McGlone and Moar 1977; A. Edmonds pers. comm.). The climate during this time therefore is considered to have been warm but subjected to severe droughts. Although other pollen diagrams from the

Plate 21. Lake Serpentine: (A) flooded area which is an important habitat for Tanytarsini;

(B) detail of edge showing algal rich sediments.

A

B

region show a similar temporary decrease in D. cupressinum at this time (Harris 1963; Lambert 1970), other North Island pollen diagrams register the highest D. cupressinum totals (McGlone and Topping 1977; McGlone pers. comm.). Harris (1963) postulated that this period was marked by oscillation in the climate, corresponding to the Allerod period of Europe. The drying phase witnessed in the Waikato cores may therefore have been only a regional event.

From 10,000 to 9,000 yr B.P. Corynocera sp. increased in numbers, indicating an expansion of the littoral zone. The Rukuhia bog was enlarging and the sediments show high levels of chlorophyll degradation products indicating a high algal content. In the pollen diagram, the D. cupressinum/podocarp ratio increases while Ascarina decreases, presumably due to shading out by the taller rimu. This suggests the return of a wet and mild climate. During this period I envisage that following the dry period of the last zone, the edges of the lake were covered with water for much of the year. The lake however was more productive than in an earlier but similar phase that occurred between 13,400 and 12,500 yr B.P. (Chironomid Zone 4a).

In the next period that lasted from 9,000 to 7,000 yr B.P., the numbers of chironomids were decreasing once again. From the chemical data there is evidence of a brief drying period. D. cupressinum numbers decreased while Ascarina was increasing which also suggests a drying of the climate. During this time Harris (1963) identified a burnt zone in the Hamilton peat. It is possible that fire was the cause of the chemical and pollen changes in the Maratoto core but this does not preclude a drying of the climate. It is possible therefore that a reduction of the littoral area was due to a lowered water table, although there is no evidence of this in the lake basin stratigraphy.

The increase in numbers and change in species composition of chironomids, as well as the chemical composition of the sediments, clearly show that the lake was dystrophic between about 7,300 and 6,000 yr B.P. Peat therefore probably had a major influence on the lake from this point. From the pollen diagram it appears that the climate was deteriorating with droughts and frost returning. This is supported by speleothem palaeotemperatures derived by Hendy and Wilson (1968).

Between 6,000 and 3,000 yr B.P. there was a marked increase in Polypedilum spp.. These species' habitat preferences suggest that one of the sandy volcanic ash layers (probably the Mamaku ash) lined much of the shore at this time and that the phytoplankton content was high. Analysis of fossil cladoceran (J. Green pers. comm.) shows a decrease of the deep water species, implying that the lake was possibly shallow at this time and/or was deoxygenated for most of the year. Since the stratigraphy of the lake does not show any evidence of marked water level fluctuations, it is likely that any water level changes would have been small, perhaps only sufficient to uncover the littoral shelf.

Chemically, the sediments show little change, the lake now being surrounded by peat and being dominated by it. In the pollen diagram there is a sharp decline in the D. cupressinum ratio and a slight drop in Ascarina which suggest a cool and dry climate. Other data sources from New Zealand also suggest a cooler and drier climate during this time interval (Lintott and Burrows 1973; Wardle 1973; McGlone and Moar 1977; McGlone and Topping 1977). I postulate therefore that there was at this time, a small drop in lake level resulting from a decreased rainfall, which led to the oxidation and wave erosion of the organic sediment along the shoreline. This not only exposed the sandy volcanic ash layers but also increased the nutrient input to the lake which became enriched and probably remained deoxygenated for most of the time.

The surrounding peat bog had its greatest effect on the lake between 3,000 and 1,700 yr B.P. This suggests that the Rukuhia peat swamp was now a raised bog, with water from this area flowing towards the lake. The climate was probably much as today.

Above the Taupo ash (1,700 yr B.P.) total chironomid numbers were still declining, probably reflecting the continuing trend towards dystrophy. The number of Paucispinigera sp. however, were increasing. This genus is most common among organic detritus, particularly in flowing water, and their increase here may well have been caused by the development of a drainage system on the swamp (natural and later man made).

In modern times, agricultural development of the catchment has resulted in the destruction of the native vegetation and in the expansion of pasture land. On the peat, major changes in the drainage patterns have taken place. The addition of fertiliser and of lime to promote pasture growth has also resulted in an increase in the trophic state and pH of the lake. Fossil remains in surficial sediments at present show little resemblance to the fauna now living in the lake (Chapter 4), doubtless reflecting the rapidity of the change, probably the fastest of all changes in the lake's history.

CHAPTER 6

CONCLUDING REMARKS

"La raison nous trompe plus souvent que la nature."

Vauvenargues (1746)

Lake Maratoto with its brown, acid water and peaty sediments is characteristic of the dy or dystrophic lake type discussed by Hansen (1962). The high benthic standing crop of Lake Maratoto places it among the more productive New Zealand lakes and it can be regarded as a eutrophic dy lake. Although productive, the lake has a low species diversity, reflecting not only the low species richness of the New Zealand fauna but also typifying the dystrophic lake type. The littoral zone is often ignored in benthic surveys, yet this study has shown that in Lake Maratoto (and other lakes of the Waikato) the reed beds and areas that flood during periods of higher water are highly productive, and should not be neglected in future studies.

Chironomid reproduction in Lake Maratoto was continuous, although there were surges in the populations of the various species. These surges involved all age groups and were usually of short duration. Yet, the number of fourth instar larvae, particularly those of Chironomus zealandicus, continued to increase after the main flight period (Figure 3.7), possibly because of a slow down in emergence during the coldest winter months. The numbers of these late instars then decreased over several months to reach a minimum in the spring, but no mass emergence as is the case in colder climates took place. In the summer, larval numbers increased once again probably because of better survivorship of young larvae caused by the availability of algal food.

Cohorts could not be recognised because of the rapidity of the life cycles. However, differences in the size of each instar, probably caused by growth at different temperatures, were noted and may be of use in future studies. It may also be possible to follow emergence more accurately by making use of the presence of a thickening of the body around the head region of the larvae which occurs close to pupation.

In the Waikato, chironomid larvae with little or no blood pigment (tanypods, podonomids, orthoclads, tanytarsines) were only found where and when the oxygen concentration was high, for example close to the water's edge near the surface on macrophytes, or in winter. When the oxygen concentration was low as was usually the case in summer, species with dissolved haemoglobin in their blood were more numerous. Even these were excluded from the deeper waters during periods of deoxygenation and returned only following the turnover. The importance of oxygen has led some authors to conclude that chironomids were better indicators of oxygen standards than of trophic standard (Brundin 1949; Mundie 1957; Megard 1964; Carter 1977). These authors suggest that it is only because eutrophic lakes are usually associated with low oxygen concentrations that there is usually a good correlation between lake type and chironomid community type. Whilst oxygen concentration is undoubtedly a major factor in determining the distribution of chironomids many other chemical and physical factors also affect them and this has given them the reputation of being good indicator organisms (e.g. Hellawell 1978).

In New Zealand chironomids have been considered unsuitable as trophic indicators because of their low species diversity (Forsyth 1978; Timms 1982). However, as a better knowledge of their taxonomy and ecological requirements is obtained it will become easier to interpret the significance of differences in both community composition and in the relative abundances of each species. Multivariate statistical analyses will be a powerful tool in exploiting the ecological potential of the group.

As chironomids leave recognizable remains in the sediment, the problem of sampling over a range of existing habitats can be largely avoided by making use instead of the surficial sediments. These will represent several years of deposition. At least in small lakes, by sampling away from potential barriers (e.g. reed beds) which tend to prevent mixing, a sample can be obtained of the remains of species living both in the profundal and the littoral. The only major difficulty with such analyses is taxonomic, as identification of chironomids to species level can involve appendages that are often not preserved in the sediment. Furthermore, although the feeding mode and habitat preference of many chironomid species have now been determined, some major gaps still remain.

In spite of these limitations, multivariate analysis of surficial sediment fossil counts was successfully used to classify the lakes and habitats sampled into meaningful categories. The analysis could be widened to include a more varied series of lakes, and it would be of interest to test it on the seven lakes investigated by Forsyth (1978) and on some of the 20 South Island lakes studied by Timms (1982).

Information gained from analyses of the surficial sediment enabled postulations to be made about earlier conditions in Lake Maratoto. An interpretation of the environmental history of the lake was thus possible. Good correlation was found between the interpretation derived here and from the results of stratigraphic, pollen and chemical analyses. Extension of the work to include other taxonomic groups e.g. cladocerans and diatoms, would permit further refinement.

The presence of easily recognisable and dated volcanic ash layers at regular intervals in the sediment of all the Waikato lakes provides a unique opportunity for comparing and confirming the climatic, edaphic

and other events in the region. In the Lake Maratoto core, there is evidence of an oscillation in the climate between 13,000 and 9,000 yr B.P. and it would be worthwhile determining whether these variations were more widespread. There is also a period between 6,000 and 3,000 yr B.P. which I postulate was dry. Unfortunately, the overwhelming effect of blanket peat around Lake Maratoto at this time did not allow the event to be recorded in the chemical composition or stratigraphy of the core. An analysis of a lake not so effected by peat (e.g. Lake Rotomanuka) would establish this hypothesis.

In the Waikato no habitats that closely resemble the early developmental stage of Lake Maratoto were recognised. The closest equivalent found are small tarns in the Urewera National Park. In these small lakes/bogs, as in the lower portion of the Lake Maratoto core, the percentage of tanypods and of the rarer orthoclads appears to be higher than in other lakes studied. Such habitats deserve further research.

Analysis of fossil chironomids is restricted by the lack of knowledge of some species, but this type of analysis can in itself prove valuable for suggesting new avenues of sampling. The discovery of fossil head capsules in the surficial sediment such as those of Corynocera sp. led to a search for living larvae, which has permitted the description of the species and its ecological requirements. There is also the possibility of utilising a greater range of chironomid remains for a better identification of the species present (e.g. pupal posteriolateral spurs of segment VIII and respiratory horns). The use of these and other appendages will only come with increased taxonomic knowledge of the group.

In conclusion, the baseline information on Lake Maratoto that has been recorded can serve as a point of comparison, as inevitable changes - due mainly to increased nutrient inflow and lowering of the water table - take place. Already major pH changes have resulted (B. McCabe pers. comm.), but it is to be hoped that these will be minimised and will stabilise now that the lake and its buffer strip are protected under the QE2 National Trust. Changes that do take place are likely to be reflected in the chironomid community, and examination of these at some future date will allow further documentation of the eutrophication process in the Waikato peat lakes.

APPENDICES

APPENDIX 1

Benthic macroinvertebrates collected in Lake Maratoto by sampling with three cores of different sizes. Samples were taken at random by S.C.U.B.A. at the 1 m station in August 1978. Values are given as numbers per core.

Appendix 1.1

Area of core: 81.7 sq. cm

Sample No.	1	2	3	4	5	6
Oligochaeta	13	17	24	18	16	46
Oecetis unicolor	4	2		2	2	6
Tanypodinae		1				
Chironomus zealandicus	6	3	13	20	4	6
Cladopelma curtivalva	4	3	2	4	2	4

Appendix 1.2

Area of core: 44.2 sq. cm

Sample No.	1	2	3	4	5	6	7
Oligochaeta	6	41	40	6	34	8	28
Oecetis unicolor			1	1		4	4
Chironomus zealandicus	2	5		3	2	2	13
Cladopelma curtivalva		3		1	1	1	
Kiefferulus opalensis				1	1		1

Appendix 1.3

Area of core: 22.7 sq. cm

Sample No.	1	2	3	4	5
Oligochaeta	8	2	1	2	4
Chironomus zealandicus	2		2	1	1

APPENDIX 2

Counts of macroinvertebrates and microfossils made in this thesis have been stored on IBM RX02 floppy diskette No. 184 at the Computer Centre, University of Waikato, Private Bag, Hamilton N.Z..

File	Content
EXPLAIN.;1	-list of codes used
CHIRO.DAT;1	-chironomids collected in Lake Maratoto from 19/9/78 to 13/3/80
CHIRO.CTL;1	-control file for "chiro.ctl"
CORE.DAT;1	-microfossils recovered from Lake Maratoto core
CORE.CTL;1	-control file for "core.dat"
FAUNA.DAT;1	-macroinvertebrates collected in Lake Maratoto from 19/9/78 to 13/3/80
FAUNA.CTL;	-control file for "fauna.dat"
SURF.DAT;1	-microfossils recovered from surficial sediments of some North Island lakes
SURF.CTL;1	-control file for "surf.dat"

APPENDIX 3

Density of macroinvertebrates (numbers per core) along three transects of Lake Maratoto. To obtain numbers per square metre multiply by 440. $\bar{x}$ = mean of five cores, S = sample variance.

Appendix 3.1

DEPTH (m)	0.5							
Date	17/10/79		25/10/79		25/10/79		1/11/79	
Transect	A		B		C		A	
	$\bar{x}$	S	$\bar{x}$	S	$\bar{x}$	S	$\bar{x}$	S
Oligochaeta	67.4	55.2	13.4	22.1	144.0	155.0	165.0	39.0
Arachnida			0.2	0.4	0.2	0.4		
Xanthocnemis zealandica							0.2	0.4
Oecetis unicolor			5.0	2.6	0.8	1.3	0.6	1.2
Triplectides cephalotes							0.2	0.4
Anisops wakefieldi	0.6	0.5	0.2	0.4			0.2	0.4
Coleoptera	0.4	0.5					0.2	0.4
Chironomidae (total)	17.2	8.9	44.4	36.4	19.4	17.5	30.0	5.1
Tanypodinae								
Podonominae	4.8	4.0	0.2	0.4				
Orthocladiinae			0.6	0.5	0.8	0.8		
Chironomus zealandicus					0.2	0.4	1.0	1.0
Cladopelma curtivalva								
Kiefferulus opalensis	2.4	5.4	18.4	24.3	1.8	1.1	3.7	5.5
Calopsectra funebris	9.8	6.7	25.6	25.2	16.8	16.1	15.0	11.3

Appendix 3.2

DEPTH (m)	1.0							
Date	17/10/79		25/10/79		25/10/79		1/11/79	
Transect	A		B		C		A	
	$\bar{x}$	S	$\bar{x}$	S	$\bar{x}$	S	$\bar{x}$	S
Oligochaeta	6.0	9.6	4.0	3.4	9.6	9.1	4.4	8.7
Arachnida								
Xanthocnemis zealandica								
Oecetis unicolor	0.8	1.3	4.8	2.3	1.0	1.0	0.6	0.8
Triplectides cephalotes	0.2	0.4						
Anisops wakefieldi								
Coleoptera								
Chironomidae (total)	2.0	1.9	0.2	0.4	0.4	0.5	1.0	2.2
Tanypodinae								
Podonominae								
Orthocladiinae								
Chironomus zealandicus	1.6	1.8					1.0	2.2
Cladopelma curtivalva	0.4	0.5						
Kiefferulus opalensis								
Calopsectra funebris			0.2	0.4	0.4	0.5		

Appendix 3.3

DEPTH (m)	2.0							
Date	17/10/79		25/10/79		25/10/79		1/11/79	
Transect	A		B		C		A	
	$\bar{x}$	S	$\bar{x}$	S	$\bar{x}$	S	$\bar{x}$	S
Oligochaeta	0.8	0.5	5,8	4.0	16.0	14.5	0.2	0.4
Arachnida								
Xanthocnemis zealandica								
Oecetis unicolor	0.4	0.5	0.4	0.6	1.0	1.2	0.4	0.6
Triplectides cephalotes								
Anisops wakefieldi								
Coleoptera			0.2	0.6				
Chironomidae (total)	2.8	2.6	1.0	1.2	1.8	2.2	1.0	0.7
Tanypodinae	0.4	0.5	0.2	0.4	0.2	0.4		
Podonominae								
Orthocladiinae								
Chironomus zealandicus	1.6	1.8	0.6	0.9	1.2	1.8	0.8	0.8
Cladopelma curtivalva	0.8	1.1	0.2	0.4	0.2	0.4		
Kiefferulus opalensis							0.2	0.4
Calopsectra funebris					0.2	0.4		

APPENDIX 4

Qualitative evaluation of gut contents in some Waikato chironomid larvae. All animals mounted whole in P.V.A. lactophenol. Values if given are percentage cover. Gn = Lake Rotomanuka South, Ki = Lake Kimihia, Km = Kaipo margin (Urewera National Park), Mh = Lake Mangahia, Mo = Lake Maratoto, Ni = Lake Ngarotoiti, Ra = Lake Rotoroa, Rk = Lake Rotokauri, Ro = Lake Rotomanuka, Ru = Lake Ruatuna, Wa = Waihaha lagoon, Wh = Waahi, Wt = Waitomo stream. D = dominant, p = present, i = mostly empty guts.

Appendix 4.1

Taxa: TANYPODINAE

Date	Jan 79	Jan 79	Feb 79	Jun 79	Jun 79	Jun 79	Jun 79	Jun 79	Jul 79	Aug 79	Feb 80	Oct 80	Oct 80	Oct 80	Oct 80	Oct 80	Oct 80	Jul 78	Sep 80	Feb 80	Feb 80	Oct 81	Dec 79
Location	Mo	Mo	Mo	Mo	Mo	Mo	Mo	Mo	Mo	Mo	Mo	Ro	Ro	Ro	Ro	Km	Km	Wt	Wt	Wa	Wa	Mh	Gn
Depth	2.0	2.0	1.0	1.0	2.0	2.0	2.0	5.0	2.0	7.0	7.0	0.1	7.0	1.0	4.0	1.0	1.0	1.0	1.0	0.5	0.5	1.0	0.2
Instar	1	1	4		1	1	2																
Algae S			p																				
Algae M																	50				p		
Detritus S																		p					
Detritus M			p						p	p			p		p		50		p	D		p	p
Detritus L				D																			
Diatoms				p			p	p	p	p	p	p	p	p	p	p				p		p	
Filamentous algae										p	p				p							D	p
Fungal hyphae												p											
Chironomid larvae																				p			
Oligochaetes			p				p																
Crustacea			D				p																
Other invertebrates				p																	p		
Sand			p																				
Undetermined	p											p				p			p				p
Melosira														p									
Pinnularia	p	p			D							p											
Surirella	p	p																					
Synedra	p																						
Tabellaria														p									
Note		i				i		i								i							

Appendix 4.2

Taxa: PODONOMINAE *Parochlus* sp.

Date	Oct	Jul	Jul	Aug	Nov	Aug	Nov	Nov
Location	Mo	Mo	Mo	Mo	Mo	Mo	Mo	Mo
Depth	0.2	5.0	2.0	0.2	0.2	0.2	0.5	0.5
Algae S								D
Algae M	90			80	5	20	95	
Algae L								
Detritus S								
Detritus M	10	p		20	95	80		80
Detritus L								
Filamentous algae						p		
Detritus filaments								p
Undetermined		p						
Frustulia				p				
Melosira	D							D
Peridinium							p	
Pinnularia	p							p
Surirella								p
Trachelomonas	p				p			
Note			i					

Appendix 4.3

Taxa: ORTHOCLADIINAE	Eukiefferiella sp.					Syncricotopus sp.			
Date	Feb 77	Nov 79	Jun 80	Oct 80	May 81	Jan 77	Feb 77	Dec 80	May 81
Location	Rk	Mo	Mo	Wh	Wh	Ni	Rk	Mo	Wh
Depth	0.5	0.5	0.5	0.5	0.5	0.5	0.2	0.2	0.8
Algae S									
Algae M	p		95		D	D	p	90	D
Algae L									
Detritus S									
Detritus M	20		p		p		D	10	
Detritus L									
Filamentous algae									D
Detritus filaments			5						
Sand	80				p				p
Frustulia								p	
Melosira		D			D				
Navicula					p				
Tabellaria		p				D		D	
Trachelomonas					p				p

Appendix 4.4

Taxa: CHIRONOMINAE	Chironomus zealandicus								Kiefferulus opalensis			Polypedilum pavidus							
Date	Feb 77	Oct 79	Dec 79	Jan 80	May 81	May 81	Jun 80	Mar 81	Feb 77	Feb 77	Aug 78	May 81	May 81	May 81	May 81	May 81	Feb 77	Feb 75	Feb 77	May 81
Location	Mo	Mo	Mo	Mo	Wh	Wh	Ro	Ra	Ki	Mo	Mo	Wh	Wh	Wh	Wh	Wh	Rk	Rk	Ra	Ra
Depth	0.2	5.0	0.5	0.5	0.2	0.2	0.5	1.0	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	1.0	0.8
Instar	II	II	I	I	IV	IV	IV	III	IV	IV	IV									
Algae S																				
Algae M	D	p	p	D	D	p	p	30		p	p	p	p	p	p		60		60	
Algae L																				
Detritus S			D			D		40				D	D	p	p		D		p	
Detritus M	p	D		p	p		p	15		p	p									
Detritus L						p		15				p	p				p	p	p	
Diatoms																				p
Detritus filaments		p																		
Sponge spicules					p	p														
Sand												p	p	p	p	p	40		40	
Anomoeneis					p															
Cyclotela								p												
Cymbella								p												
Eunotia								p												
Melosira					D	D		p			p			D						
Navicula								p												
Pinnularia								p												
Surirella					p			p												
Synedra								p												
Tabellaria								p			p				D				p	90
Trachelomonas	D				p		D	p			p		p	p						
Note									i					i						

Appendix 4.5

Taxa: CHIRONOMIDAE Cladopelma curtivalva

Date	Aug 78	Aug 78	Aug 78	Aug 78	Aug 78	Oct 78	Dec 79	Dec 79	Jan 80	Jan 80	Feb 80	Oct 79	Oct 79	Mar 81	Feb 77	Feb 77	Feb 77	Jun 80
Location	Mo	Mo	Mo	Mo	Mo	Mo	Mo	Mo	Mo	Mo	Mo	Ra	Ra	Ra	Mh	Mh	Ru	Ro
Instar				IV			I			II								
Algae S																		
Algae M	40		60							p	80		40		40	"		60
Algae L																		
Detritus S		20		p			p	D		D			60	p	60	40		
Detritus M	60		40			p	p	p		p	20		p	p	p			40
Detritus L																p		
Diatoms		80				p	D		100							60		
Filamentous algae																	d	
Detritus filaments						p												
Fungal hyphae						p												
Sand													p					
Crustacea			p			p												
Anomoeneis																	p	
Chroococcus?													p					
Frustulia						p												
Melosira																	p	
Navicula															p	p		
Peridinium																p		
Peridinium	D	D					D	p	D		D				D	D		
Surirella	p																	
Trachelomonas	p	p											p		p			p
Note					i							i		i				

Appendix 4.6

Taxa: TANYTARSINAE	Calopsectra funebris						Paratanytarsus agameta	
Date	Feb 77	Feb 79	Feb 80	Jun 80	Aug 78	Jun 80	Feb 77	May 81
Location	Mo	Mo	Mo	Mo	Ro	Ro	Rk	Wh
Depth (m)	0.2	0.5	0.5	0.1	1.0	1.0		
Algae S								
Algae M	20	60	90	50	50	90		D
Algae L								
Detritus S						10		
Detritus M	80	40		50	50		40	p
Detritus L			10				p	p
Diatoms								p
Detritus filaments	p							
Sand								p
Undetermined								p
Cyclotela						p		
Melosira					D	p		
Navicula						D		
Pinnularia						p		
Trachelomonas	p	p			p	p		

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