Factors affecting the distribution and abundance of chironomids in three Shropshire meres, with special reference to the larval tracheal systems

by

Catriona Morag Tait Bowman

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ABSTRACT

Newton Mere, Crose Mere and Blake Mere (Shropshire) are warm monomictic lakes which show thermal stratification and clinograde oxygen curves in summer but which return to isothermal conditions in winter. Crose Mere is the most eutrophic mere and Newton Mere relatively the most dilute. The physico-chemical environment of each mere is determined by the lithology and morphology of the lake basin.

The principal factors affecting distribution of chironomid larvae are the oxygen content of the water, the time of initiation of thermal stratification, both of which are dependent on the temperature regime; and the types of tracheal systems possessed by the larvae. Four apneustic tracheal patterns have been described and show sequential development. Progressive reduction of the tracheal system is associated with an increase in the concentration of haemoglobin and a decrease in the activity levels of the larvae.

Hydrogen sulphide produced by profundal sediments in Crose Mere is responsible for low abundance of chironomids in the profundal; the life-less profundal zone in Blake Mere is due to the onset of anoxic conditions before emergence and oviposition occur. Newton Mere supports the largest population of the predominant larval form, Chironomus anthracinus Zett., whose distribution is positively related to increasing depth.

Abundance in the tubiculous larvae is related to the type of substratum, its food value and the space available for each larva; and in the carnivorous Procladius choreus Mg. abundance is related to the availability of prey.

No relationship was found between the ability of larvae of C. anthracinus, P. choreus and Cricotopus sylvestris Fab. to withstand adverse temperature and oxygen conditions and the levels of stored

tissue glycogen. However, monthly monitoring of natural populations of C. anthracinus and P. choreus showed that the amount of stored tissue glycogen increases during the last larval instar and is greatest immediately prior to pupation. The rate of respiration (QO_2) was found to increase with rising temperatures.

A key to common larval chironomids has been compiled.

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1.

INTRODUCTION

The meres in Shropshire are among the few natural lowland lakes in England and represent a series quite different from the more familiar highland lakes of Cumbria, their affinities being with lakes in Southern Sweden, Denmark and North Germany (Macan and Worthington, 1972). All the Shropshire meres may be considered eutrophic and display a full range of stages in the normal succession from open water to raised bog. However despite their obvious importance and interest, these meres have, until recently, received only sporadic attention from scientists.

The phytoplankton has been studied in relation to the "breaking" or "blooming" of the meres, principally by Phillips (1884), Griffiths (1925) and Reynolds (1967; 1971a, b; 1972; 1973a, b; 1975), while Gorham (1957) analysed the chemical composition of the Ellesmere group of meres in order to correlate the variations in ionic composition between meres with differences in local geology and drainage. The geology of the area has been described by Pocock and Wray (1925) and Edmunds and Oakley (1958); the soils by Crompton and Osmund (1954) and the vegetation by Tansley (1939) and Sinker (1962). Hardy (1939) studied pollen remains from various sites and described the past, as well as the present, vegetation.

The fauna of the meres has been virtually ignored except for passing references to Asellus populations by Williams (1962), to oligochaetes by Brinkhurst (1971), the triclads by Reynoldson (1966) and to the Corixidae of Crose Mere and Sweat Mere by Macan (1967). Faunal lists for Cole Mere and for several other Ellesmere meres are contained in the theses of Pickavance (MS, 1968) and Walsh (MS, 1965).

Ecological studies from the Department of Biology, University of Keele, began in September 1971, when a preliminary investigation was made of a number of Shropshire meres including White Mere, Cole Mere, Crose

Mere, Blake Mere, Fenemere, Newton Mere, Kettle Mere and Brown Moss. Hand net samples were taken from as many sites at one mere as possible and the general environment was noted. After consulting faunal lists compiled from these investigations, published work, and bearing in mind the individual nature of each mere, Newton Mere, Blake Mere and Crose Mere were chosen as representing the widest possible range of habitats available. The choice has been, fortunately, a happy one.

The initial inspiration for the study came from the paper by Stuart (1941) who had observed a relationship between the development of the apneustic tracheal system of chironomid larvae and their environment and this observation has been investigated in relation to the distribution of chironomids in Newton Mere, Blake Mere and Crose Mere. Although Stuart had worked on small shore pools at Millport, it was apparent from the preliminary investigations in 1971, that a relationship did exist and that the distribution of the chironomids was affected by it. Several authors have alluded to the tracheae of Chironomus species (Miall, 1895; Keilin, 1944; Imms, 1951; Wigglesworth, 1953, 1972; Whitten, 1955, 1960; Faucheux, 1974) but only Stuart noted the connection between the sequential development of the tracheal system throughout the chironomid family and the environment in which individual species lived.

The distribution of chironomid larvae in lakes, reservoirs and meres has been fairly well documented in Britain principally by Humphries (1936), Mundie (1955, 1957), Weerekoon (1956a, b), Dunn (1961), Slack (1965), Brinkhurst and Walsh (1967), Hunt and Jones (1972), Maitland, Charles et al (1972), Smith and Young (1973), Charles, East et al., (1974) and Maitland and Hudspith (1974).

Although this study has been principally ecological and deductive, with excursions into experimental and physiological entomology, it has also been a pioneering study, because little or no data existed on

either the Shropshire meres, the chironomids therein, or the pattern of apneustic tracheal systems and their adaptations to the environment. Therefore much of the study was ground work, two years being spent sampling in the field with the virtual exclusion of other work.

There are no data for Blake Mere and Newton Mere during January 1974 because of an outbreak of swine vesicular disease in Staffordshire and as a result, access to farm land was prohibited. Crose Mere was visited before the ban came into operation.

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2.

METHODS

SECTION 1. PHYSICO-CHEMICAL FACTORS

INTRODUCTION

In any ecological study, it is essential to determine the physical and chemical characteristics of the chosen habitat in order to show the interaction between them and the object of the study. As the majority of lake-dwelling chironomids have a one year life-cycle, a study of the seasonal fluctuations in the physico-chemical environment over one year must be included in any description of their ecology.

Particular attention has been paid to temperature and dissolved oxygen but pH, specific conductivity, light intensity and light penetration have also been measured throughout the study. Occasional determinations for calcium, magnesium, hydrogen sulphide and the calorific value of the profundal sediments were also made. Most of the parameters were determined at the deepest point of each mere.

Initially, surveys using an echo sounder to determine depth along the long axis of each mere were carried out and stations subsequently marked by buoys were then set up at significant depths, which included the deepest point of each mere. Sampling stations were set up at 3, 4.5, 7.5, 12 and 16 m on Newton Mere; 2, 3.5, 6, 9 and 13 m on Blake Mere and 2, 3, 4.5, 6, 7 and 9 m on Crose Mere.

2.1.1. Temperature and dissolved oxygen

Measurements were recorded simultaneously at metre intervals from the surface using a Mackereth Oxygen Sampler, so that a complete profile from surface to bottom was obtained. Dissolved oxygen was recorded as the percentage saturation at the stated temperature, corrected to a pressure of 760 mm.

2.1.2. Light intensity and light penetration

An underwater photometer (Evans Electroselenium Ltd.) was used to measure light intensity at metre intervals from the water surface until a reading of 0 lumens/ft^2 was obtained on the lowest scale. This depth was recorded as the limit of penetration of white light.

2.1.3. pH and specific conductivity

Values for every station on each mere every month for the surface and bottom water were measured on return to the laboratory. The pH was recorded using a glass electrode with a Pye Model 79 and specific conductivity with an Electrolytic Conductivity Measuring Set (Model MC-1, Mark V Electronic Switchgear). Results for conductivity are quoted as µmho/cm.

2.1.4. Calcium, magnesium and hydrogen sulphide

Determinations of the concentration in mg/l of calcium and magnesium were made using an EEL 240 atomic absorbtion spectophotometer.

Samples for hydrogen sulphide analysis were taken in 100 ml stoppered glass bottles and fixed immediately in the field with 1% cadmium chloride solution and shaken vigorously. The samples were left for 48 hrs. as required (Golterman, 1969). The supernatant liquid was then decanted and any white precipitate (which was very obvious if present) dissolved in 5 ml 0.025 N iodine solution and 5 ml concentrated hydrochloric acid. Excess iodine was then titrated against 0.025 N sodium thiosulphate with 1% starch solution as indicator. Samples which had not produced any precipitate were discarded as the precipitate is indicative of the presence of hydrogen sulphide.

Water samples were obtained every month at each mere at all stations for surface and bottom water. Bottom water was obtained using a

modified Kemmerer water sampler (Welch, 1948) and taken back to the laboratory. Two 125 ml samples were taken for pH, conductivity, calcium and magnesium determinations.

2.1.5. The nutritional nature of the profundal sediments

It was not fully appreciated until late in the study that the nutritional nature of the substratum could be one of the most important factors in the distribution of chironomids in the meres. Consequently, there is little quantitative data, although notes have been made throughout the study on the appearance, texture and content of each sample. Determinations of the calorific value of the mud are quoted as kcal/g and were obtained using a Gallenkamp ballisitic bomb calorimeter.

Mud samples were taken from the deepest point of each mere using a 15 cm^2 Ekman grab and returned to the laboratory in labelled plastic buckets with lids. The samples were sieved by hand, using a sieve with 40 meshes/inch, in a deep plastic tray so that none of the sample would be lost. The coarse organic matter retained in the sieve was sorted for animals and then filtered to remove excess water. The remaining "mineral" mud was poured back into the buckets and allowed to settle. The water was then siphoned from the top of the mud and the mud weighed.

The coarse organic matter was weighed and expressed as a percentage of the total mud weight ("mineral" mud + organic matter).

11 samples of the "mineral" mud and 3-5 of the organic matter were taken for each mere, enough to fill small crucibles, the mean weight of which was 5.7 g. The crucibles and contents were then weighed and dried for 24 hrs. at 110°C. The crucibles were then weighed again and the dry weight calculated.

The samples were then separately ground in a mortar to ensure a standard size of particle. Materials of low bulk density require

special treatment to ensure the satisfactory combustion of a sample, Such materials burn extremely rapidly and so are compacted in a press, forming pellets, before testing. The actual insertion of the pellet in the bomb and the firing followed the procedure laid down in the handbook accompanying the bomb calorimeter.

The principle of bomb calorimetry is: that a known weight of a sample is ignited electrically and burned in an excess of oxygen in the bomb and that the maximum temperature rise at the top of the bomb is measured with the thermocouple and galvonometer system. This temperature is compared with that obtained when a sample of known calorific value is burnt to obtain a value for the heat release and thus the calorific value of the sample. Thermochemical grade benzoic acid is the recommended standard material to calibrate the amount of heat released by the combustion of a sample.

2.1.6. Chironomid sampling and treatment of catches

Two samples of bottom mud were collected with a 15 cm^2 Ekman grab monthly for each mere at every station and returned to the laboratory in labelled plastic buckets with lids. The samples were either sieved by hand or by using Slack's (1972) rotary sieve at 40 and 50 meshes/inch. The residues were returned to their labelled buckets and left under aeration until they could be sorted for larvae. Samples which contained a lot of residue, such as peat, were sorted using the magnesium sulphate flotation method.

Larvae sorted from the residues were put in dishes of clear water, identified, counted and species lists compiled. Numbers permitting, the catch was then divided into two groups, one group being preserved in Carnoy's fixative and the other maintained in plastic sandwich boxes (11 x 19 x 7 cm) for rearing and experimentation.

The sandwich boxes contained sieved lake mud and pond water and a

hole was cut in the lid to accommodate an aeration tube. In this manner, larvae could be kept for several months in a cold aquarium. If the larvae were overwintering, a thin paste of soya bean flour was added occasionally to the water.

If numbers were low, the whole catch was preserved.

The numbers of animals from both grab samples were combined and then converted to numbers per square metre according to Welch's (1948) formula for analysis of Ekman grab samples, in which,

$$n = \frac{o}{a\ s} \cdot 10{,}000$$

where,

n = numbers of live macroscopic animals in 1 m^2 of profundal bottom,

o = number of animals actually counted,

a = transverse area of Ekman grab in cm^2, and

s = number of samples taken at one sampling station.

Keys used in the identification of the larvae were Bryce (1960), Chernovskii (1949) and Johannsen (1937a,b). Adults were identified using Coe (1950). Larval head capsules were removed, dissected and mounted on a slide ventral side up, in polyvinyl lactophenol. The width of the capsules was measured in Chironomus anthracinus Zett. larvae to ascertain their instar group. For identification of the adult males, the hypopygium was removed, boiled in 10% KOH, washed, dehydrated and mounted in polyvinyl lactophenol.

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SECTION 2. MORPHOLOGICAL AND PHYSIOLOGICAL FACTORS

INTRODUCTION

The adaptations of a species to its environment are undoubtedly one of the most effective, if not the most important factor in determining the species' distribution. In lake-dwelling chironomids the differences in response by various species to the oxygen content of the water account in part for depth distribution. The success of the response by a species is principally dependent on the type of respiratory system and any respiratory adaptations displayed by the species. The respiratory system controls the rate of respiration and survival of the species under adverse conditions.

Special reference has been made in the study to the pattern of the tracheal systems of larvae found in the Shropshire meres and the interrelation between the pattern and the distribution of a species within a mere.

The ability to survive adverse conditions has been studied in relation to the glycogen contents of the larvae, both freshly collected and under experimental conditions. In conjunction with this study, the rates of respiration under three temperature conditions have been examined in 4th instar Chironomus anthracinus. These larvae were also subjected to three pH conditions and their survival over time noted.

2.2.1. Tracheal systems

The tracheal pattern in each species was studied mainly from the whole animal. The most worthwhile method was simply to place the living larva in a drop of insect Ringer (7.5% saline), either on a flat or concave slide and view through a cover slip at varying light intensities and magnifications. Concave slides were used for the larger, fatter larvae which were usually lightly anaesthetised in soda water. The

larvae were therefore kept alive and could be used again if the drawings needed further elaboration. An added advantage in their being kept alive was that the tracheae remained air-filled. An alternative to Ringer's solution is glycerol but there are no advantages and the slides are more difficult to clean afterwards.

The preparations were both drawn and photographed. Measurements of tracheal diameter were made with a stage micrometer and calibrated eyepiece.

Occasionally a dissection was made of the large Chironomus larvae whose tracheae were difficult to follow due to masking by subcutaneous deposits of a green bile pigment. The head, anal segments and gut were removed and the "torso" cut up one side using micro-scissors before being placed in platelet fluid (3% procaine in 0.25% saline). This fluid decolourises the haemoglobin and slightly bleaches the green pigment. Dissection was not an entirely satisfactory technique because inevitably some of the tracheae would be destroyed.

Stuart (1941) used a modified Berlese's fluid in his study of chironomid tracheal systems. A larva is placed alive in a drop of the fluid. Death follows almost immediately as the fluid penetrates and clears the tissues leaving the tracheae standing out black due to the enclosed air. This method was not considered to be very useful as larvae with haemoglobin became densely opaque and did not clear for 30 minutes or more. In addition the tracheae filled with liquid so quickly that it was impossible to either photograph or draw the entire system before it disappeared. Larvae without haemoglobin cleared quicker but they were so transparent that all the intricacies of the tracheae could be seen with the larvae in water only.

In the preparation of sections for closer study of the anatomy and tracheae, warm Bouin's fixative was most frequently used after initial

narcotisation in 1% ethyl carbamate. Preparations of tissue were then dehydrated, cleared, embedded in paraffin wax, sectioned at 5 µm and stained with either Mallory's Triple stain or else Erlich's Haematoxylin and counterstained with alcoholic eosin. Preparations were cut in both T.S. and L.S. These did not assist the study of the tracheae at all as none could be found, although the slides did bring a greater understanding of the anatomy and histology of the larval body.

2.2.2. Glycogen studies

2.2.2i Monthly monitoring

This study began in January 1974 and continued until July 1974.

Samples of profundal mud from Newton Mere were bought back to the laboratory each month and sorted for Chironomus anthracinus and Procladius choreus larvae, which were then placed in clean water for 24 hours to permit evacuation of the intestinal contents. This ensured that any glycogen which was isolated was tissue glycogen and not from a recent meal.

The method of glycogen isolation which was eventually adopted was adapted from Clark (1964) from a procedure for the extraction of glycogen from rat liver. Other methods which were tried, for example, the Folin-Wu method for determining the level of blood sugar, as described by Myers (1942) and used by Augenfeld (1967), were found to be unsatisfactory because the end-product to be measured was not glycogen, but "reducing sugar". Also, the pre-test of the Folin-Wu method which was long and detailed was followed only by a subjective comparison between the test solution and colour standards.

2.2.2ii Isolation of glycogen

After 24 hours in clean water, the larvae were sorted into species, counted, weighed and placed in a small precooled glass mortar containing 0.5 ml 10% Trichloracetic acid (T.C.A.). Keeping the mortar on a

chilled tray, the larvae were ground with a glass pestle.

The homogenate was then centrifuged in weighed, balanced 5 ml polypropylene centrifuge tubes for 10 minutes at 4,000 r.p.m. (2000 x g) in an MSE 'High Speed 18' centrifuge. The opalescent supernatant liquid was decanted into a 5 ml measuring cylinder and kept chilled.

To achieve complete extraction of the glycogen, the mortar and pestle were rinsed with 0.5 ml 5% T.C.A. and the washings poured into the used centrifuge tube. The mixture was stirred, centrifuged for 10 minutes and the supernatant liquid added to the first T.C.A. extract.

Two volumes of absolute alcohol were added to the T.C.A. extracts, the mixture stirred and left to stand on the chilled tray until the precipitate flocculated. The centrifuge tube was thoroughly washed and dried ready for use in the second part of the procedure.

The suspension from the measuring cylinder was then centrifuged for 3 minutes at 4,000 r.p.m. The supernatant liquid was discarded and the white precipitate dissolved in 1 ml distilled water and reprecipitated in 2 ml absolute alcohol. The precipitate was collected by centrifugation and washed again with 1.5 ml absolute ethanol followed by 1.5 ml diethyl ether. The ether was left to evaporate. The tubes were placed in a desiccator until they could be weighed. The white precipitate in the bottom of the tube is the isolated glycogen.

The purity of this glycogen and thus the effectiveness of the extraction procedure was determined by the anthrone reaction (Rendina, 1971). For comparison, the purity of B.D.H. (oyster) biochemical glycogen was also determined.

2.2.2iii The anthrone reaction

The 9.0 mg samples of the extracted glycogen were crushed and weighed quantitatively, then dissolved in 100 ml distilled water. 4.0 ml of

anthrone reagent (0.2% w/v anthrone in concentrated sulphuric acid) was then added to each of the following:

duplicate 1 ml aliquots of the glycogen solution;

duplicate 1 ml aliquots of a standard 0.5 μmoles/ml glucose solution and 1 ml distilled water.

All the tubes were cooled to $0^{o}C$ in an ice bath and then heated in a boiling water bath for 10 minutes. The tubes were then put in cold water to stop the reaction and brought to room temperature. A 3 ml sample from each tube was transferred to individual cuvettes and the absorbance read at 620 mμ.

Calculations

$$\frac{A_{620} \text{ of glycogen}}{A_{620} \text{ of glucose}} \times 100 = \text{purity of glycogen}$$

2.2.2iv Survival under adverse conditions related to the glycogen content of the larvae

In this experiment an attempt was made to correlate survival by larvae of three chironomid species kept under 4 different temperature and oxygen conditions, with the amount of glycogen which can be stored by a larva. The experiment lasted 14 days and the conditions simulated as nearly as possible environmental conditions which had been found in the meres over one year. The species involved were Chironomus anthracinus, Procladius choreus and Cricotopus sylvestris.

The experimental conditions were as follows:

low oxygen (5%), low temperature ($5^{o}C$) representing decaying matter in the littoral zone in winter;

low oxygen, high temperature ($20^{o}C$) representing conditions under the thermocline in summer;

high oxygen (95%), low temperature representing the benthos in winter;

high oxygen, high temperature representing the littoral zone in summer.

High oxygen conditions were maintained by aeration and low oxygen by using boiled pond water which had been kept in sealed flasks. The larvae were housed in either sealed conical flasks ('low oxygen') or in sandwich boxes with an airline through the lid ('high oxygen').

Cricotopus larvae were given no substratum as they spin their nets readily on either plastic or glass but the containers for the other larvae were filled to a depth of 2 cm with sieved lake mud and topped up with water.

The boxes and flasks were put in incubators set at 5°C for the 'low temperature' larvae and at 20°C for the 'high temperature' larvae. Air lines were passed into the incubators for the 'high oxygen' boxes.

Larvae from the same batch as the experimental larvae were used to determine the pre-experimental content of glycogen.

After 14 days the flasks and boxes were removed and inspected for larvae. Any larvae still alive were counted and left for 24 hours in clean water to allow evacuation of the intestinal contents. The larvae were then analysed for the post-experimental glycogen value.

2.2.3. Rate of respiration of 4th instar Chironomus anthracinus larvae

3 Gilson Differential Respirometers (Gilson Medical Electronics Inc.) were set up at 6.5°, 15° and 21°C. These respirometers are a type of constant pressure manometric apparatus used to measure gaseous exchange.

10 reaction flasks were used in each respirometer although not all gave reliable results. 10 weighed 4th instar Chironomus anthracinus larvae were placed in each reaction flask and covered with 2 ml distilled water. 0.2 ml 20% KOH was placed in the centre well to absorb the carbon dioxide. A control reference flask was also set up but containing only distilled water. The rate of shaking was set at 100 shakes/minute.

2.2.4. Effect of 3 pH conditions on 4th instar Chironomus anthracinus and Procladius choreus larvae

3 repli-dishes were set up each containing filtered pond water made up with buffer powders to 3 pH conditions: pH 4, pH 7 and pH 9. Repli-dishes are square plastic petri dishes with close fitting lids and are separated into 25 individual cells.

15 Chironomus anthracinus larvae and 7 Procladius choreus larvae were used per repli-dish, each larva being placed in an individual cell. P. choreus larvae were given chopped Tubifex for food and the C. anthracinus larvae were left in their tubes with a small amount of sieved mud. The dishes were placed in the cold aquarium.

Each larva was examined at 24, 48 and 72 hours and C. anthracinus larvae allowed to go on to 96 hours. If the water with P. choreus larvae became foul because of the Tubifex, it was replaced with fresh water of the appropriate pH. Larvae were considered healthy if they curled around the forceps when picked up.

At the end of the experiment, the living larvae were removed, counted, and the % survival was calculated.

This brief experiment was run to find out if the pH of water has any significant effect upon chironomid larvae.

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3.

THE PHYSICO-CHEMICAL ENVIRONMENT

SECTION 1. DESCRIPTION OF GEOGRAPHICAL FEATURES

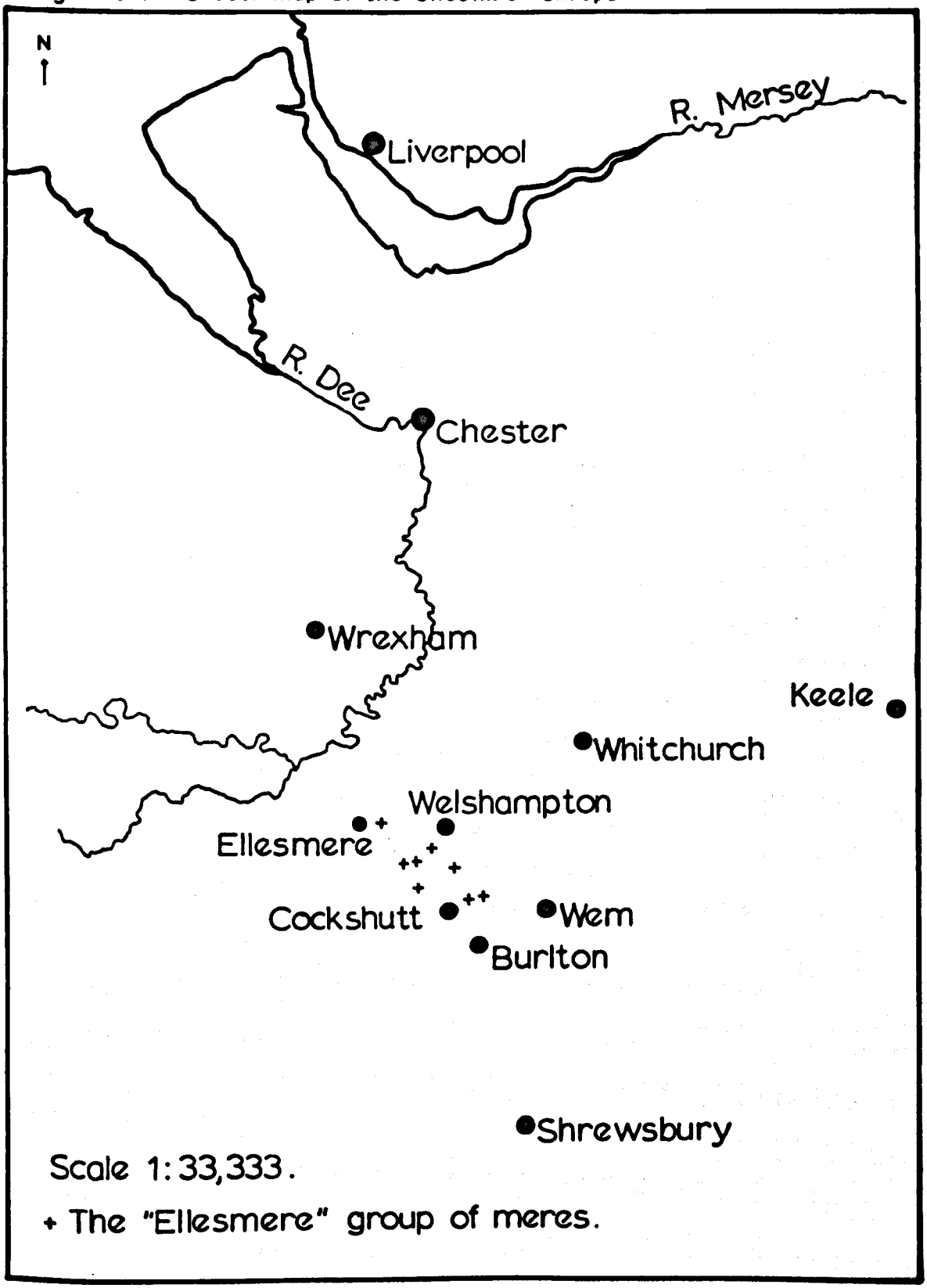
INTRODUCTION

The North Shropshire Meres are small shallow lakes lying in kettle holes and hollows amongst the thick glacial drift which covers much of the Cheshire-Shropshire Plain (Fig. 3.1). The distinctive character of this area, and its complexity, arises from its once being the meeting place for two ice sheets, the greater of which came down from the Lake District by way of the Irish Sea, while the lesser originated in Wales. The medial moraine marking the boundary between the two sheets remains as a belt of unusually hilly country, extending from Ellesmere (SJ 400348), through Cockshutt (SJ 435292) to Shrewsbury, in which the meres and mosses are surrounded by numerous steep-sided moraine hummocks (Crompton and Osmund, 1954). The sand, gravel and boulder clay form a distinct belt, widening south from Ellesmere towards Burlton (SJ 458260), which is of considerable thickness. Bore holes reveal that at Welshpool (SJ 435349), the drift is 58.5 m thick; more than 28 m at Ellesmere and a well, sunk in Colemere Woods (SJ 422318) failed to bottom the sand and gravel at 23 m (Pocock and Wray, 1925). So it can be concluded that all the meres lie on glacial drift and are not affected by the solid geology.

Keuper deposits underlie the drift which has great variety: outwash sands and gravel, lacustrine clays and "till" which varies from sandy loam to compact clay.

Peake (1961) considered that glacial lakes covered the area below 300 ft. (91.4 m) after the retreat of the ice and some of the larger meres, such as Cole Mere, Crose Mere, White Mere and Ellesmere may be remnants of these extensive lakes. Newton Mere, Blake Mere and Kettle Mere are all at higher altitudes and are perhaps kettle holes, formed when large chunks of dead ice were left stranded in the moraine.

Figure 3.1 Sketch map of the Cheshire - Shropshire Plain



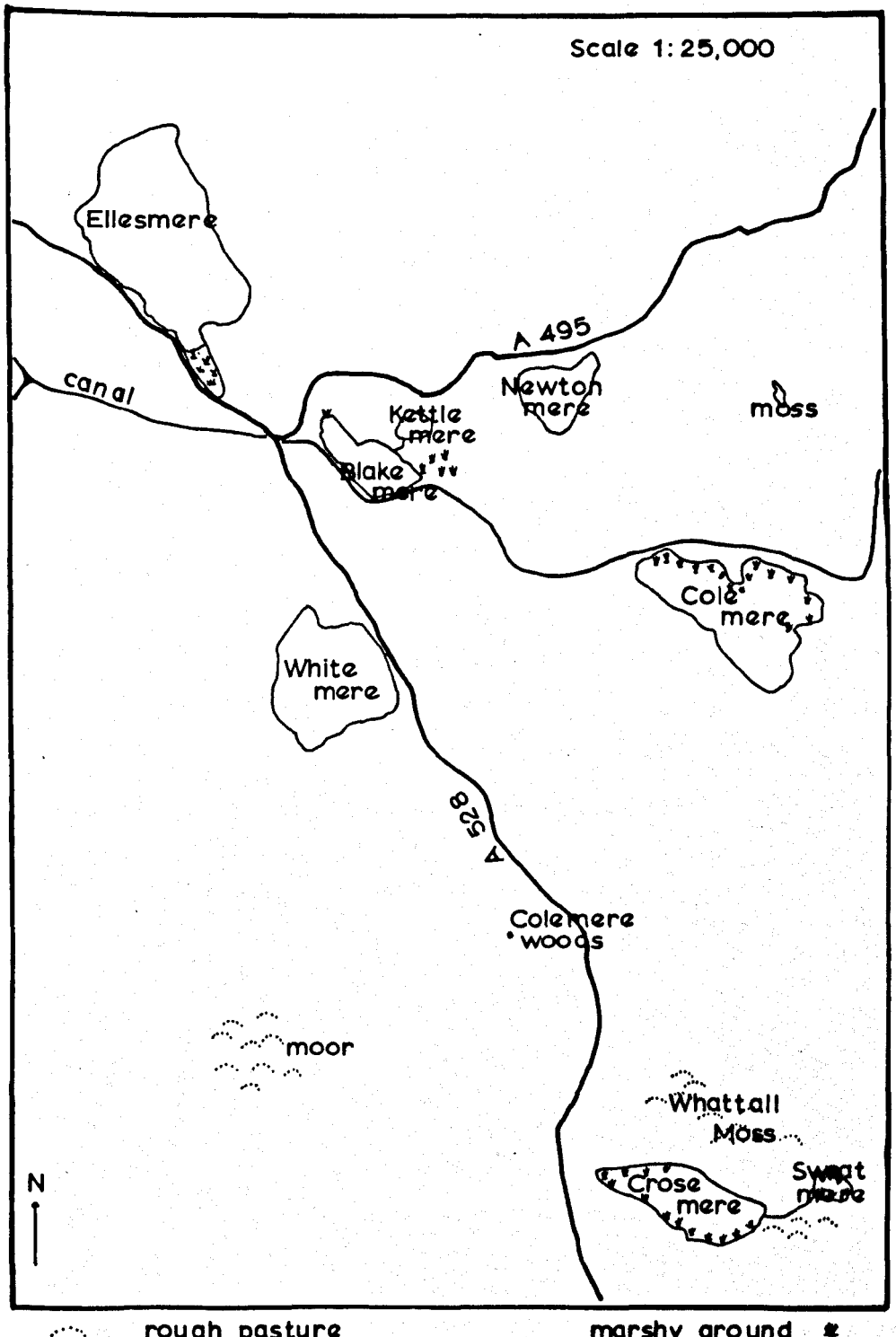


Figure 3.2 Sketch map of the Ellesmere group of meres.

North Shropshire lies in the rain shadow of the Welsh mountains upon which the prevailing Westerlies deposit much of their rainfall, and is therefore one of the drier parts of Britain with 27.5 - 30" rainfall annually, (Howell, 1941).

The meres are comparatively sheltered, lying amongst moraine hummocks but the amount of exposure varies considerably between meres. The secluded setting of Blake Mere, for instance, is perhaps the single most important factor in its hydrology. The amount of exposure of each mere has considerable bearing on the onset and breakdown of thermal stratification.

Crose Mere, Newton Mere and Blake Mere are three of the smallest waterbodies in the Ellesmere group (Fig. 3.2), which is spread over an area of twenty-three sq. km. The most attractive feature of this group is their ecological diversity and although they can all be described as "eutrophic" according to Thienemann's (1915) definition, the term oversimplifies the uniqueness of each mere.

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Newton Mere

Newton Mere (National Grid Reference SJ 425342), (Fig. 3.3), has an area of 9 hectares and a maximum depth of 16.7 m. The mere is orientated SW - NE and is therefore moderately exposed to the prevailing westerly winds (Plate 3.1). It is an unfringed mere (Sinker, 1962), lying predominantly on sands and gravel except for the NW tip which penetrates boulder clay. A small patch of Iris pseudacorus L. marks the change in the drift.

The soils overlying the drift are Brown Earths (Baschurch Series) which give free drainage, being composed of loam, sand and stones. The Baschurch Series are depleted in bases and have low pH values (Crompton and Osmund, 1954). The catchment area is very restricted as the mere is in a hollow bounded on all sides by abrupt moraine hillocks. There are no inflows or outflows and therefore the water level must be maintained by surface runoff and ground water seepage. Gorham (1957) considered that surface runoff played a larger part than deep percolation in maintaining water levels in Newton Mere, Blake Mere and Kettle Mere, because of their restricted drainage areas and dilute waters, which are exceptional in the Ellesmere group in being acidic.

The basin is simple, roughly triangular in shape with the deepest point being approximately central, revealing its origin as a kettle hole.

The mere can be divided into littoral, sublittoral and profundal zones although there is no emergent vegetation except for the small patch of Iris in the NW corner. The shores of the mere, which abutt partly on to pasture, are sand and gravel down to 2-3 m depth (Plate 3.2), with thick banks of leaves overlying the sand when some irregularity in the shoreline occurs. Griffiths (1925) noted then that for several years past Newton Mere had been treated annually with copper sulphate crystals to reduce algal blooms. The present agent continues this practice, throwing the crystals into the water along the shore. A total of 2 cwts. is used every year.

Figure 3.3 Sketch map of Newton Mere and Blake Mere.

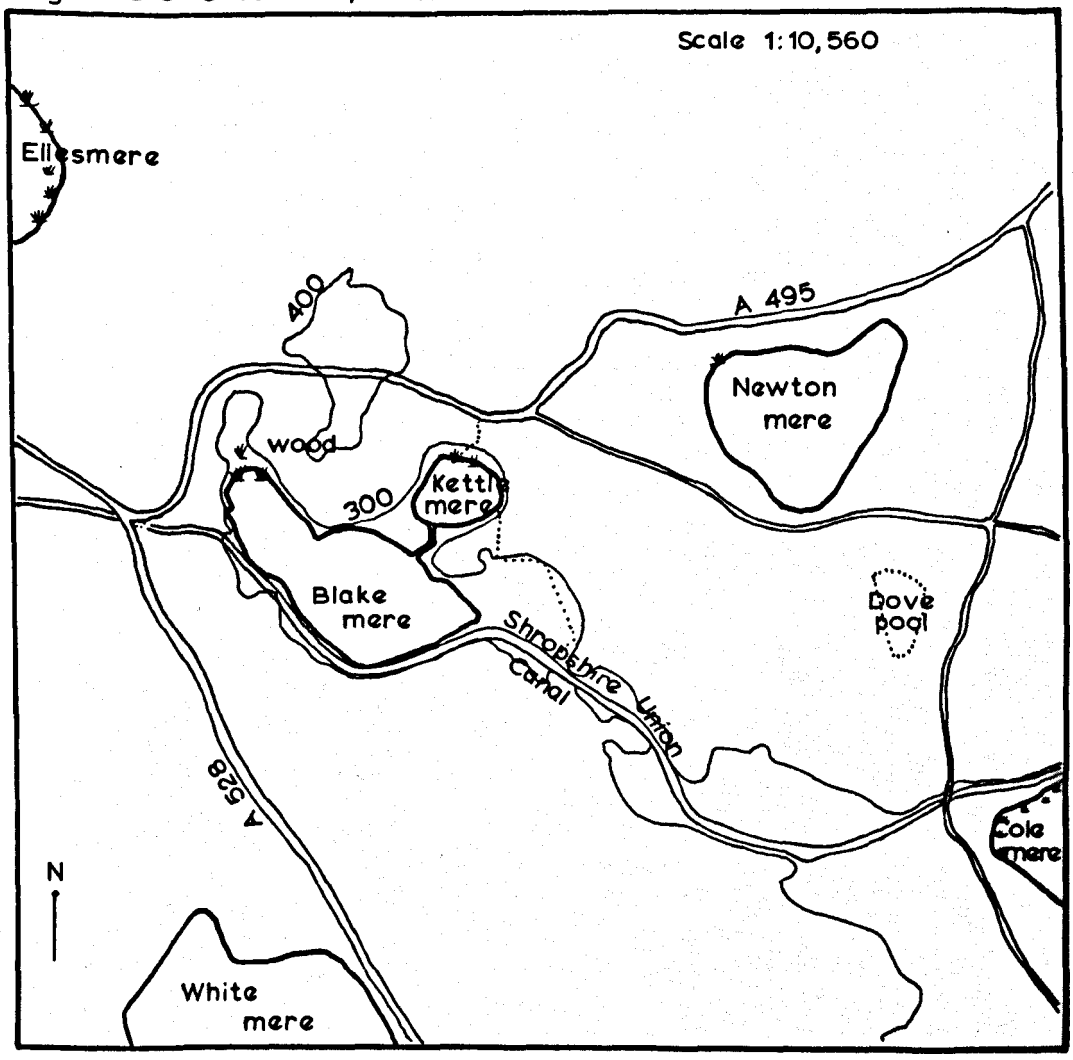

Plate 3.1 Newton Mere, looking north-east towards Welshampton

Plate 3.2 Newton Mere, looking south towards the sand and gravel shore

A sublittoral zone, where mixing of littoral and profundal fauna occurs, is evident from 3 - 5 m depth and a true profundal zone, defined as the area beneath the hypolimnion and characterised by uniform bottom deposits, low hypolimnetic oxygen in summer and a fauna composed of a few species, is established below a depth of 6 m. The sediments on the floor of Newton Mere beyond a depth of 6 m are composed almost entirely of smooth dark brown mud mixed with varying amounts of organic matter, much of it finely shredded, or as twig and leaf fragments.

The substratum at the deepest point (Station 16 m) has a very distinctive character quite different from the other profundal sampling stations (12 m and 7.5 m). The sediments are paler brown and very sticky; balls of gelatinous matter lie mixed in the fine surface mud with twig fragments, much leafy material and the occasional battered Phryganea case. It seems that because of the shape of the basin, ie. the deepest point being central, water currents tend to carry materials down.

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Blake Mere

Blake Mere (SJ 416339) is an unfringed mere, 8 hectares in area, completely surrounded by mixed woodland (Plates 3.3 and 3.4) and lying in a deep drift hollow within the 300 ft (91.4 m) contour line (Fig. 3.3). A wide shallow ditch connects Blake to Kettle Mere, which is circular and 2 hectares in area. Surrounding the two meres and separating them, are peat deposits up to the 300 ft contour line, indicating that the area of open water might once have been substantially greater. There are no inflows, the water level being maintained by seepage and surface runoff.

Blake Mere comprises two basins, the larger being 13 m deep, the smaller 6 m deep. A ridge of grey glacial clay, coming to within less than 2 m of the water surface, separates the two basins.

There is no shore, and the banks frequently plunge steeply and treacherously into the mere. The east side merges into the slightly upraised peat platform separating Blake Mere and Kettle Mere and where indentations occur, they are filled with a semi-liquid mass of peat and decomposing leaves. Silver birch and ornamental rhodendendrons grow to the water's edge (Plate 3.3), in contrast to the west side where there is a bare, narrow towpath between the mere and the Shropshire Union Canal. A small patch of Iris pseudacorus L. and Sparganium minimum Hart. has managed to find a foothold in the SW corner of the mere. The canal flanks the south and west sides of Blake Mere but there is no connection with the mere. The northern end of Blake Mere merges with and is lost in a peat, alder and willow swamp.

The peat hollow in which Blake Mere lies is formed amongst glacial sand and gravel. At the SW corner, marked by the patch of Iris, a wedge of boulder clay interrupts the sandy drift. The surface soils which have formed post-glacially reflect the underlying drift. Brown Earths (Baschurch Series) cover the sand and gravel as at Newton Mere and Gley soils (Salop Series) overlie the boulder clay. Gley soils are non-

Plate 3.3 Blake Mere from the 6 m station showing typical vegetation along the bank

Plate 3.4 Blake Mere, looking north-east towards Kettle Mere

calcareous clay loams and indicate impeded drainage and an acid pH (Crompton and Osmund, 1954).

The sediments on the floor of the mere are varied and are considered to reflect the underlying drift. Peat deposits containing little mud are found at 3.5 and 9 m and are very homogenous in appearance with few twigs or leaves. At the deepest point of each basin, 6 and 13 m, the sediments are similar in being composed of fine silt with no trace of peat or coarse organic matter, except for strips of decomposing silver birch leaves.

On top of the ridge separating the two basins at 2 m, the substratum is coarse sand, pebbles of flint thickly covered with Cladophora, pieces of waterlogged wood and twigs. There is no trace of peat or silt.

Blake Mere is very secluded, set in its hollow amongst tall trees, not at all exposed to the prevailing winds. Its sheltered position is possibly the single most important factor in its physico-chemical environment, affecting primarily the temperature and oxygen regimes and thus the chironomid population. That Blake Mere has had a remarkably constant environment is indicated by a patch of the "glacial relic" Nuphar pumila Timm, a local plant in lakes of central and northern Scotland but found south of the border only in Merioneth and Shropshire (Clapham, Tutin and Warburg, 1968).

* *

Crose Mere

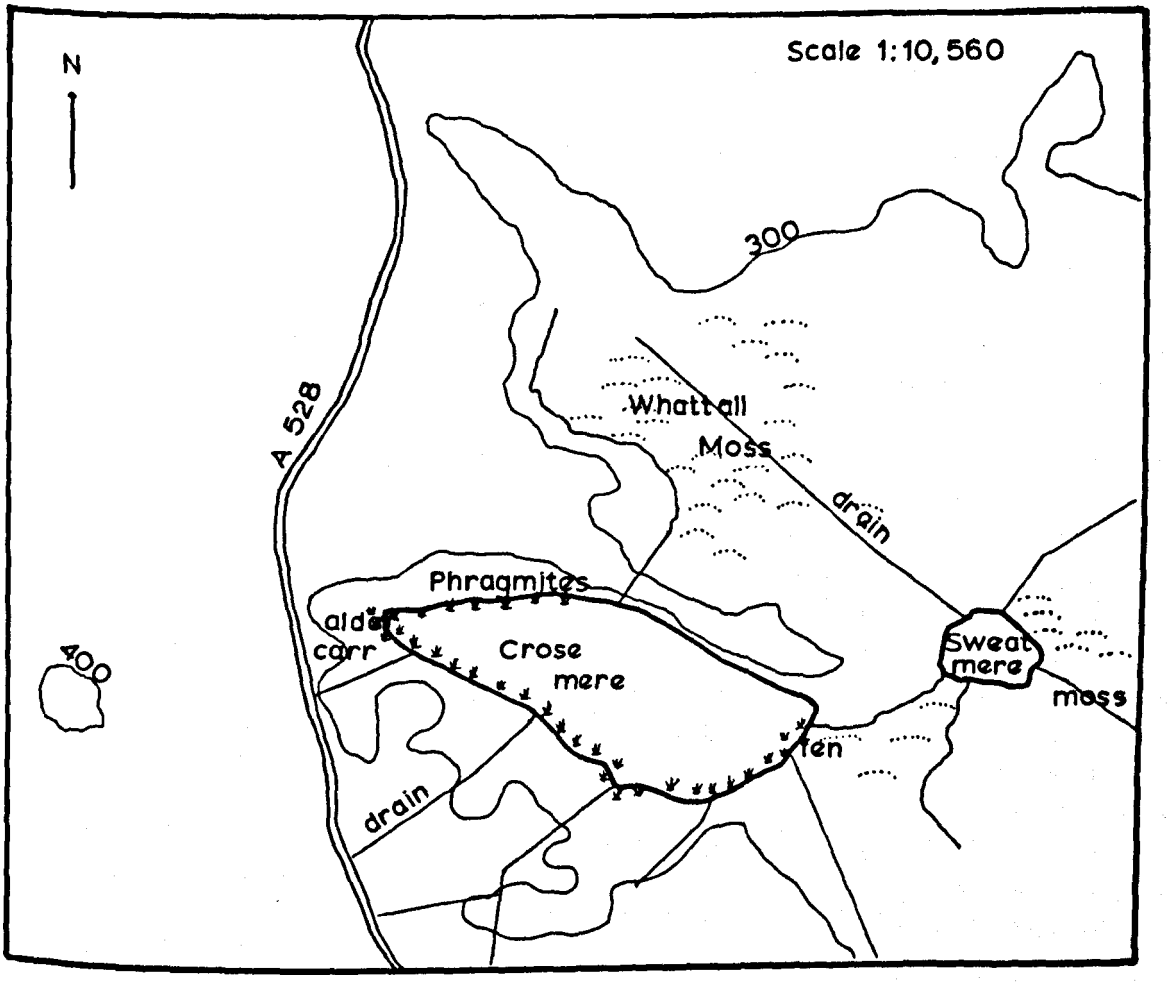
Crose Mere (SJ 435305) is the largest (15 hectares) of the three meres, the shallowest (9.2 m) and the most productive (Ca^{++} 63 mg/l). The basin is simple, oval-shaped and is orientated W-E (Fig. 3.4), thereby being the most exposed to the prevailing westerly winds. Crose Mere is also the only fringed mere in the group although the Phragmites beds are narrow and backed by peat, fen and fen/carr (Plate 3.5). Hardy (1939) reported that drainage operations on Whattall Moss (SJ 433310) in 1864 lowered the level of the mere by 4 m and Crose Mere now lies 285 ft. (86.8 m) above sea level. The former greater extent is marked by deposits of waterlogged peat around the shores up to 300 ft. except where a gravel ridge separating Crose Mere from Whattall Moss is exposed.

The basin lies entirely on sand and gravel, overlain by Brown Earths (Baschurch Series).

The drainage area of Crose Mere is more extensive than either Blake or Newton Mere and includes fields under arable cultivation as well as cattle pasture. There are several field ditches draining into the mere, one of which serves a cow byre and is heavily polluted with organic matter. A drainage culvert at the east end flows into Sweat Mere (Plate 3.6). The water level is maintained principally by deep percolation of ground water (Reynolds, 1975).

Crose Mere is the most thoroughly studied in the Ellesmere group and excellent descriptions of the general environment, flora and phytoplankton have been given by Gorham (1957); Griffiths (1925); Reynolds (1971a, b; (1973a, b; 1975) and Sinker (1962).

The sediments in Crose Mere range from large stones, coarse sand and gravel of the small "rocky" shore, through shelly, silty sand to brown mud containing large amounts of coarse organic matter. The substratum at the deeper stations is silty sand which is dark khaki in colour and



rough pasture

Figure 3.4 Sketch map of Crose Mere.

Plate 3.5 Crose Mere from the gravel bank
separating the mere from Whattall Moss
Note foreground area of drained land

Plate 3.6 Crose Mere, looking towards the fen
and the woods surrounding Sweat Mere.
Drainage culvert at northern edge of reeds.

which produces hydrogen sulphide in summer.

The shallowest station (2 m) has a sandy substratum overlain by decomposing Phragmites leaves, chunks of stalks and also twigs and pieces of waterlogged wood from the thin line of spindly alder trees growing behind the reeds. The sand contains large quantities of bleached mollusc shells as do all the substrata.

A littoral zone with emergent vegetation is clearly evident but because of the steeply shelving sides of the basin immediately beyond the littoral, the sublittoral is narrow.

* *

SECTION 2

A COMPARISON OF SOME OF THE PHYSICO-CHEMICAL FACTORS

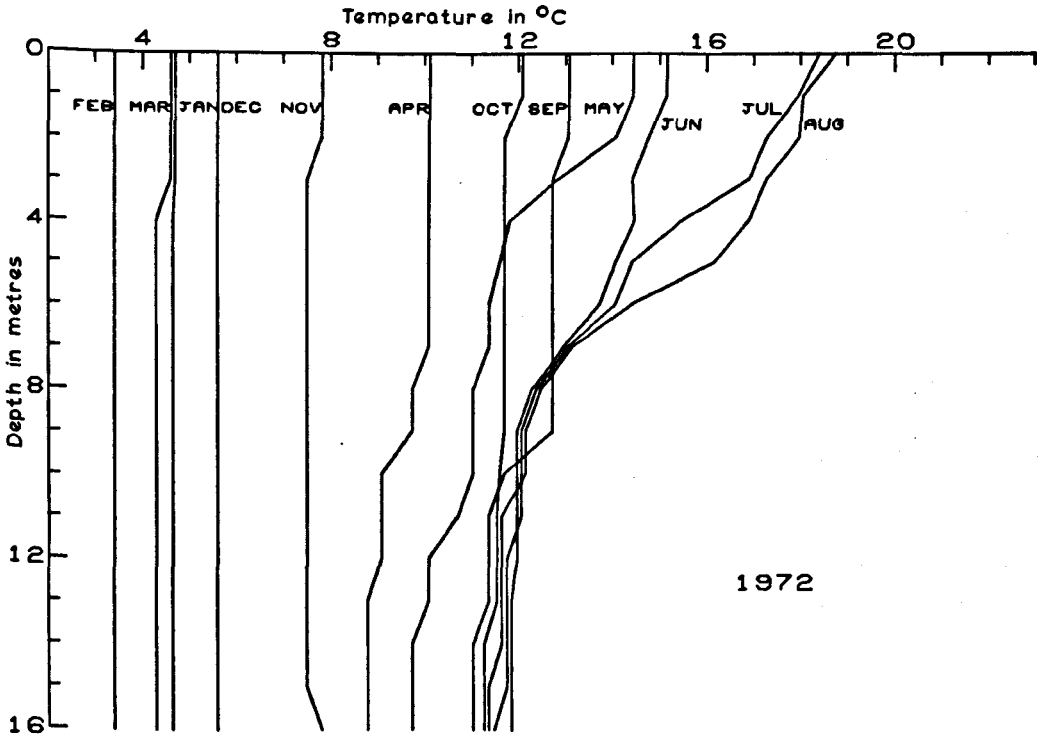
3.2.1 Temperature regimes

Temperature readings taken every month at each metre depth from the surface to the floor of each mere (Figs. 3.5, 3.6 and 3.7) show that the temperature range of the three meres is between 4 and 20°C throughout the year, although infrequent short periods outside this overall range have occurred (Appendix 1). This range classifies Newton Mere, Blake Mere and Crose Mere as warm monomictic lakes according to Hutchinson's (1957) definition.

Each mere follows the same general pattern of summer stratification and isothermal conditions in winter but the duration of each period differs markedly.

Newton Mere stratifies each Spring in May after being isothermal for at least 5 months during the winter. The mere begins to warm up steadily after February and once established, the thermocline persists until October when cooling of the surface waters lowers the thermocline and the hypolimnion is eroded. The thickness of the thermocline and its depth are dependent on temperature and the intensity of wind induced currents in the epilimnion. Once the thermocline has become established, the temperature of the hypolimnion rises very little - less than 2°C throughout the summer - remaining remarkably constant: 1972, 9.76 - 11.4°C; 1973, 8.5 - 10.4°C. Monthly differences throughout 1972 and 1973 of surface and bottom temperature at 16 m are shown in Fig. 3.8.

Fig. 3.10 shows that thermal stratification in Blake Mere develops by April and persists until the autumn overturn which occurs in November. Therefore during both 1972 and 1973, Blake Mere was stratified continuously for 7 months. The thermocline which develops is very stable and the metalimnion correspondingly deep, the greatest fall in temperature being



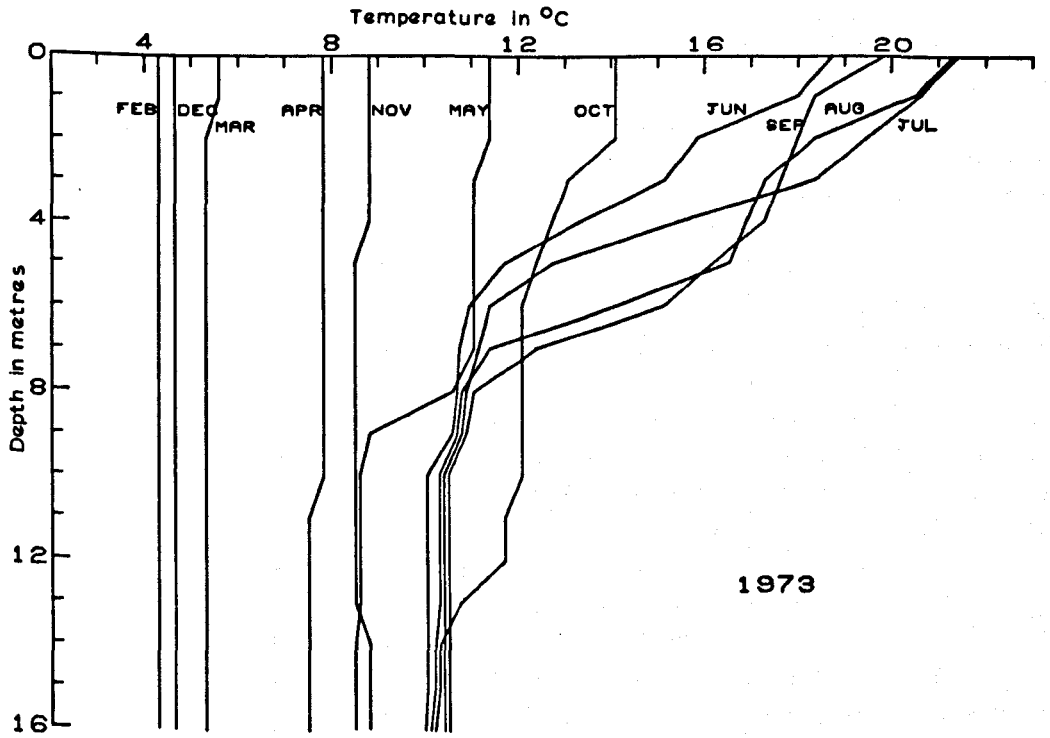


Figure 3.5 Temperature profiles during 1972 & 1973 in Newton Mere

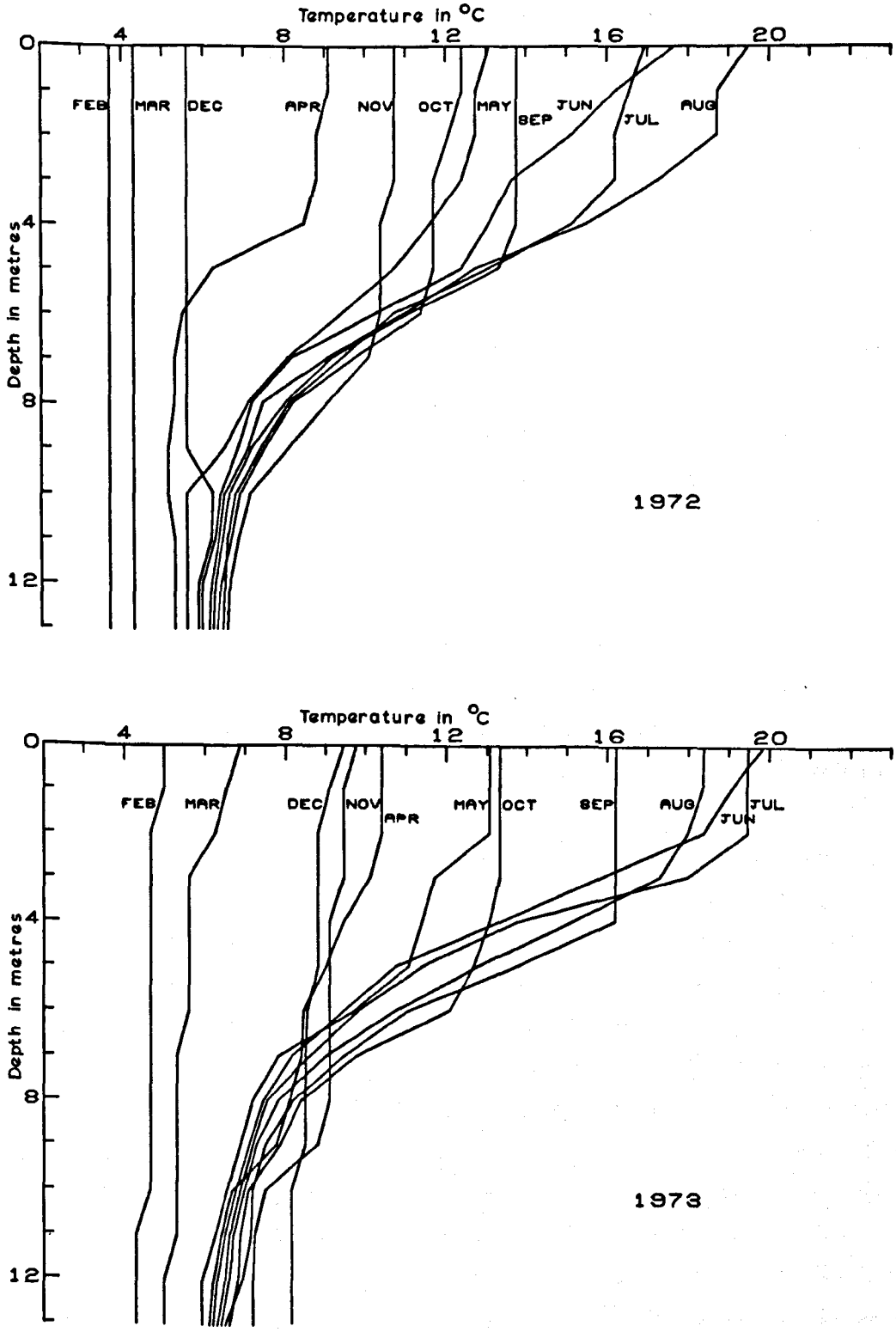


Figure 3.6 Temperature profiles during 1972 & 1973 in Blake Mere

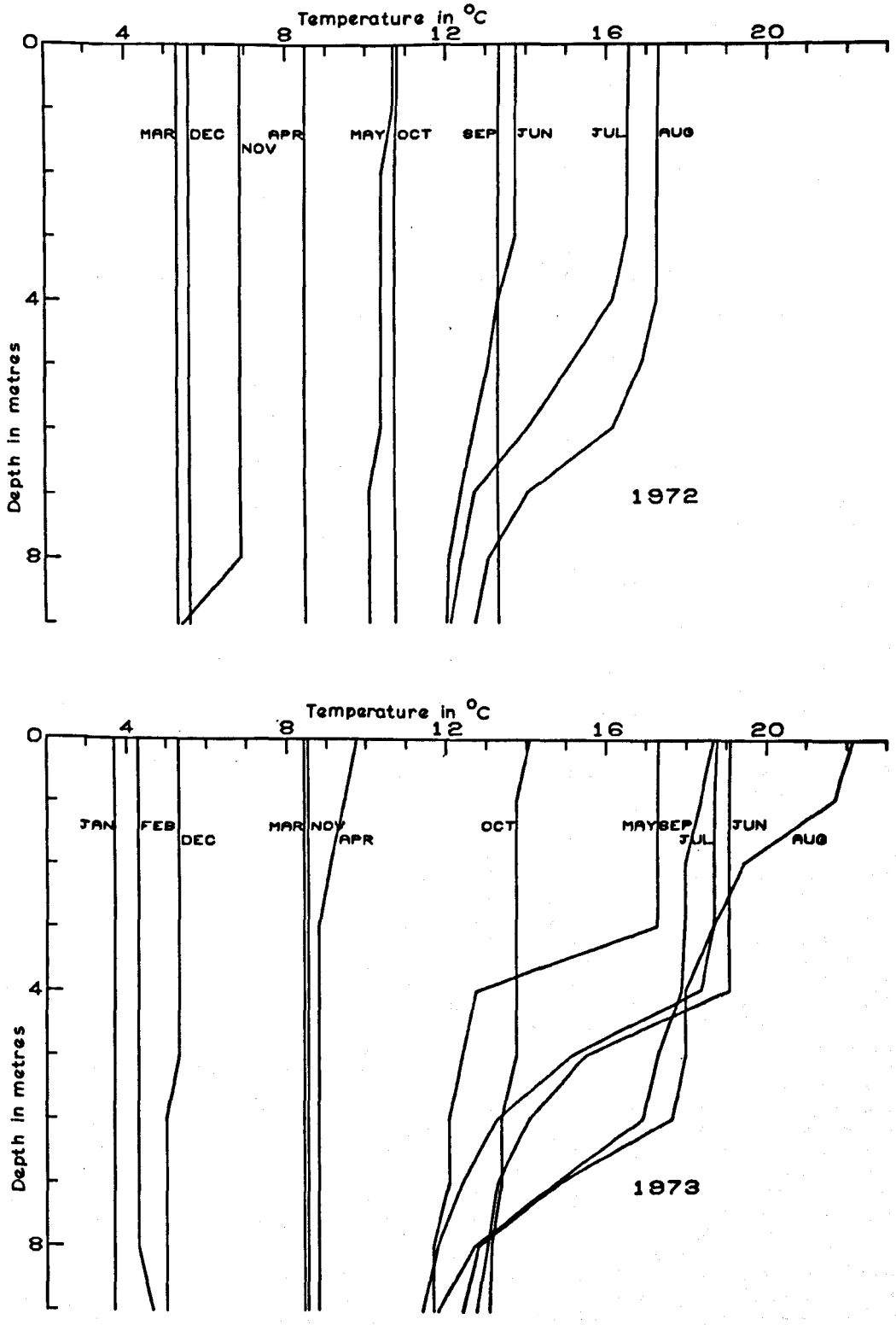


Figure 3.7 Temperature profiles during 1972 & 1973 in Crose Mere

in the 3 - 8 m zone. Unlike Newton Mere, the hypolimnion is not progressively eroded during the summer; on the contrary the metalimnion is eroded as the epilimnion cools, thus facilitating mixing. This is vital to Blake Mere, because the greater the disparity between epilimnion and hypolimnion temperatures, the more difficult it is for autumn gales to induce the overturn.

The mean temperature range at 13 m between February and November was 2.25°C, which is exceedingly narrow. Apart from two exceptional readings of 7.18 and 8.15°C for November and December, 1973, the temperature at 13 m hardly rose above 6.55°C even during summer.

When the mere finally turned over in November, 1973, the bottom water temperature began to rise as mixing occurred and resulted in the temperature for December being higher than in June. These continuous low temperature, "refrigerator" conditions have a disastrous effect on the potential chironomid population.

Readings were also taken in the smaller northern basin which show that although the two basins are virtually isolated from each other in summer, a similar pattern of stratification and overturn can be followed.

Despite its shallowness and exposed position, Crose Mere stratified in both 1972 and 1973, although not very successfully in 1972, as shown in Fig. 3.7. Following a very cold winter (1971-1972), the water took a long time to warm up and was still virtually isothermal in May. A violent storm in June kept Crose Mere freely circulating although there was a 2.04°C difference between surface and bottom water at 9.2 m (Fig. 3.12). A thermocline finally developed between 4.5 and 6.5 m during July but persisted only until early August when it was eroded and the mere returned to isothermal conditions.

Reynolds (MS, 1971) noted the vulnerability of Crose Mere to the prevailing winds and the tendency to appear polymictic, ie. short phases

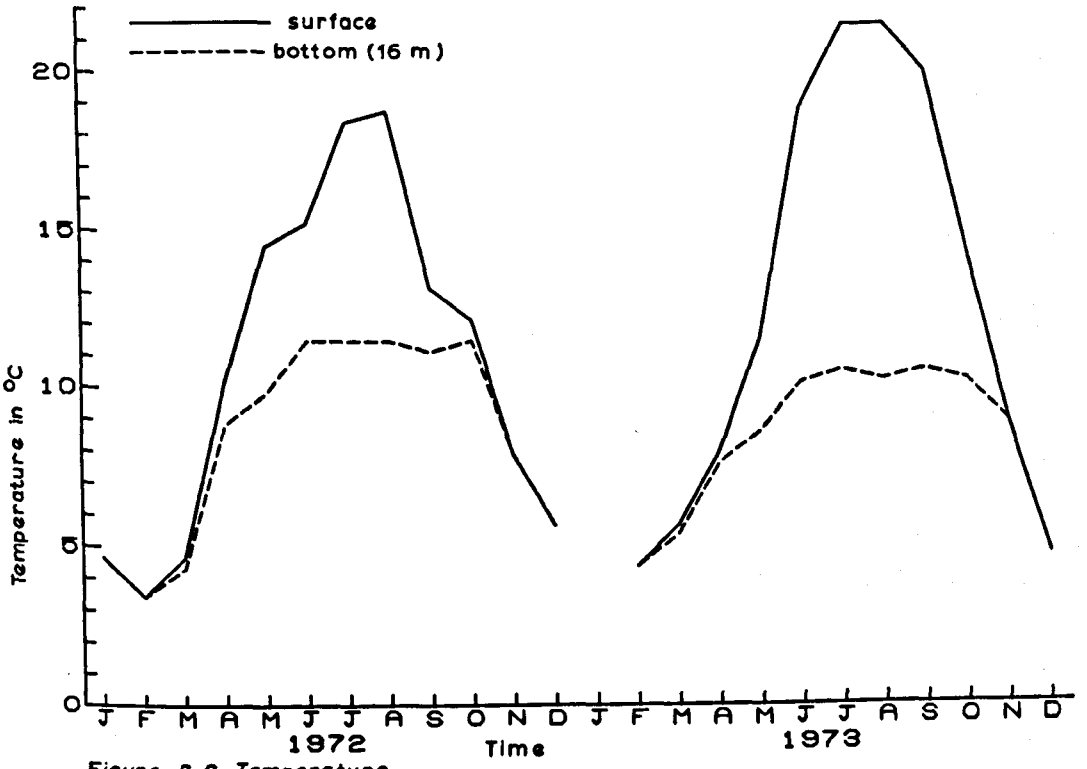


Figure 3.8 Temperature

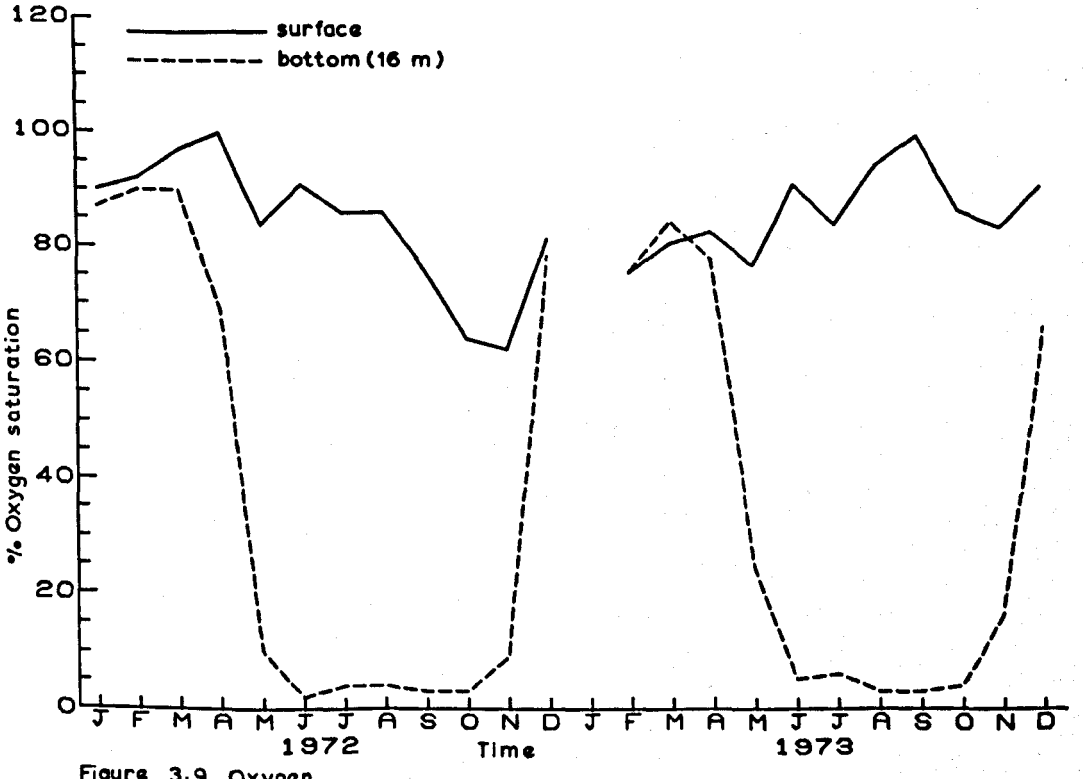


Figure 3.9 Oxygen

Figures 3.8 & 3.9 Newton Mere: surface and bottom temperature and oxygen values.

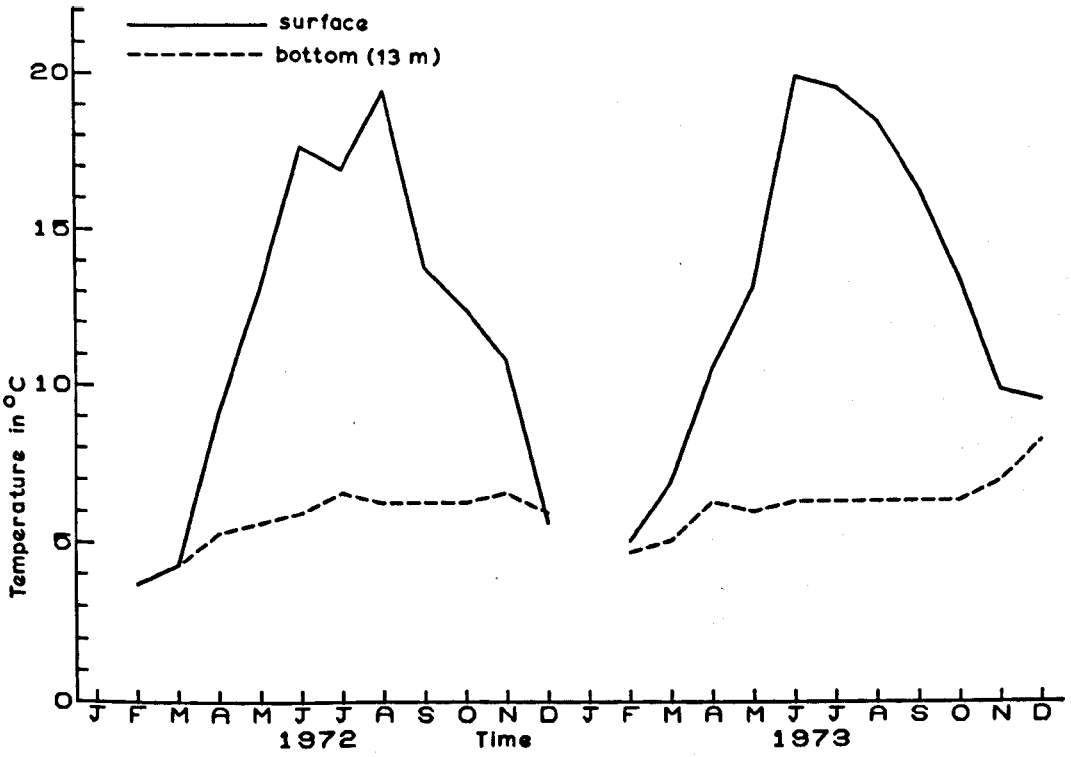


Figure 3.10 Temperature

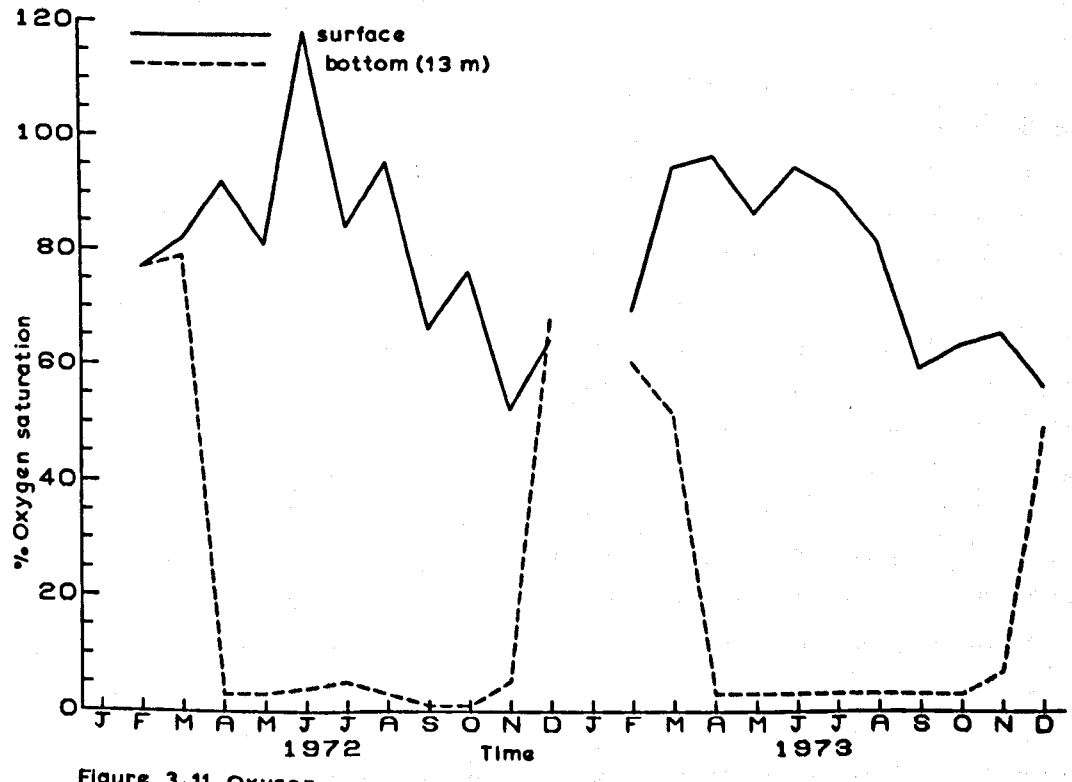


Figure 3.11 Oxygen

Figures 3.10 & 3.11 Blake Mere: surface and bottom temperature and oxygen values.

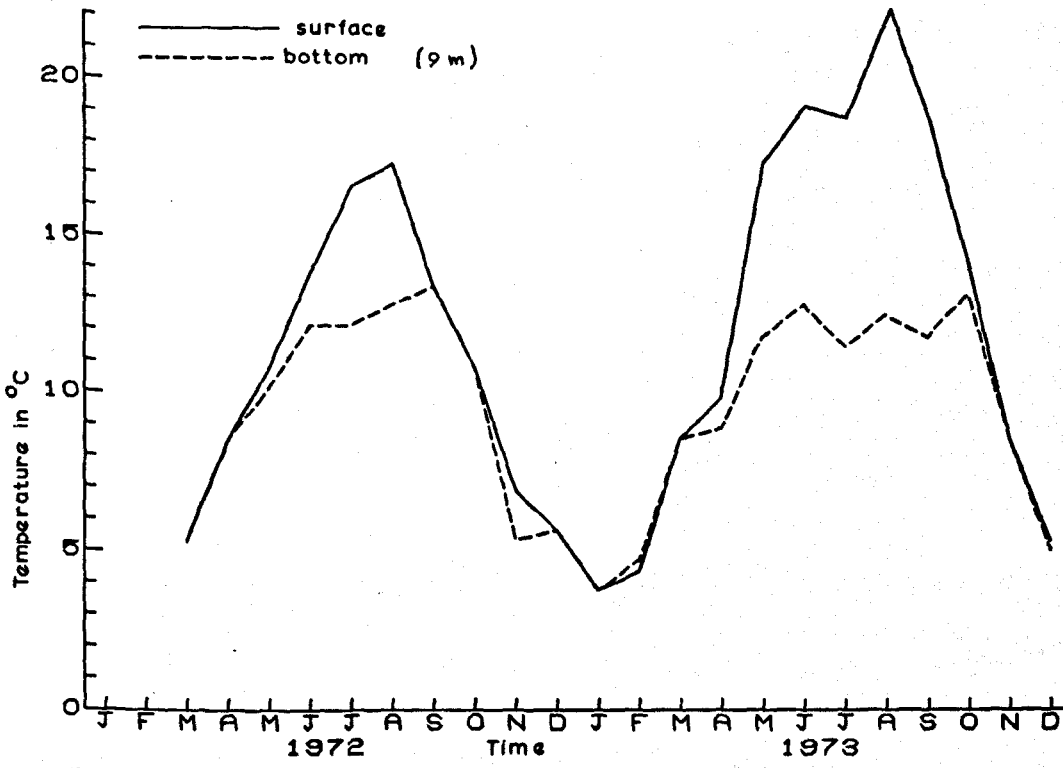


Figure 3.12 *Temperature*

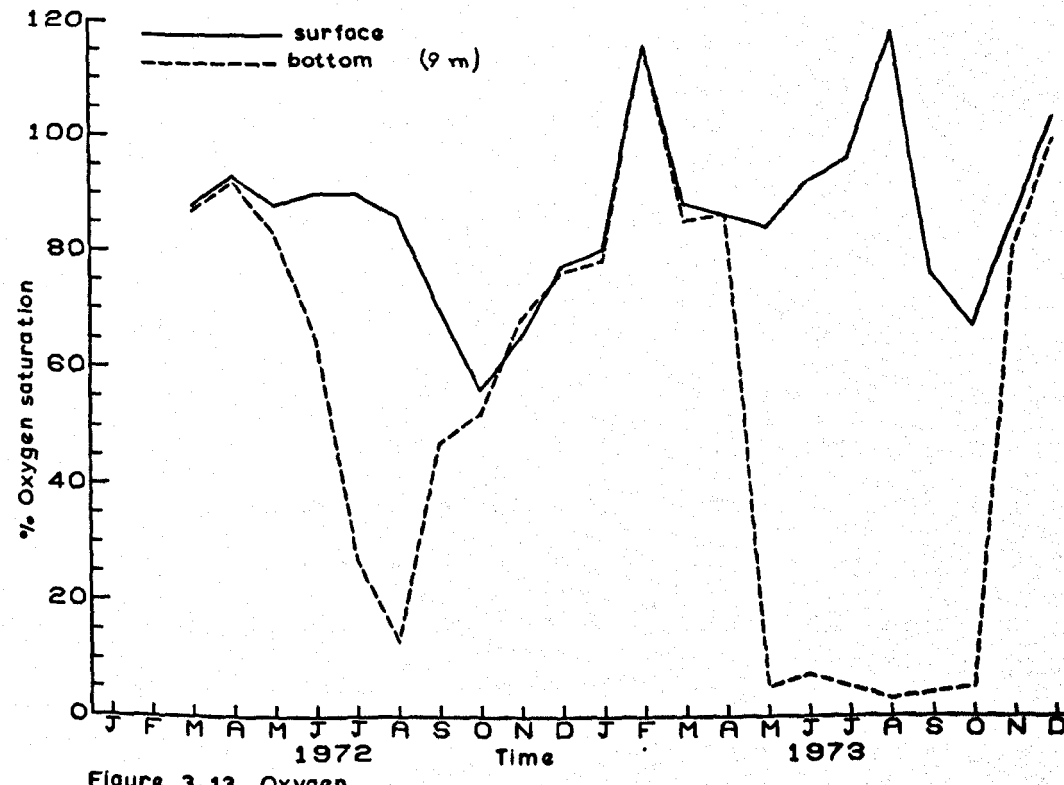


Figure 3.13 Oxygen

Figures 3.12 & 3.13 Crose Mere : surface and bottom temperature and oxygen values.

of stratification interspersed with free circulation. That Crose Mere is not polymictic can be seen from the data for 1973 in Appendix 1.

Profundal temperatures, because of the shallower depth of Crose Mere, were the warmest of the three meres, reaching a peak at 13.08^{o} in September 1972 and averaging 11.8^{o} each year. Reynolds (1975) believes that the variation in temperature at the bottom of the mere reflects the temperature of the ground water percolating through the sand and gravel.

3.2.2 Dissolved Oxygen

The distribution of dissolved oxygen in Newton Mere, Blake Mere and Crose Mere is "clinograde" according to Hutchinson's (1957) description of small productive lakes which lose oxygen from the hypolimnion during summer. During the winter months from December to March, the meres are fully oxygenated and freely circulating.

The fall in oxygen below the surface starts as soon as the meres begin to warm up, ie. after March, when a temperature differential exists between the surface and floor of the mere (Figs. 3.9, 3.11 and 3.13). The shape of the graph for eutrophic bottom waters has been described as a "trough" by Collins (F.B.A. Annual Scientific Meeting, 1974). The development and demise of the thermocline in each mere in 1973 and the corresponding oxygen levels can be seen in Figs. 3.14, 3.15 and 3.16.

The greatest drop in oxygen occurs between April and May in the profundal of Newton Mere as the mere begins to stratify, but the lowest oxygen conditions (less than 10%) do not set in before June. This month's "grace" has a significant effect on the chironomid population and will be discussed later.

The profundal zone of Blake Mere could well be described as an anaerobic "refrigerator". The monthly recordings of percentage oxygen saturation in Fig. 3.11 show that during the 7 months of thermal stratification, oxygen levels were below 10%. Oxygen levels plummetted

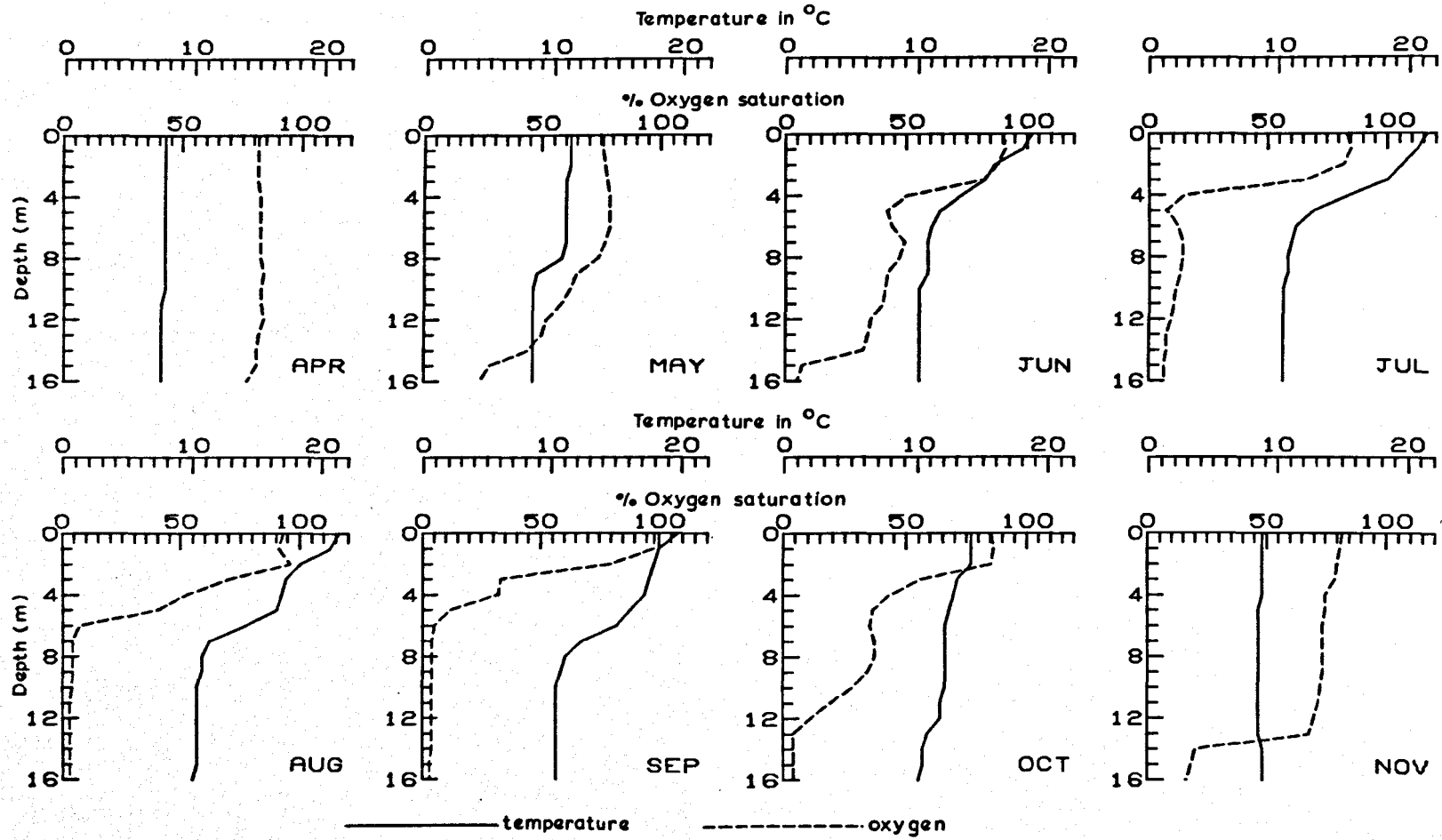


Figure 3.14 Newton Mere 1973: development and demise of the thermocline.

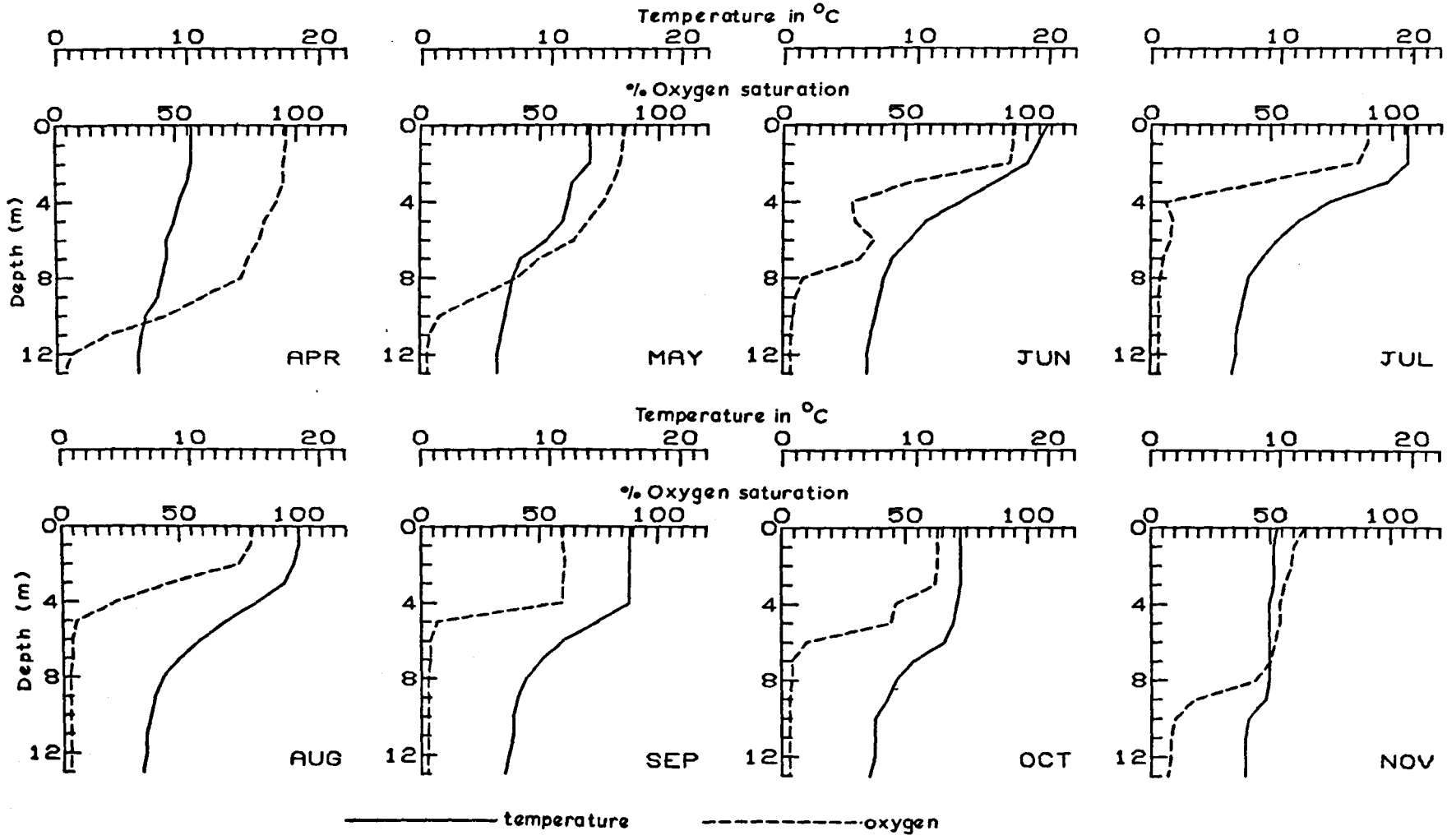


Figure 3.15 Blake Mere 1973 : development and demise of the thermocline.

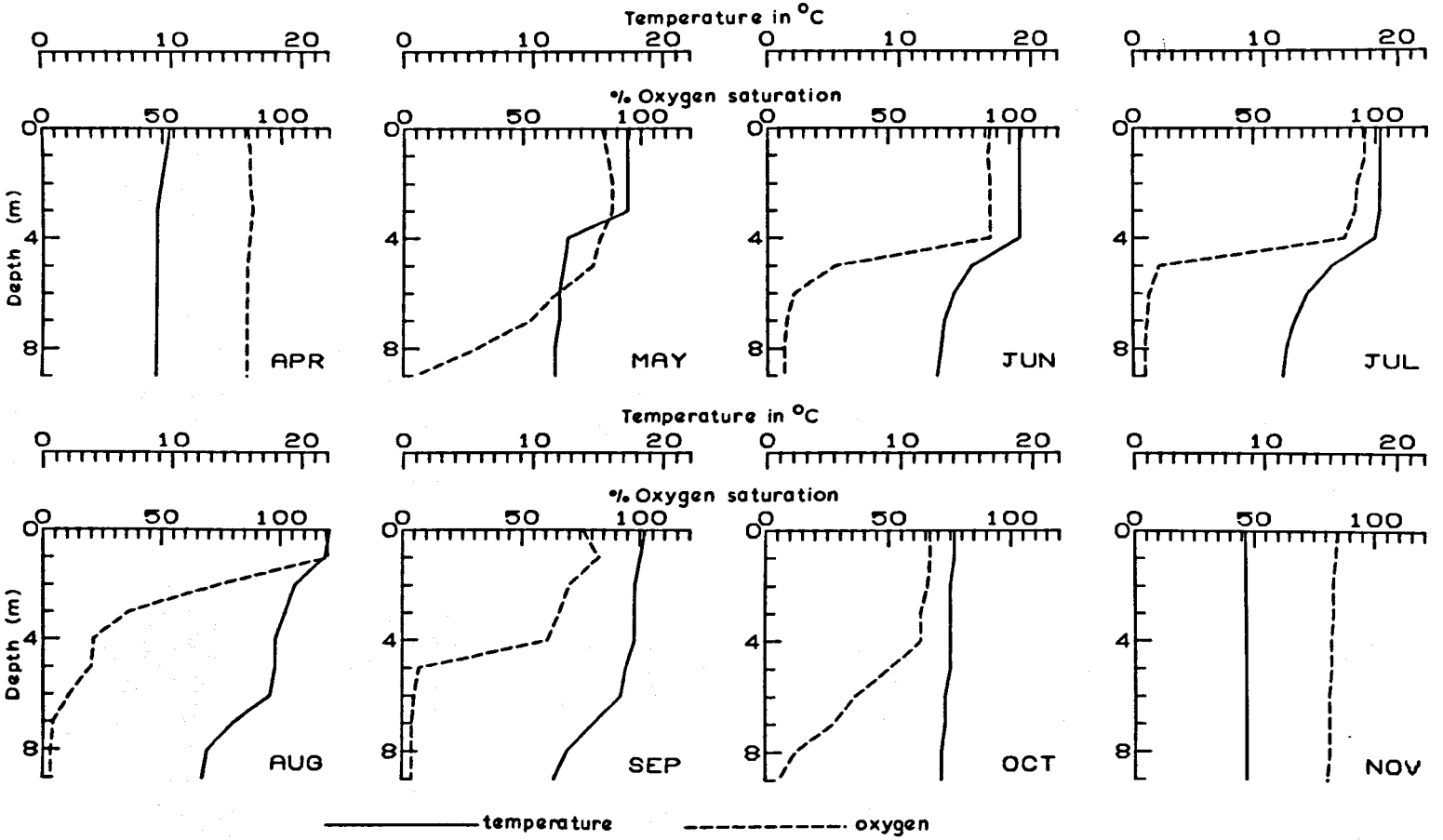


Figure 3.16 Crose Mere 1973 : development and demise of the thermocline.

between March and April 1972, from 79% to 3%, with the onset of stratification and remained low until the overturn in November, when the mere returned to isothermal conditions. A similar fall occurred in the spring of 1973 but not so spectacularily, as levels had begun to fall after February. This sudden drop in oxygen during the spring, and the long summer stratification also has an adverse effect on the chironomid population. The consequences of the combination of low temperatures and low oxygen levels will be discussed later.

The surface levels for percentage oxygen saturation vary according to the local weather conditions, high levels being reached on calm days when an algal bloom occurred.

Fig. 3.13 shows that despite freely circulating conditions during spring and early summer in 1972 at Crose Mere, oxygen levels began to fall at 9 m after April. The mere did not stratify until July and so the fall in oxygen would seem to be initiated by the rise in temperature. The period of low oxygen conditions, represented by the trough was of 5 months duration in 1973, indicating how stable the anticyclonic weather conditions were that year.

3.2.3(i) pH

The data collected show that during summer stratification in each mere, a pH gradient exists from surface to bottom and the deeper the water, the more acid was the reaction. The pH of the profundal waters begins to fall concurrently with the decline in O_2, although this fall is more marked in the less eutrophic Newton Mere and Blake Mere which are poorly buffered. The fall in pH from the epilimnion to the hypolimnion in lakes with a clinograde distribution of oxygen is well known (Strøm, 1933; Ohle, 1934). If the water is poorly buffered, then any CO_2 liberated into the water will produce a reduction in the pH.

During the winter months, however, when the meres are isothermal, there is no pH gradient as the waters are freely circulating, eg. Newton Mere, Dec. 1972: surface - pH 6.1; 16m - pH 6.0.

Monthly variations in surface values are affected by the pattern of phytoplankton production. A bloom on Crose Mere (July, 1973) raised the pH to 8.9 and another on Newton Mere (Sept. 1973) resulted in the pH increasing to 9.3 from 7.1.

The monthly variations for each mere in pH at the surface and the deepest station are presented in Figs. 3.17, 3.19 and 3.21, and show that Newton Mere is acidic, Blake Mere is neutral to slightly acidic and Crose Mere, with a range between 7.7 and 8.05 is alkaline. Compared with the ranges for the other two meres (Newton Mere: 5.8-9.3; Blake Mere: 5.9-9.3), Crose Mere has a narrow range which is due to buffering by bicarbonate ions.

The generally lower pH values in seepage lakes such as Newton Mere and Blake Mere is attributed to the absorption of metallic cations, either in peaty organic matter in the basin (Williams and Thompson, 1936), or in some cases, by clay minerals in the soil, (Gorham, 1955).

Occasionally, the pH in the profundal of Newton Mere rose during summer stratification. In a hypolimnion considerably deficient in oxygen, diffusion of ferrous and manganous bicarbonates from the sediments raises the bicarbonate alkalinity and thus buffers the water, causing an increase in pH. Occasionally, an acid heterograde curve may result (Yoshimura, 1932; Juday, Birge and Meloche, 1935), as on August 15, 1973 when the deepest water had a higher pH than the rest of the profundal.

3.2.3(ii) The effect of three pH conditions on larvae of Chironomus anthracinus and Procladius choreus

A brief experiment on the effect on survival of Chironomus anthracinus and Procladius choreus larvae under three different pH conditions revealed that a higher percentage of anthracinus larvae survived at pH 7 than at pH 4 or 9 and that a higher percentage of choreus larvae survived at pH 4 than at 7 or 9, (Table 3.1).

No anthracinus larvae survived pH 4 and only 2 of the original 15 were left after 96 hrs. in water of pH 9. A comparison of the two sets of results indicates that choreus larvae appear to be more tolerant than anthracinus larvae to the extremes of pH, and this supports observations made in the field that choreus is a ubiquitous species able to colonise a wide range of habitats.

The results obtained for anthracinus larvae support field observations rather better than do those for choreus. In the field it was found that Crose Mere, the most alkaline mere, supported the highest population of choreus larvae, whereas in the experiment, choreus survived best in the low acid conditions. None of the meres studied were as low as pH 4 but choreus larvae were found in an acid pool (pH 5) in Brown Moss, Whitchurch.

However, pH is not considered now to be a major ecological factor which can determine distribution of fauna. Macan and Worthington (1972) state that pH ".. gives only a rough indication of conditions obtaining in a body of water." However, Shires (1976, in press) believes that the pH of certain tributaries in the North Tyne river system is a causal factor in the distribution of Ephemeroptera.

Table 3.1 Results of expt. into effects of pH conditions on larvae of Chironomus anthracinus and Procladius choreus

	Chironomus anthracinus (nos. alive)					%	Procladius choreus (nos. alive)				%
pH/hrs	0	24	48	72	96	survival	0	24	48	72	survival
4	15	10	3	0	0	0%	7	7	6	6	86%
7	15	15	15	12	10	67%	7	7	7	4	57%
9	15	15	15	10	2	13%	7	7	5	4	57%

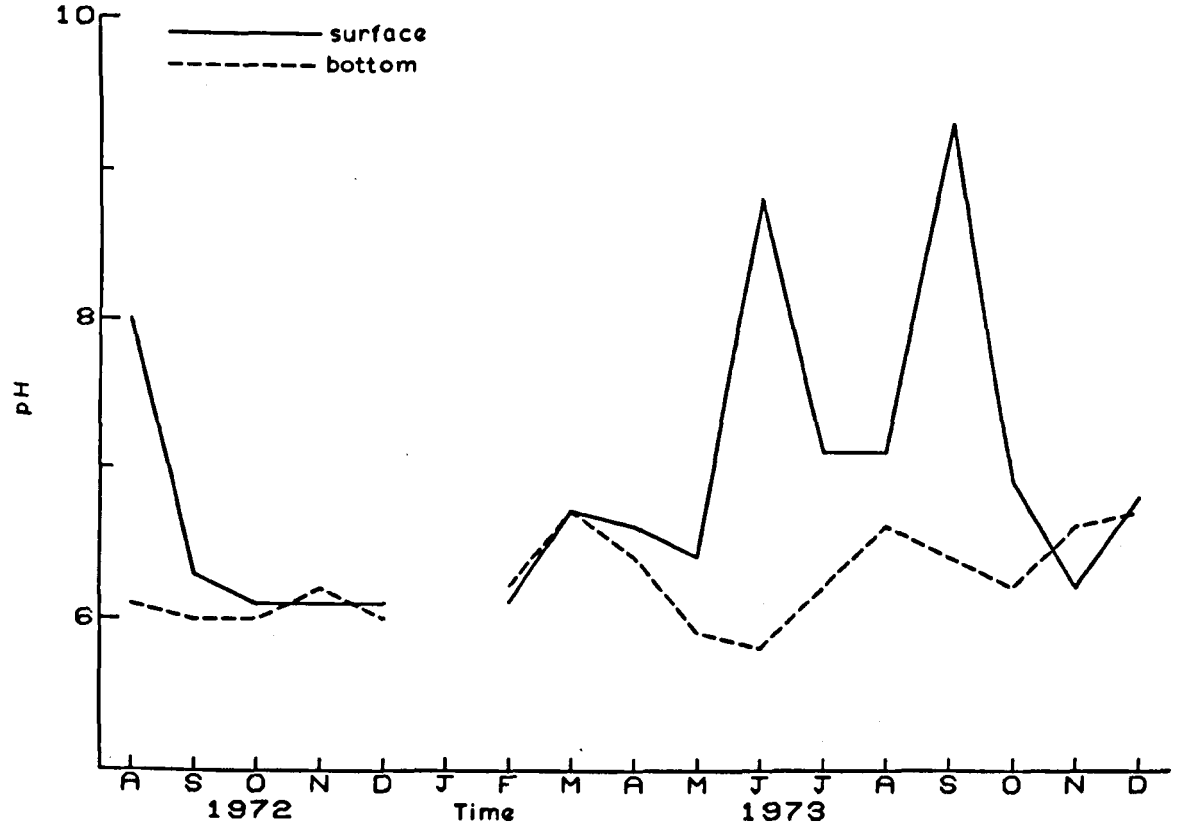


Figure 3.17 pH

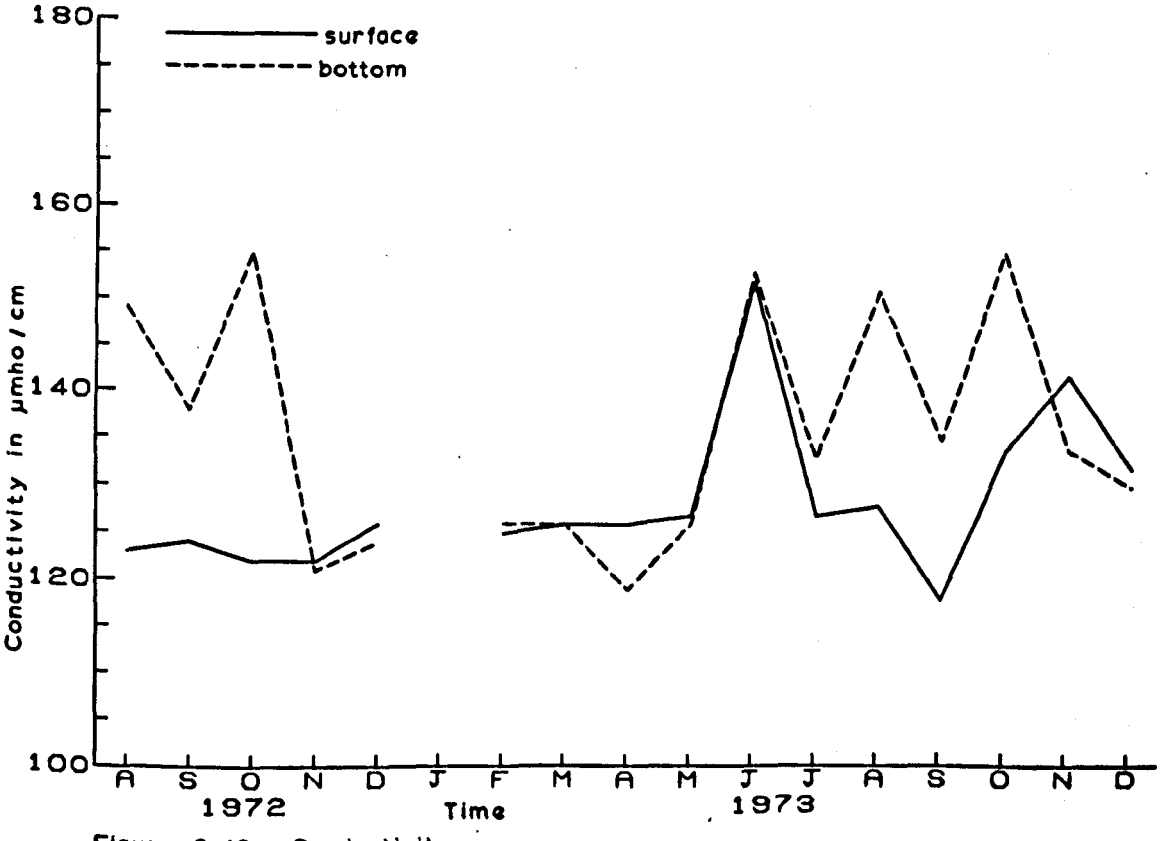


Figure 3.18 Conductivity

Figures 3.17 & 3.18 Newton Mere : surface and bottom pH and conductivity values.

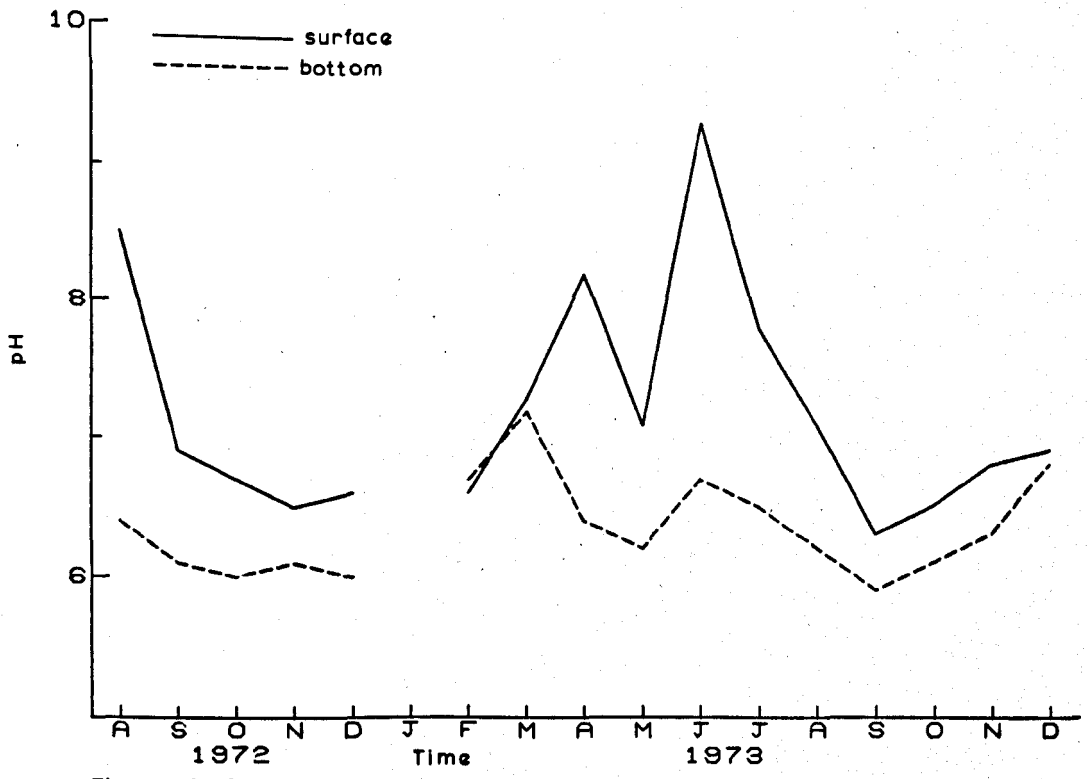


Figure 3.19 pH

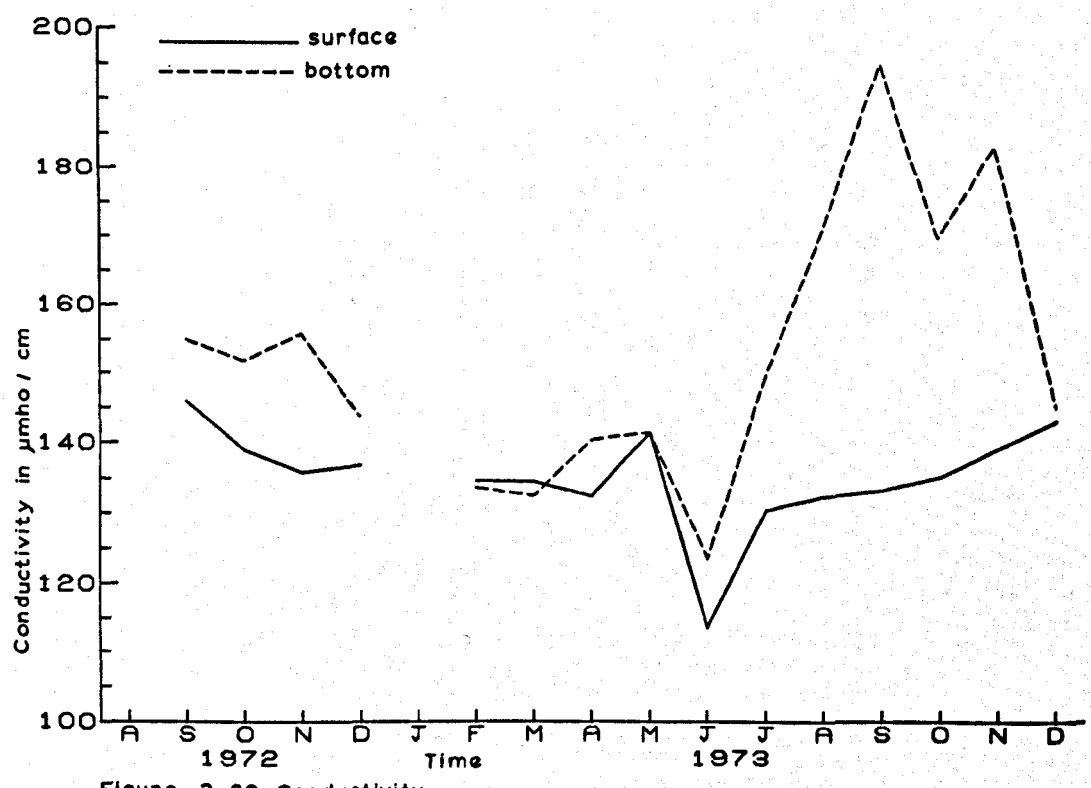


Figure 3.20 Conductivity

Figures 3.19 & 3.20 Blake Mere: surface and bottom pH and conductivity values.

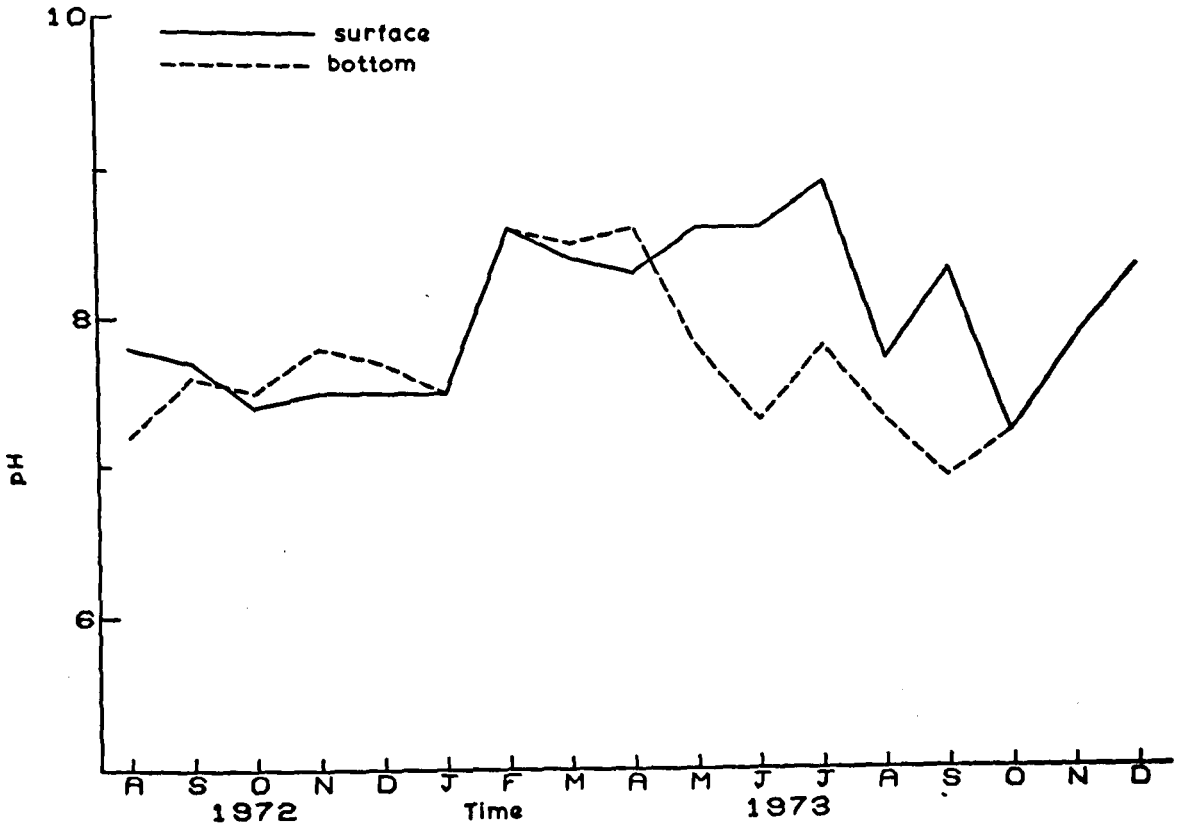


Figure 3.21 pH

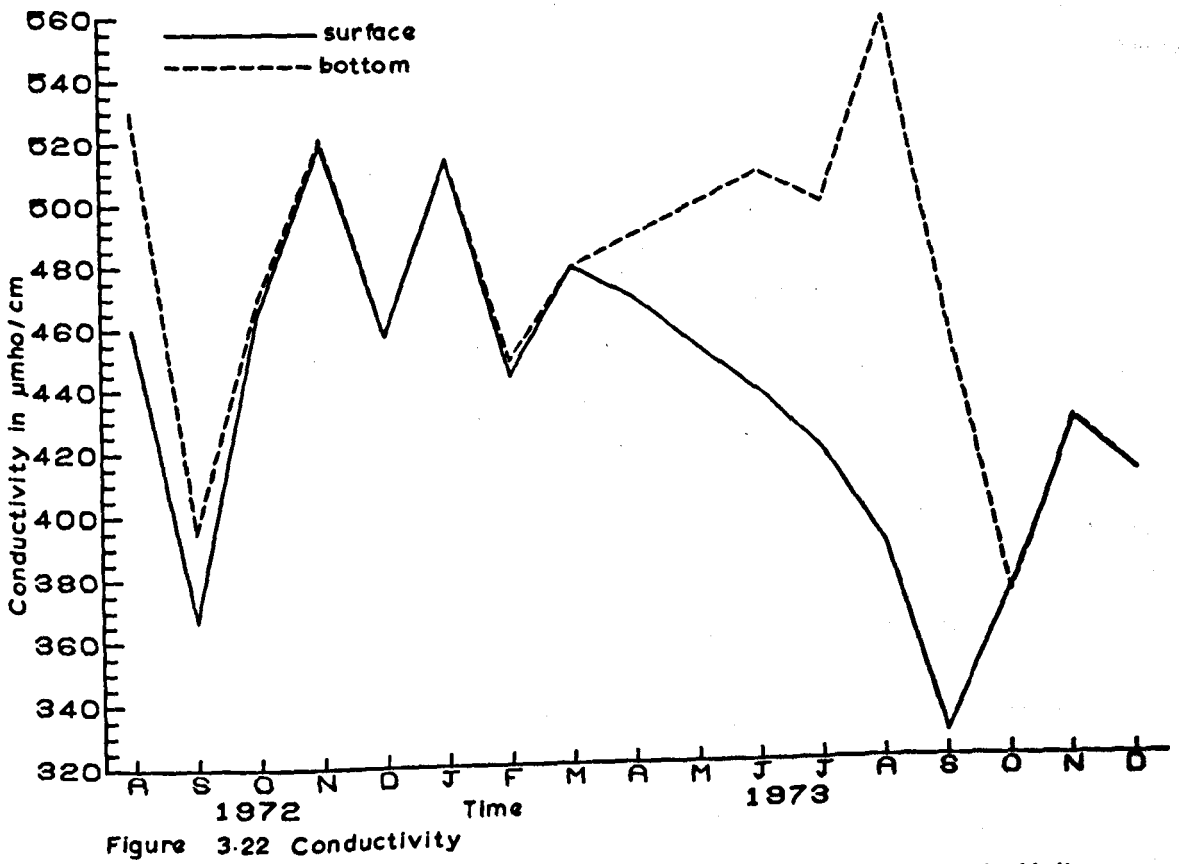


Figure 3.22 Conductivity

Figures 3.21 & 3.22 Crose Mere: surface and bottom pH and conductivity values.

3.2.4 Specific conductivity

The monthly fluctuations in specific conductivity of the three meres (Figs. 3.18, 3.20 and 3.22) reflect the ionic content and productivity. Gorham (1957) showed Newton Mere to be the most dilute of the Ellesmere meres (Total salts: 1.06 - 1.08 m.eq/l) and present data show that this is still the case (range: 100 - 170 µmho/cm). A range between 112 and 195 µmho/cm for Blake Mere indicates low to medium productivity compared with the far higher range for eutrophic Crose Mere (328 - 560 µmho/cm).

When the meres are freely circulating in winter, there is no significant difference between surface waters and those of the profundal, eg. Dec. 13, 1972, Crose Mere: surface - 458 µmho/cm; 9 m - 458 µmho/cm. As summer stratification develops, so the conductivity increases in the hypolimnion, eg. Aug. 15, 1973, Crose Mere: surface - 390 µmho/cm; 9 m - 560 µmho/cm. This increase is due to the liberation of ions under low oxygen conditions, as described by Mortimer (1941, 1942). This supports the suggestion made in the preceding section that the increase in pH at the deepest points was due to an increase in bicarbonates.

Heavy algal blooms can reduce the conductivity markedly, due to the algae utilising available ions. The fall usually coincides with an increase in alkalinity because of the uptake of CO_2 by the algae. On Crose Mere during spring and summer of 1973, the conductivity of the surface and shallow water fell continuously from 480 to 328 µmho/cm due to ion uptake by phytoplankton.

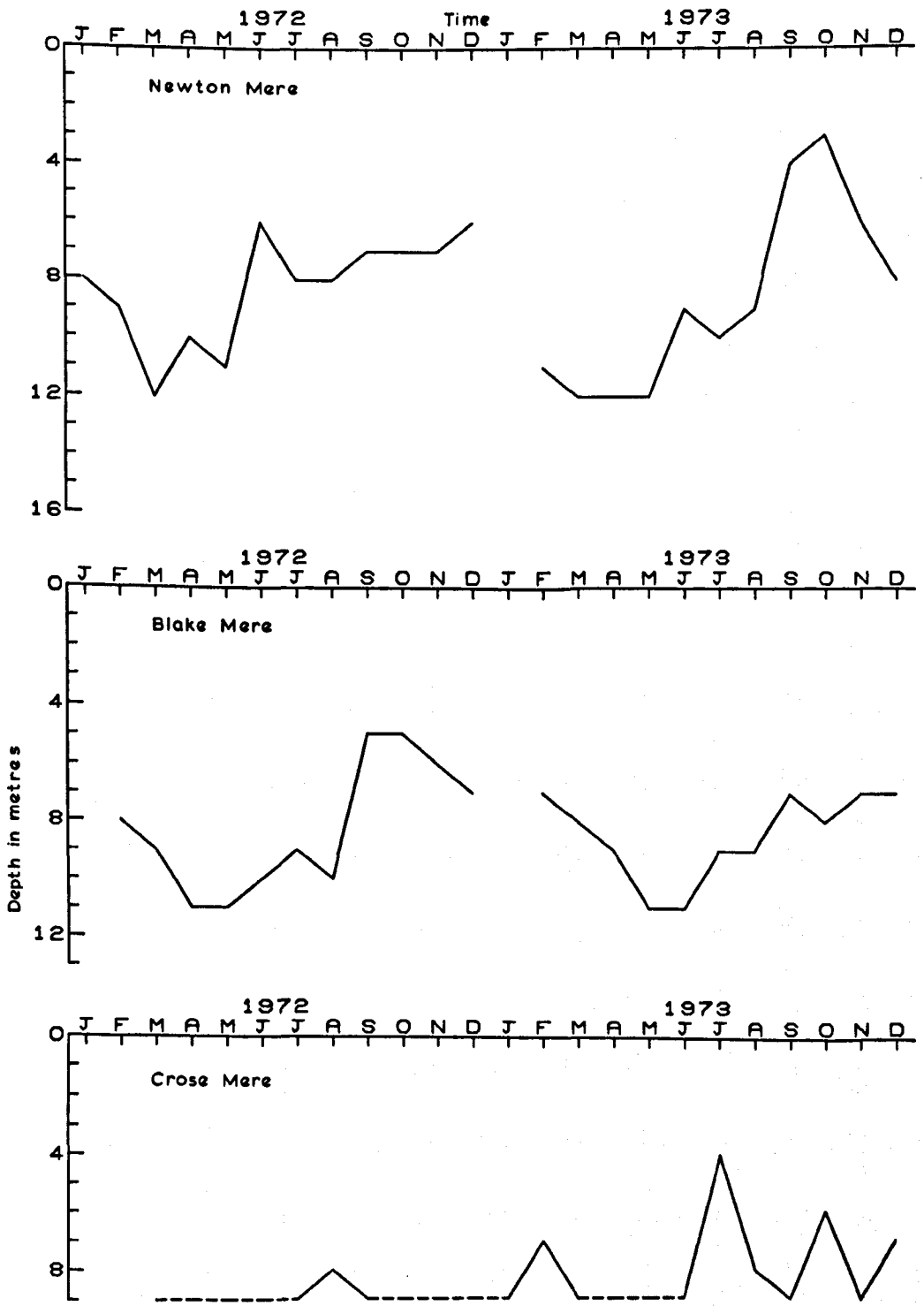


Figure 3.23 Light penetration in Newton Mere, Blake Mere and Crose Mere. Each reading equals 0 lumens/ ft^2.

3.2.5 Light Intensity and Light Penetration

Light intensity measurements were taken to ascertain the penetration depth of sunlight. However, the limitations of the light meter used must be recognised; i.e. a recording of 0 lumens/ft^2 indicates the limit of light measurable by that meter and not the absolute limit of light penetration.

Crose Mere is the shallowest mere and light generally was measurable at the deepest point except on particularly overcast and dull days or when there was a heavy bloom. Light measurable by the EEL meter never penetrated to the deepest point in either Newton or Blake Mere but generally Newton Mere was more transparent presumably due to less suspended solids. The period of maximum transparency in these two latter meres was during the spring months of March, April and May which coincided with the main period of pupal development and emergence of adult chironomids from the profundal.

Jónasson (1970) records a discussion between himself and Varley, in which it was suggested that light is the immediate mechanism for the diurnal emergence of chironomid pupae to the surface.

Fig. 3.23 presents light penetration data for Newton Mere, Blake Mere and Crose Mere during 1972 and 1973. The graphs represent the depth each month at which a recording of 0 lumens/ft^2 was taken with the EEL meter.

3.2.6 Calcium and Magnesium

Calcium is probably the most variable ion in freshwaters, thus enabling a distinction to be made between hard and soft waters and the related distribution of fauna. Macan (1963) suggested that calcium works indirectly on freshwater fauna through its correlation with productivity and the amount of organic matter decomposing in a lake.

Using Macan's (1955) definition of "hard", "intermediate" and "soft" waters (Tables 3.2 and 3.3), Newton Mere has soft - intermediate water, Blake Mere is intermediate and Crose Mere has hard water. These descriptions complement Reynoldson's (1966) classification of lake productivity relative to the calcium content, as shown in Table 3.4.

Table 3.2 also presents the fluctuations in the calcium and magnesium content during stratified and isothermal conditions in each mere at the surface and at the deepest point of each mere. The data show that the concentration of calcium and magnesium increases in the hypolimnion during summer relative to the epilimnion but that when isothermal conditions return, there is little difference throughout the lake; indeed, profundal waters appear to be slightly more dilute during winter.

Gorham (1957) stated that calcium was the dominant cation, followed by magnesium in all the Ellesmere meres except Newton Mere in which chlorides and sulphates exceeded calcium. The ratios Ca:Mg have remained virtually as Gorham found them, with perhaps a slight increase in calcium in Blake Mere.

In view of the general similarities of bicarbonate waters, Rodhe (1949) determined the relationship between total salinity, the standard composition (which included calcium and magnesium) and specific conductivity. Table 3.3 presents a comparison between the observed range of calcium, magnesium and conductivity for each mere calculated from samples taken between May and December 1973, and the expected range, as determined by Rodhe.

The upper limit for observed calcium and magnesium in Crose Mere goes higher than the expected range, as Rodhe calculated the standard composition for waters only up to 400 µmho/cm. Nevertheless, the observed calcium and magnesium range fit the expected Crose Mere range

Table 3.2 Concentrations of Ca and Mg in mg/l at two depths in Crose Mere, Blake Mere and Newton Mere during stratified and unstratified (isothermal) conditions.

	July, 1973 (Stratified)		December, 1973 (Isothermal)	
	Ca	Mg	Ca	Mg
Crose Mere:				
surface	57.00	10.00	55.00	11.40
profundal	69.00	10.50	55.00	11.30
Blake Mere:				
surface	10.60	1.88	10.10	1.90
profundal	14.30	2.70	9.75	1.82
Newton Mere:				
surface	6.55	1.76	5.70	1.40
profundal	7.55	1.90	5.85	1.45

Table 3.3 Observed range in mg/l of Ca and Mg in Crose Mere, Blake Mere and Newton Mere compared with the expected range related to total conductivity in μmho/cm, as given by Rodhe (1949).

	Ca		Mg		μmho/cm
	observed	expected	observed	expected	range
Crose Mere	50.0-72.2	46.4-59.0	8.8-11.6	7.8-9.9	328-560
Blake Mere	8.0-15.0	13.5-28.1	1.4- 2.80	2.3-4.7	112-195
Newton Mere	3.3- 9.2	13.5-22.0	1.1- 1.90	2.3-3.7	108-165

Table 3.4 Mean concentration in mg/l of Ca and Mg in Crose Mere, Blake Mere and Newton Mere, Lake Esrom (Denmark) and some highland Cumbrian lakes. Data for Lake Esrom, Esthwaite, Windermere S. and Buttermere adapted from Macan (1970). Productivity classification adapted from Reynoldson (1966).

	Ca	Mg	Productivity
Crose Mere	60.50	10.30	very high
Lake Esrom	42.00	5.60	very high
Blake Mere	11.11	1.89	high
Esthwaite	8.30	3.50	intermediate
Newton Mere	6.46	1.51	intermediate
Windermere S.	6.20	0.70	intermediate
Buttermere	2.10	0.72	very low

quite closely. The same cannot be said for either Blake Mere or Newton Mere (although there is a small overlap with the Blake Mere data) as the observed range is well below the expected range. A possible explanation for this discrepancy could lie in the lithology of the drainage area of the latter two meres, which are both atypical, being isolated with no inflows and with restricted drainage areas.

There is always the danger of not putting lakes in their true perspective and to avoid this pitfall, Table 3.4 presents the mean concentration of calcium and magnesium in these three Shropshire meres, Lake Esrom in Denmark and a selection of highland Cumbrian lakes, ranging from the extremely dilute Buttermere to the eutrophic Esthwaite. An adaptation of Reynoldson's (1966) classification of productivity according to the calcium content is included for further comparison.

Although Newton Mere is considered dilute in relation to the other Shropshire meres, in fact, it is more concentrated than the eutrophic southern basin of Windermere. Blake Mere, considered to be comparable to Newton Mere, is in fact highly productive and quite calcareous, having a higher concentration than the eutrophic Esthwaite.

The table confirms that not only is Crose Mere the most calcareous of all the lakes listed, but is also one of the most eutrophic lakes in Britain.

3.2.7 Hydrogen Sulphide

Profundal sediments of warm monomictic lakes often produce hydrogen sulphide during low oxygen conditions in the hypolimnion. H_2S is freely soluble in water and behaves as a weak acid. Usually free H_2S is fixed as ferrous sulphide which is insoluble in neutral or alkaline waters, but if the production of H_2S is in excess of iron, or if stratification is prolonged and organic matter sedimented in the hypolimnion, then appreciable amounts of H_2S are found in deeper zones.

The sediments of all three meres produce H_2S although in varying amounts as shown in Table 3.5. Production was negligible in Newton Mere and although tested for each month, the gas was detectable only during April 1973. Taylor (1958) states that ".. the most delicate test for the presence of this gas is given by its odour". Although oxygen levels were lower after April in Newton Mere, no H_2S could be smelled when profundal mud samples were brought to the surface. This contrasted markedly to collecting in Crose Mere, when mud samples were accompanied to the surface by an overpowering stench of "rotten eggs".

Detection of H_2S from profundal sediments in Blake Mere was intermittant, although levels were appreciably higher than in Newton Mere during the same period.

Levels of H_2S in Crose Mere were higher than in Newton Mere or Blake Mere and the gas was detectable over a longer period which included thermal stratification in 1973. Levels were consistently higher at 9 m ($\bar{x}$ of 2.44 mg/l) than any other station, reaching a peak of 6.02 mg/l in July, although sediments at 2 m, off the Phragmites zone, produced on average (2.18 mg/l) almost as much gas. This is thought to be due to the thick layers of undisturbed organic matter lying along the shores.

Sulphides are present in natural waters as a result of bacterial

Table 3.5 Concentrations of H_2S in mg/l at two depths in Newton Mere, Blake Mere and Crose Mere during part of 1973.

	mg/l Hydrogen sulphide				
Mere / Month	March	April	May	July	September
Newton Mere:					
surface	0	0.867	0	0	0
profundal	0	0.170	0	0	0
Blake Mere:					
surface	0	2.920	0	0	0
profundal	0	6.010	0	0	0.170
Crose Mere:					
surface	0	1.200	1.200	1.370	0
profundal	0.340	2.050	1.360	6.020	0

action on organic matter under anaerobic conditions. Gorham (1957) noted that in the dilute Shropshire meres (Blake Mere, Newton Mere and Kettle Mere) chloride exceeded sulphate but as the ionic concentration increased, so sulphate increased sharply to about double the chloride values. This was attributed to the fact that Crose Mere lies entirely on glacial till and is fed by ground reserves of water, whereas Blake Mere and Newton Mere lie on sand and gravel and are fed more by surface runoff than deep percolation.

The reduction in pH values at profundal sampling stations during the period of thermal stratification is thought to be due to the production of H_2S by the sediments. As previously stated, H_2S behaves as weak acid when in solution.

3.2.8 Nutritional nature of the profundal sediments

Table 3.6 summarises the data appertaining to the study of the nutritional nature and composition of the profundal sediments from Crose Mere, Newton Mere and Blake Mere.

There are two objections to the data; firstly, that the samples were collected during the summer and so do not present a complete examination and secondly, that the samples were from the profundal sediments only and possibly valuable comparisons between stations within one mere are therefore lacking. Despite these drawbacks it is considered that useful information concerning the nature of the sediments and their value to detritivores has been obtained.

The data have been presented in the following fashion: the DW (dry weight in g) is expressed as a mean % of the FW (fresh weight), the latter being the weight of a sample when excess water had been removed by filtering. The inorganic material left after combustion is

expressed as a mean % of the actual DW. The coarse organic material retained by hand seiving and the fine organic matrix which passed through the seive are expressed as %'s of the total mud sample. The mean calorific value is expressed in kcal/g.

From a statistical evaluation (Downie and Heath, 1965) of the raw data (Appendix I) for the profundal sediments of Newton Mere and Crose Mere, no significant differences are apparent between the % values for coarse organic material, inorganic content or fine organic matter. Where the two types of sediment do differ however is in the mean DW expressed as a % of the FW where $p = 0.001$. Newton Mere sediments therefore have a higher water content than Crose Mere sediments. This is to be expected in view of the gelatinous nature of the Newton Mere sediments.

The profundal sediments from Blake Mere differ markedly from those of Newton Mere and Crose Mere in having a lower inorganic content ($p = 0.05$-0.001) and very low amounts of coarse organic material but a higher % value of fine organic matter. There is no significant difference between the DW values for Blake Mere and Newton Mere.

Blake Mere sediments show a high calorific value for decomposing material (for which the average range is between 1.5 and 2.5 kcal/g) and at 4.08 kcal/g are nearer to values for fresh grass (4.5 kcal/g). Calorific values for Newton Mere and Crose Mere are not significantly different ($p = 0.1$) and at 2.76 and 1.86 kcal/g respectively are very much lower than those values for Blake Mere ($p = 0.01$ and 0.001).

Calorific vlaues are positively correlated with the amount of fine organic matter and negatively correlated with the values for coarse organic and inorganic material.

Table 3.6 Results from study on nutritional nature of profundal sediments from three meres

Mere	$\bar{x}$ D.W. as a % of F.W.	$\bar{x}$ wt. non-combustible material as a % of actual D.W.	wt. of coarse organic material as a % of s	estimated wt. of fine organic material as a % of s	$\bar{x}$ calorific value in kcal/g
Blake Mere	7.14%	30.20%	0.59%	69.21%	4.08
Crose Mere	12.37%	51.02%	3.35%	45.63%	1.86
Newton Mere	7.35%	47.90%	3.39%	48.71%	2.76

s = sample

Newton Mere, Blake Mere and Crose Mere are warm monomictic lakes which stratify thermally and show clinograde oxygen curves in summer. After the autumnal overturn caused by a breakdown in anticyclonic weather conditions, the three meres become isothermal. The development, establishment and demise of the thermocline is accompanied by changes in the pH, conductivity, certain ionic factors such as levels of calcium, magnesium and hydrogen sulphide and also the transparency of the lake water.

Crose Mere is the most eutrophic mere (Ca^{++} 63 mg/l; pH 7.9; conductivity 444 µmho/cm) and Newton Mere is relatively the least eutrophic (Ca^{++} 6.46 mg/l; pH 6.4; conductivity 136 µmho/cm). Blake Mere is slightly more productive than Newton Mere.

The particular conditions prevailing in each mere are thought to be intimately connected with the lithology of the drainage basin. Crose Mere has a wide drainage area and its basin lies entirely on glacial till. It is also the only mere with drainage inflows or outflows. Newton Mere and Blake Mere are isolated, surrounded by moraine hummocks and have no outflows or inflows.

The sediments of each mere vary and calorific values, calculated by bomb calorimetry, are positively correlated with the amount of fine organic matter present in the sediments. The sediments of Blake Mere have the highest calorific value, expressed as kcal/g.

The effects on the chironomid population of each mere are discussed in later chapters.

* * * *

4.

TAXONOMIC PROBLEMS

SECTION 1. KEY TO COMMON CHIRONOMID LARVAE FOUND IN MERES AND PONDS

INTRODUCTION

Possibly the biggest single problem in British chironomid studies is the confused and inadequate state of the larval taxonomy. Nothing is more disappointing than to read an otherwise interesting and important article and to find one's particular interest dealt with under a single title - "Chironomidae" - when other groups are identified to species level. Macan (1963) illustrated this neglect when he wrote: "...it is unfortunately necessary to except the Chironomidae, a family with some 400 species, most of which cannot be distinguished as larvae".

The reason for this neglect by workers in other fields is quite simple and very understandable: the keys which exist for the larvae are generally too detailed and by the time the subfamilies have been conquered, one can hardly face the barrage of "...some 400 species".

There have been two keys relevant to British chironomid larvae, those by Bryce (1960) and Bryce and Hobart (1972). Johannsen's (1937a, b) keys, although extremely useful for subfamilies and genera, are for the North American species. The Russian publications of Chernovskii (1949) and Pankratova (1970) are difficult to use primarily because they have not been written as dichotomous keys, which is the format generally accepted in the West. Also, Chernovskii's tome suffers from a deadweight of unverifiable Soviet species and the appearance of the same species several times under various synonyms.

It is, of course, advisable to rear the larvae to adults and then to use the keys of Coe (1950) and Edwards (1929) but this does not further the study of the larval forms. Shilova (1966) and Credland (1973a) have rightly pointed out the disparity between the "German" school of

Thienemann and Lenz, which has studied larval forms, and the "British" school of Edwards and Coe which studied the imagines. Recently however, Strenzke (1959) and Reiss and Fittkau (1971) have, respectively, published keys to the adults of Chironomus s.s. and Tanytarsus van der Wulp; and Bryce in Britain attempted to correct the imbalance with his 1960 and 1972 larval keys.

A new development has been in the use of salivary gland preparations and mention must be made of work by Acton (1955) and by Keyl and Keyl (1959) who produced a key to Chironomus larvae based on features displayed by the chromosomes. Cytotaxonomy is, however, of interest only to the esoteric few and from personal experience, what is most needed is an introductory key to common chironomid larvae which can be used by workers in other fields of limnology, research students beginning their projects and undergraduate students taking freshwater biology courses.

A key to common chironomid larvae of meres and ponds has therefore been written and follows. The part dealing with Chironomus s.s. is based on Bryce (1960).

The ventral external toothed plate found in the Chironominae, Diamesinae and Orthocladiinae has been called variously the submentum (Chernovskii, 1949); the hypostomium or hypostomial plate (Bryce, 1960); the labial plate (Johannsen, 1937) and the hypochilum (Gouin, 1959).

It was decided, after reference to Snodgrass (1935), Gouin (1959) and Matsuda (1965) that it was morphologically correct to refer to the toothed plate as the hypochilum.

KEY TO COMMON CHIRONOMID LARVAE FOUND IN MERES AND PONDS

Notes on using this key:

* Quickly read the key first and look at the diagrams.
* Always look at the larvae alive to note colour, type of movement etc. before killing.
* Kill in 70% alcohol or dilute formalin; very hot water may be used but many chironomids resist hot tap water.
* Some of the characters can be seen in the whole animal but removal of the head is essential for identification from mouthparts. Do not throw away the body; it may be needed for other characters, eg. lateral tubules in Chironomus s.s.
* Cut off the head on a slide with scalpel or sharp pins. If in a hurry, simply mount in glycerol but never in water. Put on a cover slip and press down gently to open up the mouthparts. This method can be disappointing as the capsule is hard and may break up the weak median suture, thus ruining the hypochilum.

  To make a good preparation, boil the head in 10% KOH for 5-10 mins., wash in water, dehydrate in alcohol and mount in polyvinyl lactophenol. The slide is permanent when dry. Gently press the cover slip to open up the mouthparts. This treatment can destroy soft parts of the antennae, eg. in Tanytarsus, so remove one antenna before boiling. The head can also be cut up the side and opened out before mounting. Always mount ventral side up.
* If the mouthparts are inside the head, as in subfamily Tanypodinae, cut open the head capsule to see the glossa and paraglossae.
* To see the lateral tubules properly, turn the body onto its ventral surface and gently press the last two segments. If small tubules are present on 10th segment, they will move away from the body wall. They are about ½ the size of the tubules on the 11th segment.
* Dissecting pins can be made from surgeon's needles (Straight

Triangular No. 20) inserted into lightweight aluminium innoculating needle holders.

Check list of species featured in this key

CLASS Insecta; ORDER Diptera; SUBORDER Nematocera; FAMILY Chironomidae; SUBFAMILIES Chironominae, Tanypodinae, Diamesinae, Orthocladiinae.

(Subfamilies not included in this key: Podonominae, Clunioninae).

CHIRONOMINAE

Chironomus Mg.

Chironomus dorsalis Mg.

Chironomus plumosus L.

Chironomus lugubris Zett.

Chironomus riparius Mg.

Chironomus anthracinus Zett.

Camptochironomus tentans Fab.

Einfeldia Th.

Tanytarsus van der Wulp

Microtendipes Kieff.

Glyptotendipes Kieff.

Glyptotendipes polytomus Kieff.

Polypedilum Kieff.

Endochironomus 'nymphoides'

Limnochironomus Kieff.

Cryptochironomus Kieff.

Phaenospectra Kieff.

TANYPODINAE

Anatopynia varia Fab.

Pentaneura monilis L.

Procladius choreus Mg.

DIAMESINAE

Prodiamesa olivacea Mg.

ORTHOCLADIINAE

Cricotopus van der Wulp

1. Larvae distinctly blood-red in colour; redness may be masked by extensive green mottling..... part of genus Chironomus Mg....2

-- Larvae not blood-red in colour; may be pink, brown, green, yellow, etc. * 15

*Early Chironomus s.s. instars are sometimes not so blood-red as the final stage. Check for lateral tubules as in Couplet 2. If present, proceed to Couplet 3.

2. Possessing either 1 or 2 or 3 pairs of lateral tubules on 10th or 11th body segment (Figs. 4.1 and 4.3) See "Notes" 3

-- Not possessing any tubules on any segment 10

3. With one pair of lateral tubules on 11th segment 4

-- With 2 pairs of lateral tubules on 11th segment 5

4. With Chironomus s.s. mouthparts ie. 15 teeth on hypochilum (Plates 4.1, 4.2 and 4.3) ..... series Einfeldia Th.

-- With Glyptotendipes mouthparts ie. 13 teeth on hypochilum; 4th laterals usually smaller than others (Plate 4.4) .... Glyptotendipes barbipes Staeg. or G. polytomus Kieff.

5. With one pair of short lateral tubules ("tubiculi") on 10th body segment - "plumosus" type (Fig. 4.3) 6

-- Without short lateral tubules on 10th body segment - "thummi" type (Fig. 4.1) 8

6. Head capsule dark only on postocciput (like a black collar) (Plate 4.1) ..... Chironomus dorsalis Mg.

-- Head capsule dark on postocciput and ventral plates (Plate 4.1) .7

7. Head black on fronto-clypeus (Plates 4.5 and 4.6) .... includes Camptochironomus tentans Fab.

-- Head not black on fronto-clypeus ..... Chironomus plumosus L.

8. Head capsule dark only on postocciput (like a black collar) (Plate 4.1) ..... Chironomus lugubris Zett.

-- Head dark on postocciput and ventral plates (Plate 4.1) 9

9. Ventral plates pale brown to moderately dark .....
..... Chironomus riparius Mg.

-- Ventral plates black ..... Chironomus anthracinus Zett.

10. With 6 antennal segments (Plate 4.8); median teeth pale, often colourless, separated by a notch (Plate 4.7) .....
..... subgenus Microtendipes Kieff.

-- With 5 antennal segments 11

11. With less than 16 teeth on hypochilum 12

-- With 16 teeth on hypochilum 14

12. With 13 teeth on hypochilum 13

-- With 10, 12 or 14 teeth; central area rounded, pale, usually colourless, often not toothed; 5 - 7 teeth either side of central area (Plate 4.9) ..... part of group Cryptochironomus Kieff.

13. Head capsule heavily built and black on fronto-clypeus but darkening smudged onto ocular lobes; anterior margin of fronto-clypeus markedly concave (Plate 4.5). 1st and 2nd lateral teeth fused basally and equal in length; 4th laterals often very small in relation to others (Plate 4.4)..subgenus Glyptotendipes Kieff.

-- Head capsule not heavily built and black only on fronto-clypeus (Plate 4.6); anterior margin of fronto-clypeus not markedly concave, but with distinct notch; 1st and 2nd laterals on hypochilum fused; 1st laterals equal in length with median tooth and longer than 2nd laterals (Plate 4.10) .....
..... group Limnochironomus Kieff.

14. Median pair of teeth longer than 1st laterals (which are very small); 2nd laterals longer than 1st laterals but not as long as median pair (Plate 4.11) ..... subgenus Polypedilum Kieff.

-- Median pair of teeth smaller than 1st laterals; 2nd laterals smaller than both median pair and 1st laterals (Plate 4.12) ..... group Phaenospectra Kieff.

15. Paralabial plates not external; hypochilum (correct term for this subfamily: glossa) not developed as external but as internal toothed plate (See "Notes"); anal papillae pointed (Figs. 4.2, Plates 4.13, 4.14, 4.15) ..... subfamily Tanypodinae 16

-- Paralabial plates (if present) and hypochilum external; paralabials may also have whiskers OR be 4 times as wide as deep OR merely wing-like extensions of the hypochilum OR absent; anal papillae rounded .... subfamilies Diamesinae, Chironominae, Orthocladiinae ...18

16. Glossa with 5 teeth; paraglossae with inner prong (Plate 4.14) ... .17

-- Glossa with 4 teeth, paraglossae serrated with no inner prong (Plate 4.13); lateral fringe of swimming hairs .... Anatopynia varia Fab.

17. Antennae half as long as head, which is very long and narrow; no lateral fringe of swimming hairs on body; teeth on glossa all approximately equal in length (Plate 4.14)..Pentaneura monilis L.

-- Antennae short, about ¼ the length of head; body with fringe of swimming hairs laterally; glossa usually showing black through head capsule but may be amber in colour; teeth on glossa not of equal length; median tooth smallest and 2nd laterals longest (Plate 4.15) ..... Procladius choreus Mg.

18. "Paralabial plates" (which are actually only extensions of the hypochilum) whiskered; whitish body (Plate 4.17) .... Prodiamesa olivacea Mg.

-- Paralabials not whiskered 19

19. Paralabial plates about 4 times as wide as deep; long antennae always borne on a protuberance (Plates 4.18 and 4.19) .... genus Tanytarsus van der Wulp

-- Not like this 20

20. Median pair of teeth entirely separated by a distinct incision; median teeth always smaller than 1st laterals; median teeth and 1st laterals slightly raised above other teeth; 16 teeth on hypochilum; body yellow (Plate 4.16) .... subgenus Endochironomus, 'nymphoides' group

-- Single median tooth longer than lateral teeth; 2nd laterals as auxiliary teeth on 1st laterals; 13 teeth on hypochilum which has an especially distinct convex curve (Plate 4.20) .... part of genus Cricotopus van der Wulp

* *

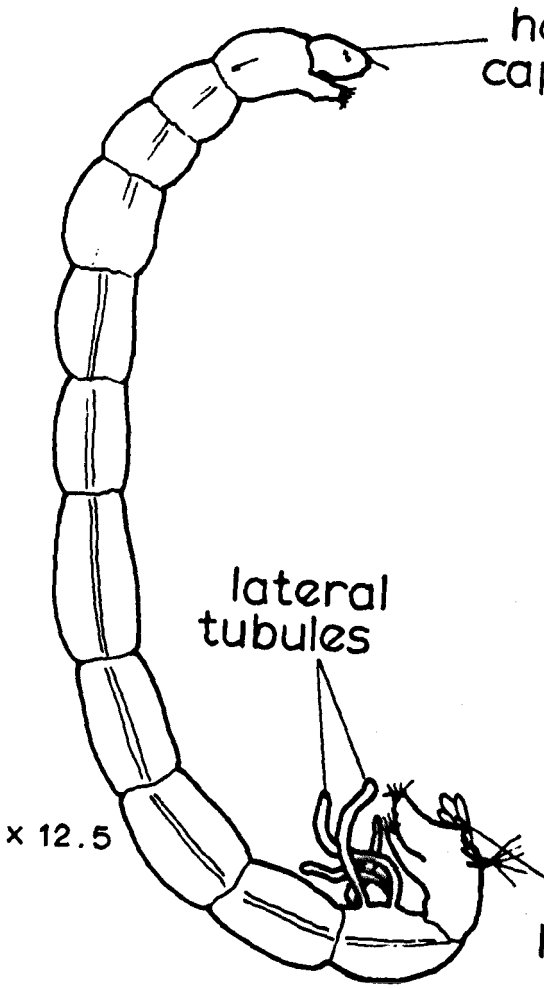


Figure 4.1 Chironomus s.s. larva

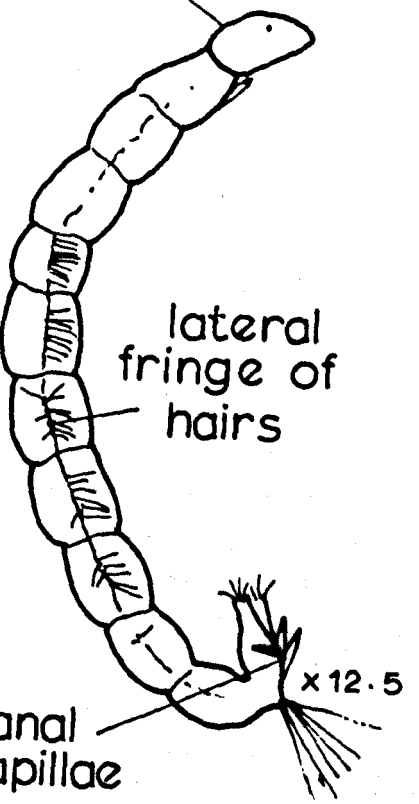


Figure 4.2 Procladius choreus larva

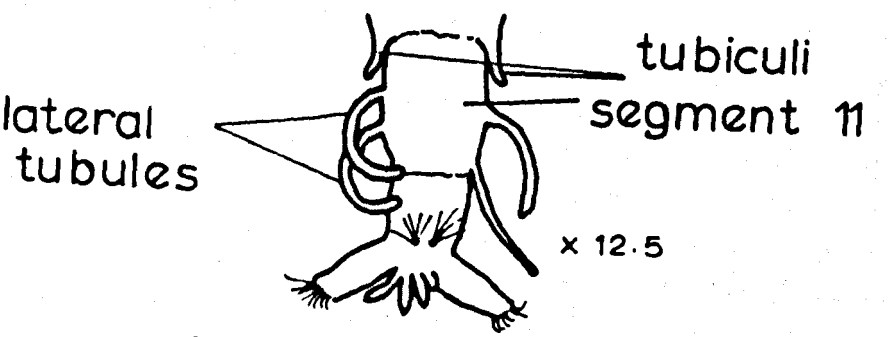


Figure 4.3 Chironomus s.s. "plumosus" type.

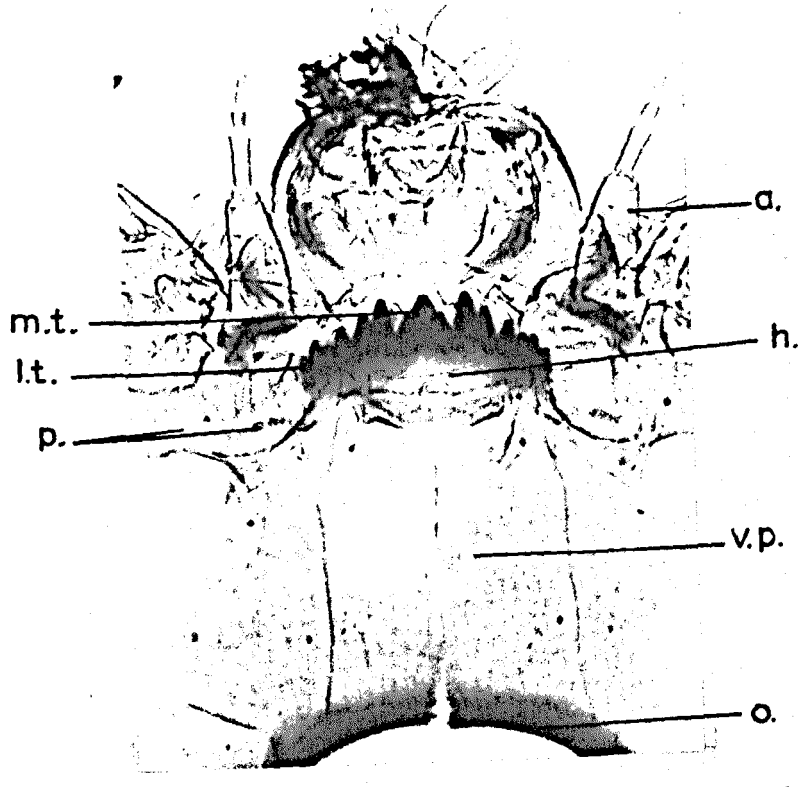


Plate 4.1 Ventral aspect of Chironomus s.s. head capsule showing features referred to in text:

o. = post-occiput; v.p. = ventral plates; a. = antenna; m.t. = median tooth

h. = hypochilum; l.t. = lateral teeth; p. = paralabial plates

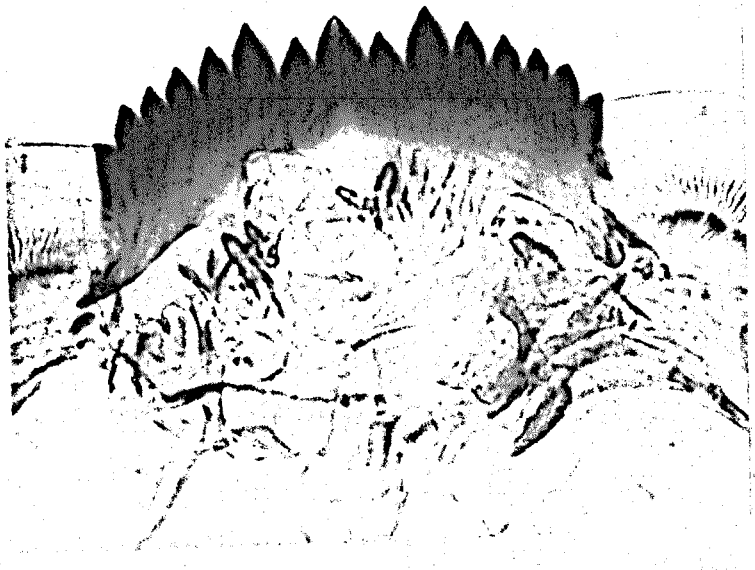


Plate 4.2 Chironomus s.s. - hypochilum and paralabial plates (in part).

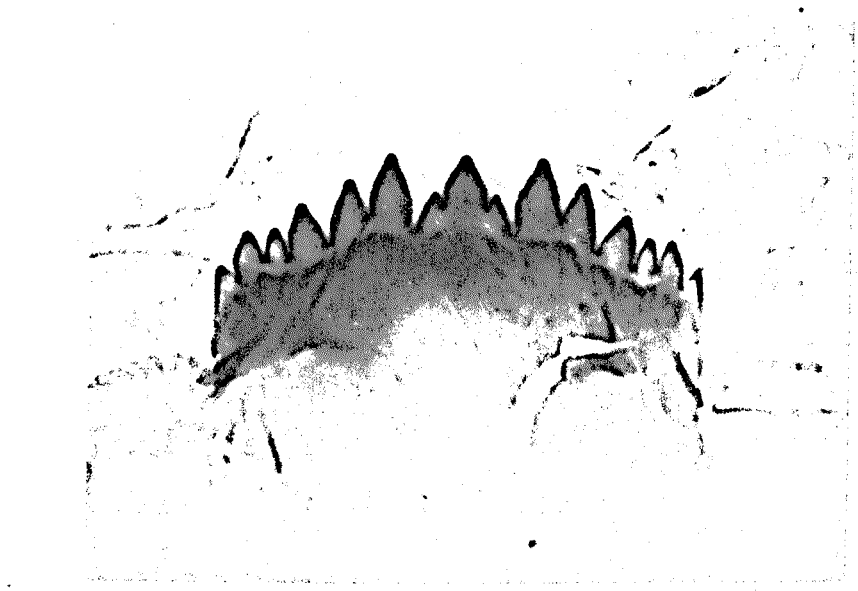


Plate 4.3 Chironomus s.s. - hypochilum (early instar)

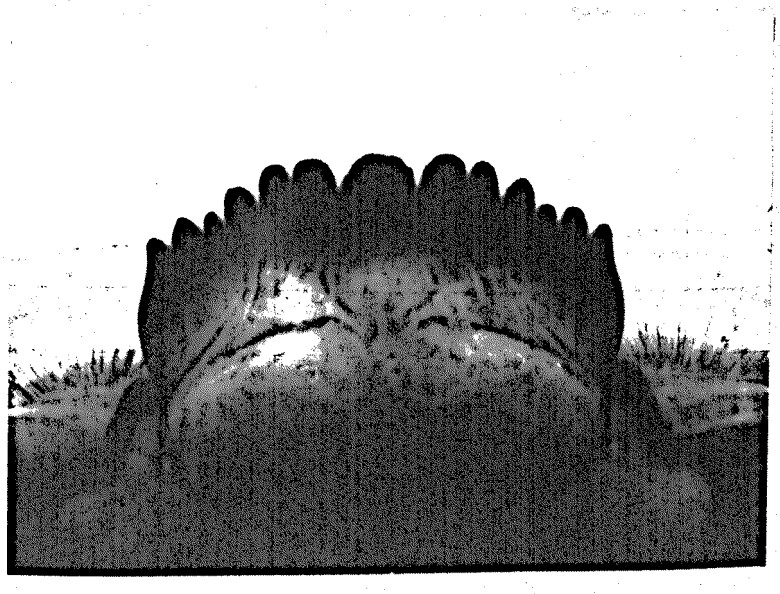


Plate 4.4 Glyptotendipes sp. - hypochilum and paralabial plates

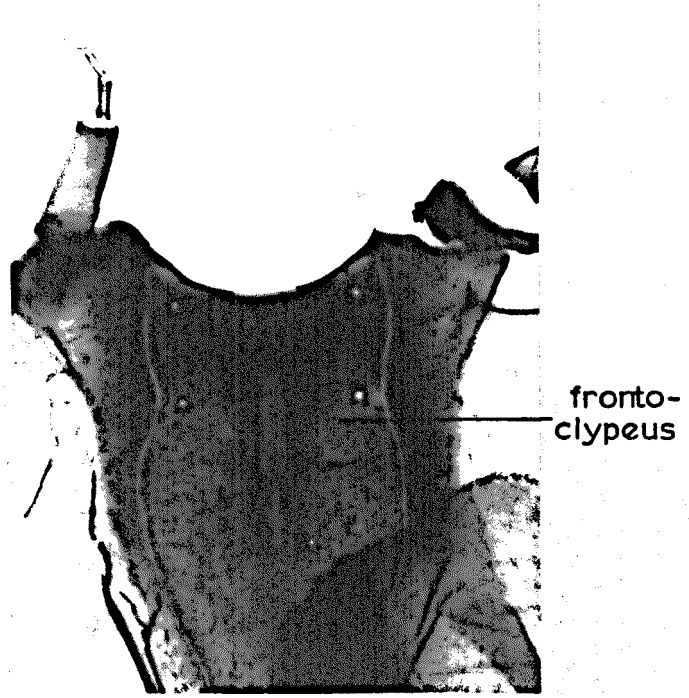


Plate 4.5 Glyptotendipes sp. - dorsal aspect of head capsule - fronto-clypeus

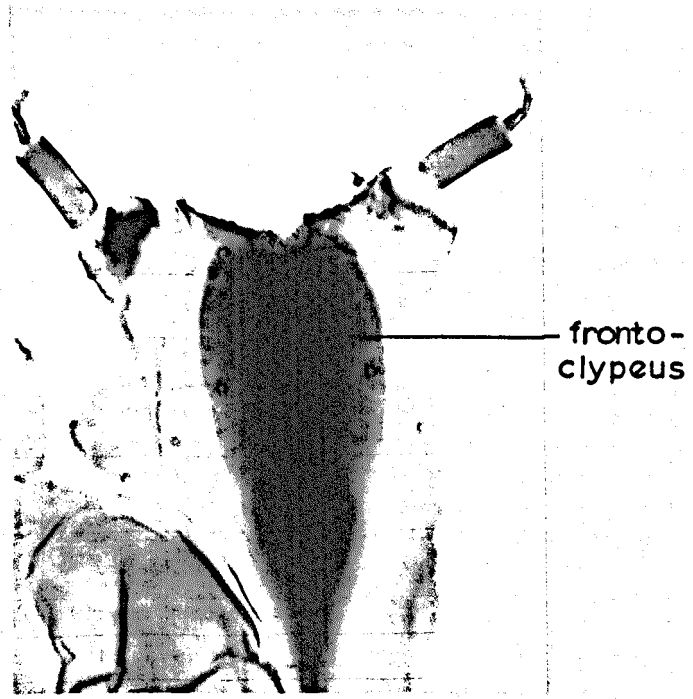


Plate 4.6 Limnochironomus sp. - dorsal aspect of head capsule - fronto-clypeus

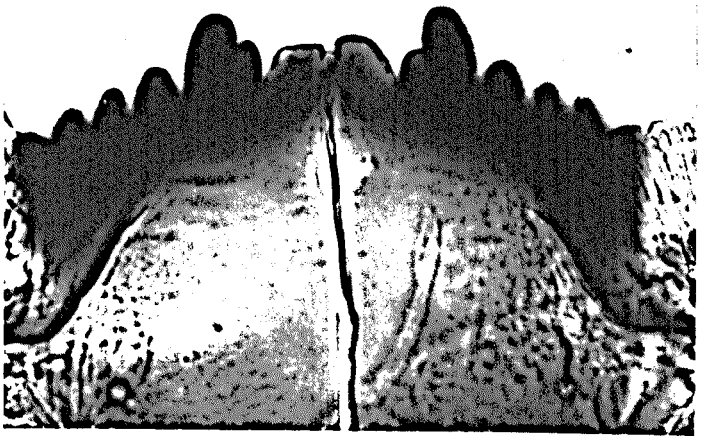


Plate 4.7 Microtendipes chloris - hypochilum

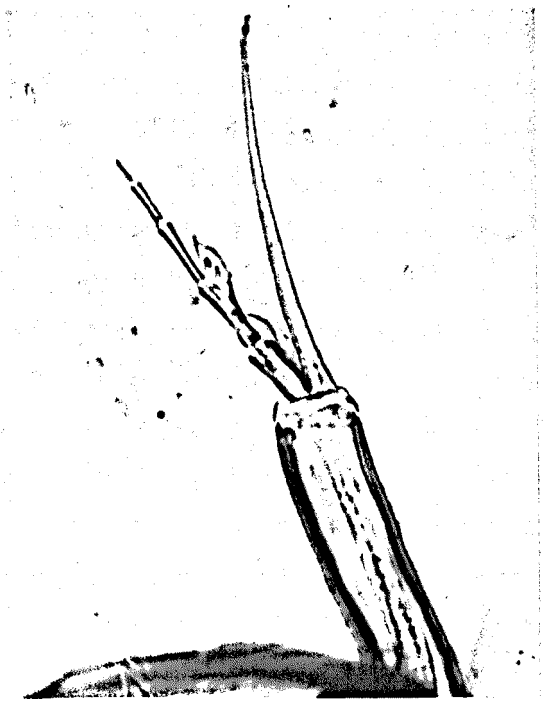


Plate 4.8 Microtendipes sp. - antenna

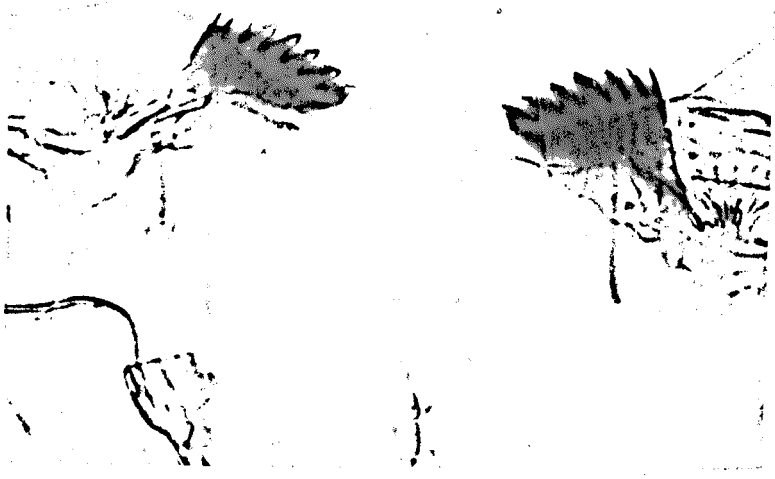


Plate 4.9 Cryptochironomus 'defectus' - hypochilum and paralabial plates

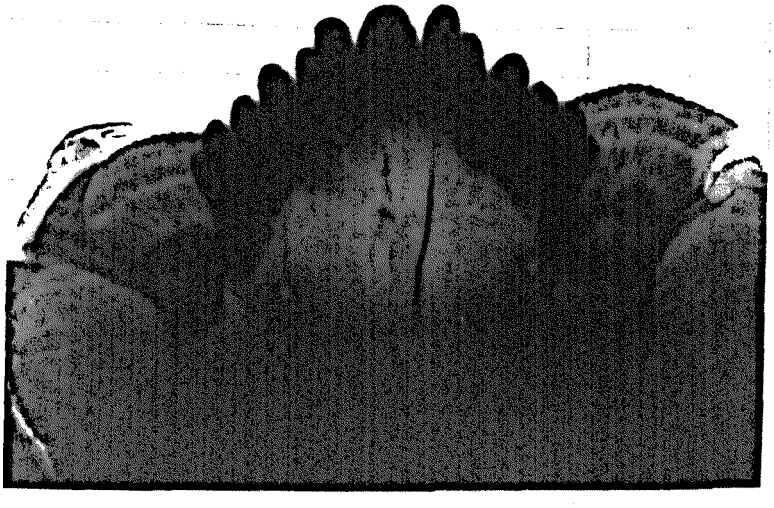


Plate 4.10 Limnochironomus sp. - hypochilum and paralabial plates

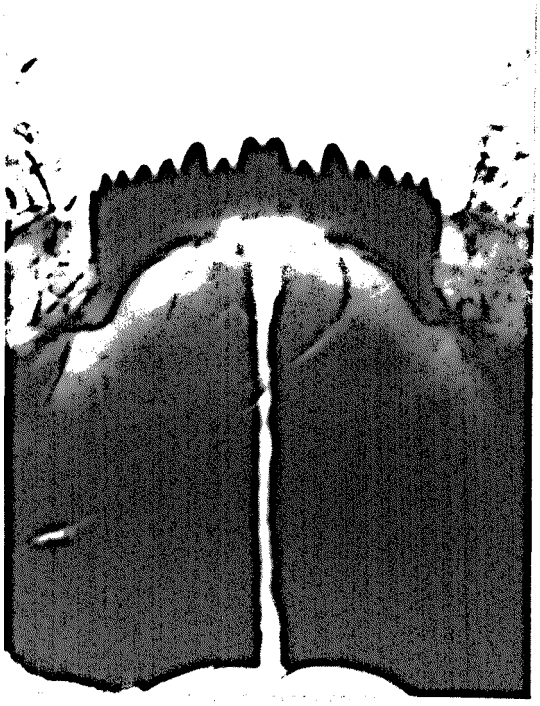


Plate 4.11 Polypedilum sp. - hypochilum

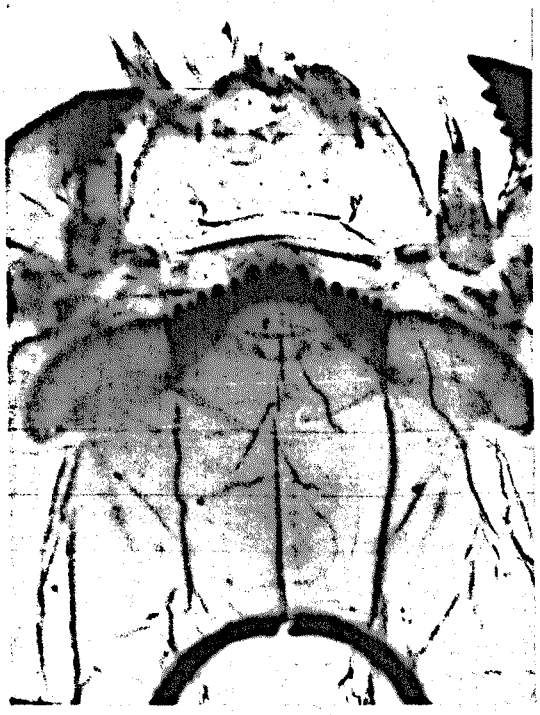


Plate 4.12 Phaenospectra sp. - ventral aspect of head capsule showing hypochilum

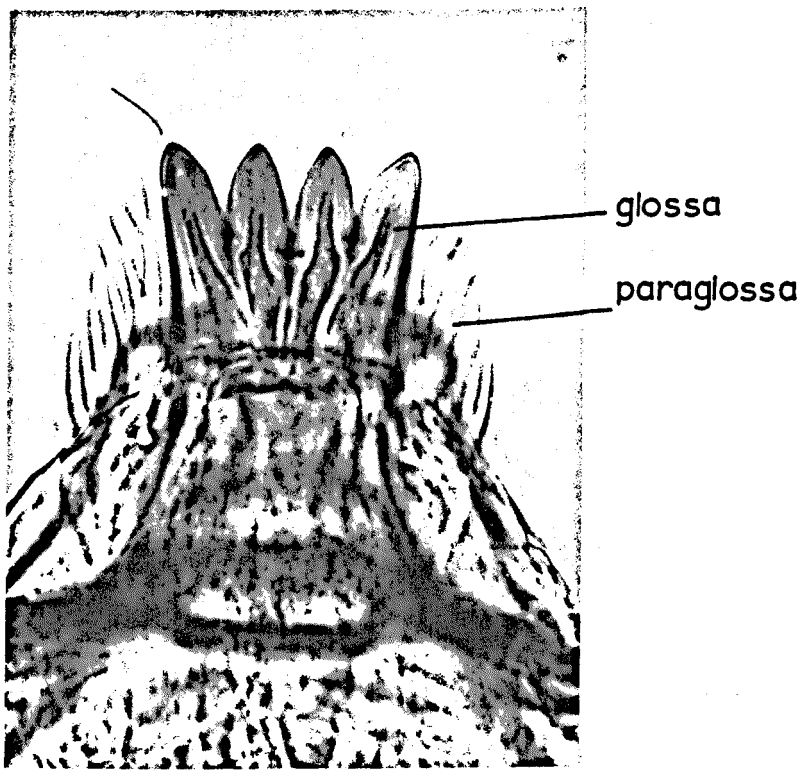


Plate 4.13 Anatopynia varia - glossa and paraglossae

Plate 4.14 Pentaneura monilis - glossa

Plate 4.15 Procladius choreus - glossa and paraglossae

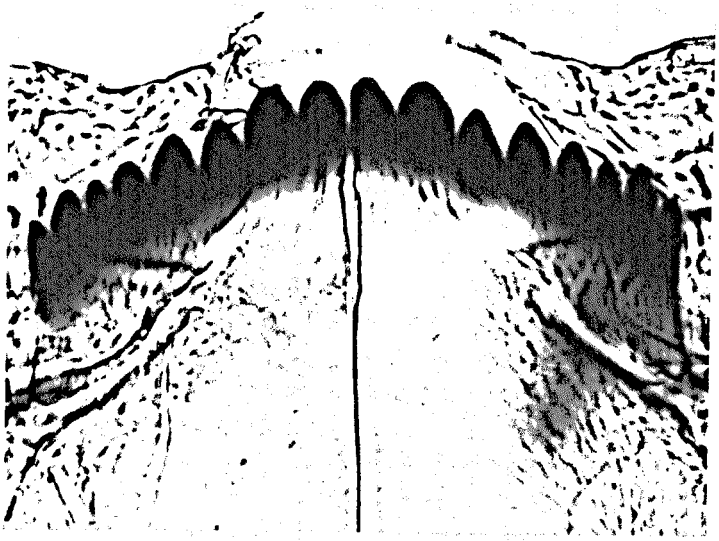


Plate 4.16 Endochironomus 'nymphoides' - hypochilum

Plate 4.17 Prodiamesa olivacea - hypochilum and whiskered "paralabial plates" (actually extensions of the hypochilum)

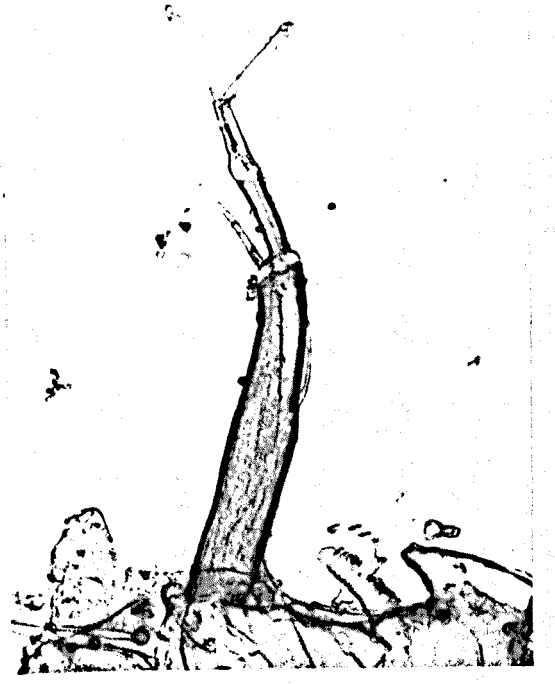


Plate 4.18 Tanytarsus sp. - antenna

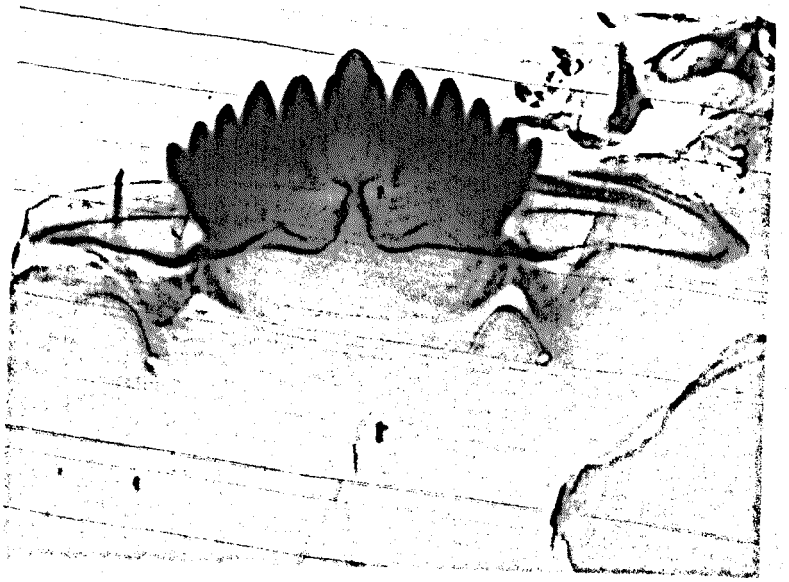


Plate 4.19 Tanytarsus sp. - hypochilum and paralabial plates

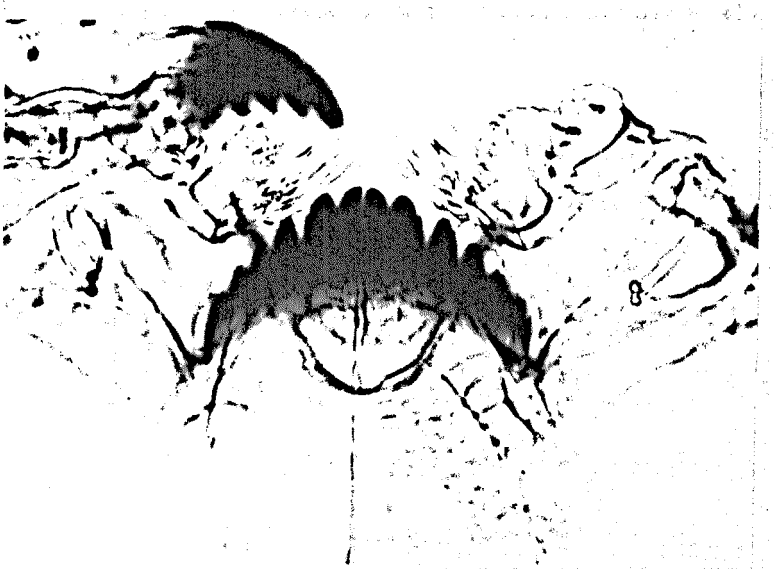


Plate 4.20 Cricotopus sp. - hypochilum

*Due to its extreme convexity, the hypochilum splits down the single median tooth when pressure is applied to cover slip

SECTION 2. TAXONOMY OF CHIRONOMUS ANTHRACINUS ZETT. AND PROCLADIUS CHOREUS MG.

INTRODUCTION

The two great taxonomic problems in the present study were concerned with Chironomus anthracinus Zett. and Procladius choreus Mg.. Although 65 species have been identified, only these two can be considered to be predominant, having been taken in samples consistently and in large numbers. It was therefore essential that the two most abundant and widely distributed species were correctly identified.

Chironomus anthracinus Zett. (syn. bathophilus Kieff., liebeli Kieff.)

Following Bryce (1960), larvae of C. anthracinus were originally identified as Chironomus longistylus Goet., a "thummi" type larva with two pairs of lateral tubuli in segment 11 only, black ventral plates and a black rim on the posterior border of the head capsule - the post-occiput. After the emergence of several imagines from these larvae, it was evident that reidentification of the larvae was necessary because all the adults were C. anthracinus, which, according to Bryce has a "plumosus" type larva, ie. with one pair of lateral tubiculi on the 10th body segment in addition to the two pairs of tubuli on segment 11. The adults were clearly anthracinus, having a mean leg ratio of 1.2, a long tarsal beard and an almost entirely black body. The leg ratio, as defined by Coe (1950) is the length of the first segment of the tarsus in relation to the tibia and is expressed as a decimal. Reference is usually to the front legs.

Imagines of C. anthracinus from Shropshire have also been checked against Edward's collection in the British Museum (Natural History).

Berg (1938) described larvae from the liebeli-bathophilus group in Lake Esrom, as being 17 - 18 mm long, with "...two pairs of filiform tubili (so-called blood gills)" which he found ventrally "...on the second

last segment of the body" and depicted in diagrams a "thummi" type larva and its antenna with the annual ring situated in the proximal half of the first antennal segment. In 1972, Berg's colleague Jónasson described "..Chironomus anthracinus Zett. (syn. bathophilus Kieff., liebeli Kieff.)" as having "..four ventral papillae (the blood gills)..... on segment 11" and added that ".. segment 4 through 10 have small lateral bulges".

In a personal letter (10.1.73), Bryce wrote that in his original account (MS, 1958), he described his 'anthracinus' as a "plumosus" type because it had small lateral tubiculi on segment 10.

This problem has been remarked upon by others. Hunt and Jones (1972) found in Llyn Tegid, "thummi" type larvae whose adult forms were indistinguishable from anthracinus adults. Slack (16.10.72 - pers. comm. in reply to a query) stated that, in his experience, anthracinus larvae looked very like those of longistylus, in having melanin over the posterior or ventral surface of the head, two pairs of ventral gills but no dorso-lateral appendages.

Finally, Mrs. H. D. Slack kindly examined some preparations of salivary gland chromosomes and pronounced them to be from C. anthracinus. This was later confirmed by consulting drawings from Keyl and Keyl (1959).

The characteristics of the larva of C. anthracinus have been described many times by Jónasson (1961, 1964, 1970, 1972) and need not be repeated here.

Procladius choreus Mg.

Procladius crassinervis Zett. has been included with P. choreus following a suggestion by Dr. Paul Freeman that crassinervis was but a minor variant of choreus, which could be distinguished in the adult but not in the larval form. Mundie (1957), in an account of the taxonomy of these two species, suggested they may be sibling species, subspecies or

variants of one species.

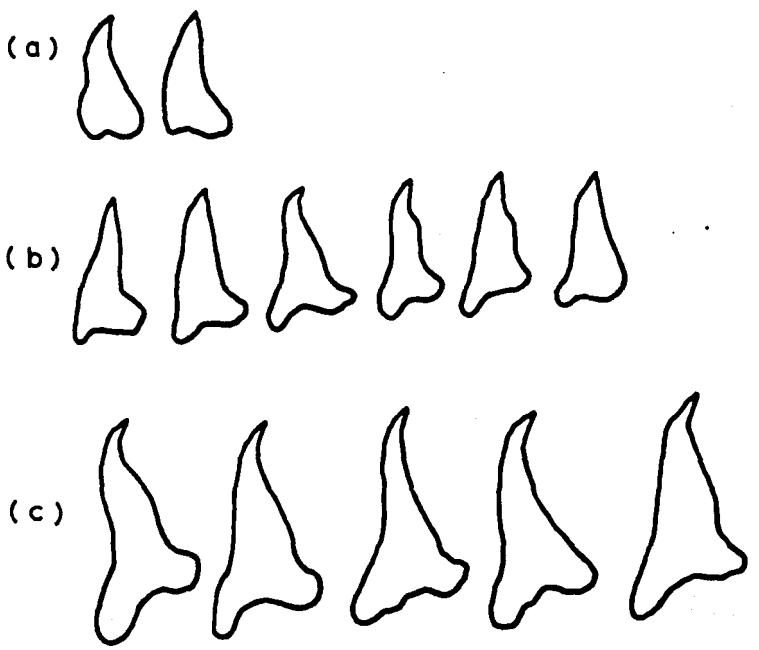
An examination of the hypopygia of 64 male Procladius sp. imagines revealed a 3:1 ratio (49:13) between numbers of choreus and crassinervis, as well as two specimens of sagittalis Kieff. Drawings made of some of the styles using a camera lucida are presented in Fig. 4.4. The lengths of all the styles from the point of the claw at the end of the style, to the concavity between the backward process and the insertion into the coxite, was measured, to the nearest mm, on paper. The lengths fell into 3 groups: one which had its mean at 19 mm (sagittalis - 2 specimens), another at 21 mm (choreus - 49 specimens) and the other at 29 mm (crassinervis - 13 specimens).

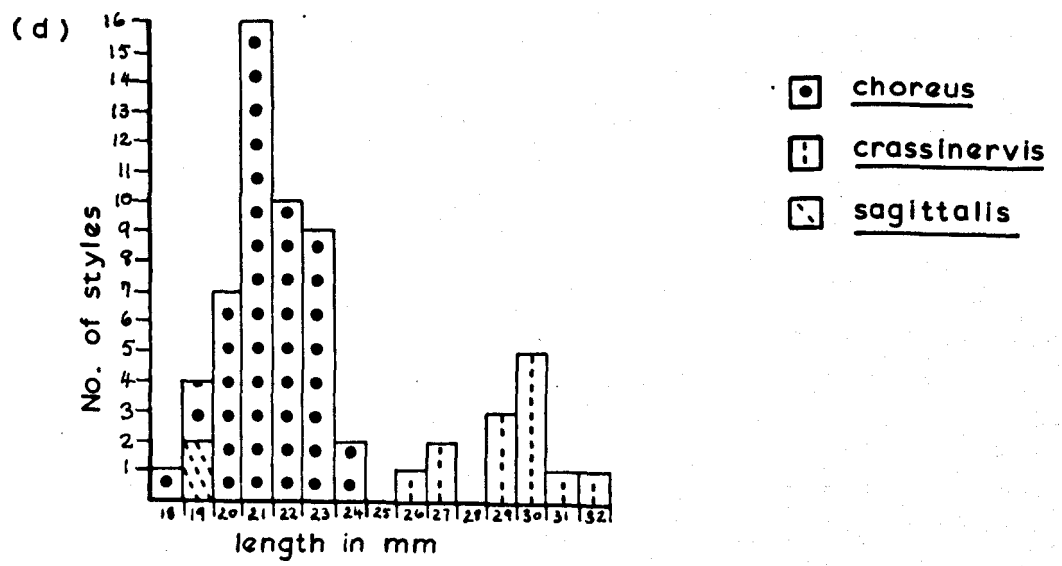
Specimens preserved in Carnoy's preservative are simple to distinguish because the yellow abdominal bands of choreus are more clearly visible than in the pinned specimen.

An examination of the number of teeth on the paralabial plates of preserved larvae revealed, in 4th instars only, a ratio of 3:1 between numbers of plates which had 7 pairs of teeth and those with 8 pairs of teeth. Johannsen (1937), Mundie (1957) and Zavrel (1921) all state that choreus larvae have 7 pairs of paralabial teeth but Bryce (1960) describes choreus as having about 8 pairs of teeth on the paralabial plates. It would therefore be inaccurate to conclude that because of the similarities in the 3:1 ratios mentioned, that choreus larvae have 7 pairs of teeth and crassinervis have 8. Also, should live larvae be required for experimental work after examination, the number of teeth on the paralabial plates would not be a good criterion for identification as they are situated internally in the head capsule.

A final justification for using choreus as a "blanket" name is found in Bryce (1960), who also reared adults referable to sagittalis and crassinervis from types indistinguishable from choreus larvae.

Figure 4.4 (a - c) Right style, dorsal aspect (x 10) of male hypopygium of Procladius sp. - (a) P. sagittalis Kieff. (b) P. choreus Mg. (c) P. crassinervis Zett. (d) histogram of style length groupings.





Descriptions of P. choreus may be found in Morgan (1949), Mundie (1957) and Kajak and Dusoge (1970).

* * * *

5.

DISTRIBUTION AND ABUNDANCE

SECTION 1 DATA APPERTAINING TO LARVAL CHIRONOMID DISTRIBUTION AND ABUNDANCE

INTRODUCTION

The data which will be presented in this chapter are the first detailed records of the chironomid fauna from any of the Shropshire meres. Walsh (MS, 1965) gave a list of organisms, which included some chironomids, found in a survey of Cole Mere, Crose Mere, Sweat Mere and Ellesmere, undertaken to provide a contrast to Rostherne Mere in Cheshire which had been found to have a life-less, deep-water zone (Brinkhurst and Walsh, 1967). Sinker (1962) and Walsh (MS, 1965) both mention that in brief surveys undertaken in 1960 by Brinkhurst and by Kennedy in 1961, the deeper sediments were found to support populations of tubificids and chironomid larvae, but no species lists have yet been published.

65 chironomid species have been identified, representing four subfamilies: the Chironominae, Orthocladiinae, Tanypodinae and Diamesinae. Table 5.1 shows an analysis of the number of species from each mere representing each subfamily. It is immediately obvious that the Chironominae is the most numerous of the groups in these meres.

TABLE 5.1 Number of species from each mere representing each subfamily

Subfamily	No. of species per mere		
	Newton Mere	Blake Mere	Crose Mere
Chironominae	26	23	23
Orthocladiinae	0	7	11
Tanypodinae	3	4	5
Diamesinae	0	0	1
Total:	29	34	40

The complete species list has been divided into three parts which are presented separately in Tables 5.2, 5.3 and 5.4. Those species common to all three meres, or to any two are included in Table 5.2, while Table 5.3 presents those species found only in Newton Mere or in Blake Mere; those species unique to Crose Mere are presented in Table 5.4. Some species appearing in these tables are from hand netting as well as from the Ekman grab samples.

Species have been described as "regular and abundant", "regular and few", "regular and sparse" or "occasional and sparse". The criteria for each category depicted in the Legend applying to each Table are as follows. A species is considered to be:
"regular", if listed in >33% of the monthly faunal lists/mere, or
"occasional", if listed in <33% of the monthly faunal lists/mere, and
"abundant", if numerically >20% of the total number of larvae collected/mere, or
"few", if numerically 2 - 20% of the total number of larvae collected/mere, or
"sparse", if numerically <2% of the total number of larvae collected/mere.

Tables 5.5, 5.6, 5.7 and 5.10 summarise the distribution and abundance of those species, mostly identified as larvae, which were collected in the monthly grab samples. Full lists for each mere may be found in Appendix 2. The values for each species represent mean densities/m^2/sampling depth and are presented as percentages of the total/m^2 in Figs. 5.1, 5.2 and 5.3. These show, particularly Fig. 5.1 for Newton Mere, the predominance of Chironomus anthracinus over all other species, except in the littoral zones down to 3 - 4 m. Microtendipes chloris, accompanied by Procladius choreus, Glyptotendipes glaucus, Endochironomus albipennis and C. anthracinus, predominates at 2 m in

Figure 5.1 Newton Mere: mean densities/m^2 for the 7 most abundant chironomid species (represented as a % of the total density/m^2) at each sampling depth.

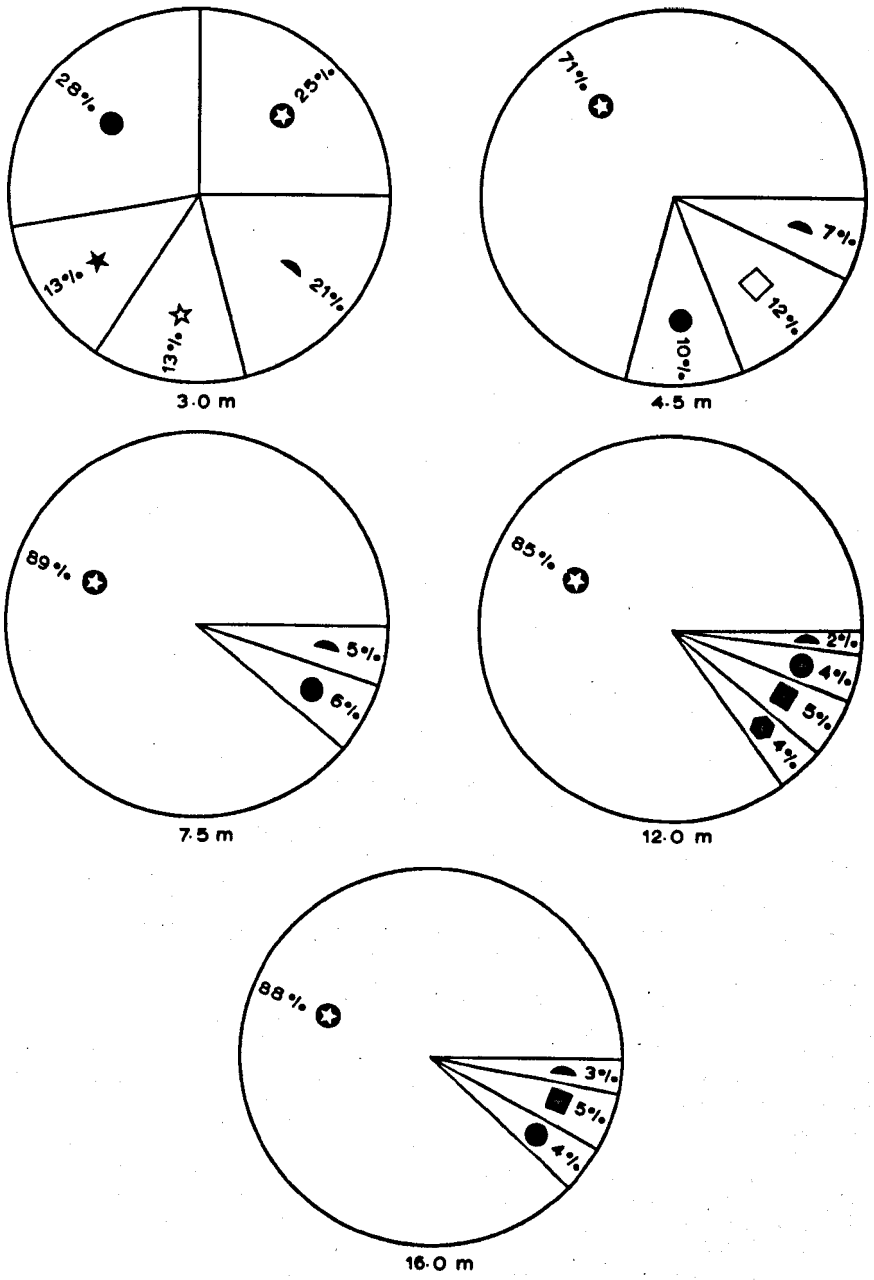
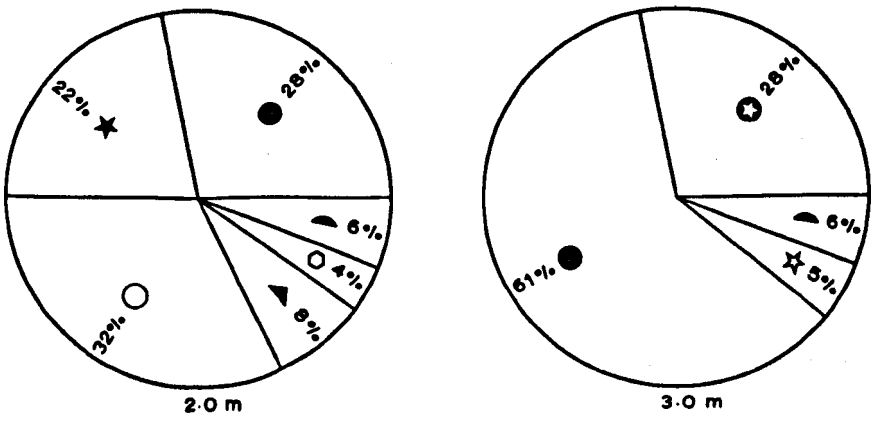
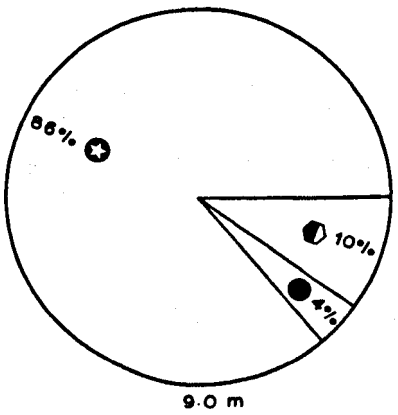


Figure 5.2 Blake Mere : mean densities/m^2 for the 8 most abundant chironomid species (represented as a % of the total density/m^2) at each sampling depth.



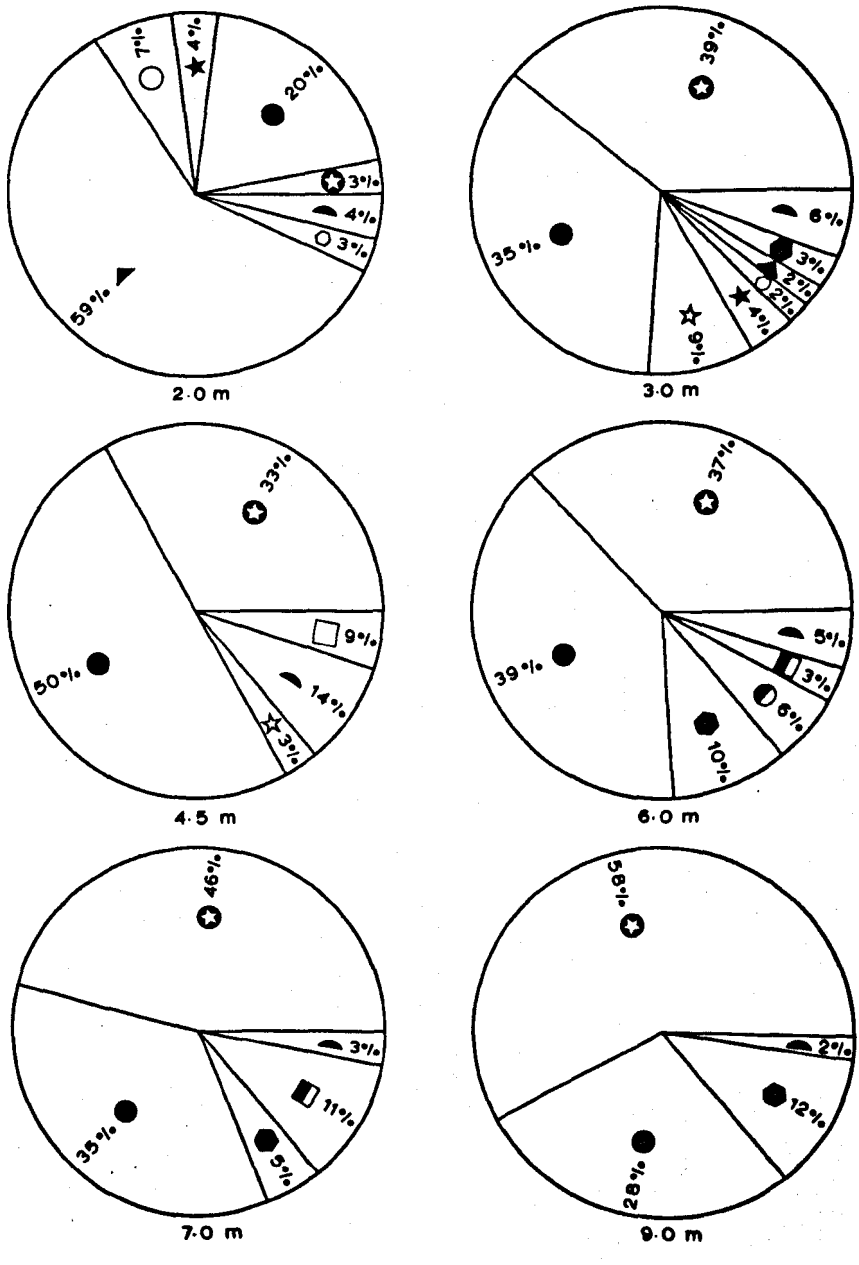
All species scarce or absent from stations 6.0 & 13 m.



LEGEND

- Chironomus anthracinus
- Procladius choreus
- Limnochironomus pulsus
- Tanytarsini sp.
- Glyptotendipes glaucus
- Microtendipes chloris
- Endochironomus albipennis
- Chironomus riparius
- Chironomus annularius
- Chironomus s.s.
- Chironomus plumosus
- Chironomus lugubris
- Chironomus dorsalis
- Others

Figure 5.3 Crose Mere: mean densities / m^2 for the 11 most abundant chironomid species (represented as a % of the total density / m^2) at each sampling depth.



Crose Mere but falls off to 2% of the total at 3 m, against the sublittoral and profundal forms which increase in number.

14 species, 10 of which have been recorded for all three meres, have been ranked in order of predominance (Table 5.2) according to their relative abundance and distribution.

In Blake Mere, G. glaucus, accompanied by P. choreus and Limnochironomus pulsus, M. chloris and E. albipennis, is the dominant form at 2 m, the station on the ridge of grey glacial clay. All other stations support sublittoral and profundal forms.

As the meres increase in ionic concentration, so a higher percentage of the species are confined to the littoral and sublittoral zones. 64% of the species are littoral - sublittoral in Newton Mere, compared with 75% in Blake Mere and 80% in Crose Mere. This is thought to be related to the particular environment in each mere and the effect of summer stratification. Fig. 5.4 shows the depth distribution of the total population at each sampling depth in each mere which illustrates this point. In Newton Mere, the number of animals increases with depth but in Crose Mere and Blake Mere, the maximum density occurs between 3 and 3.5 m and declines thereafter.

A consistent pattern for the deepest sampling depth in the profundal zone of all three meres is a predominant Chironomus anthracinus, ranging from 58 - 88% of the total, accompanied by another Chironomus s.s. species and Procladius choreus.

Figure 5.4 Depth distribution of total populations at each sampling depth in Newton Mere, Blake Mere and Crose Mere (expressed as the mean number of larvae / m^2).

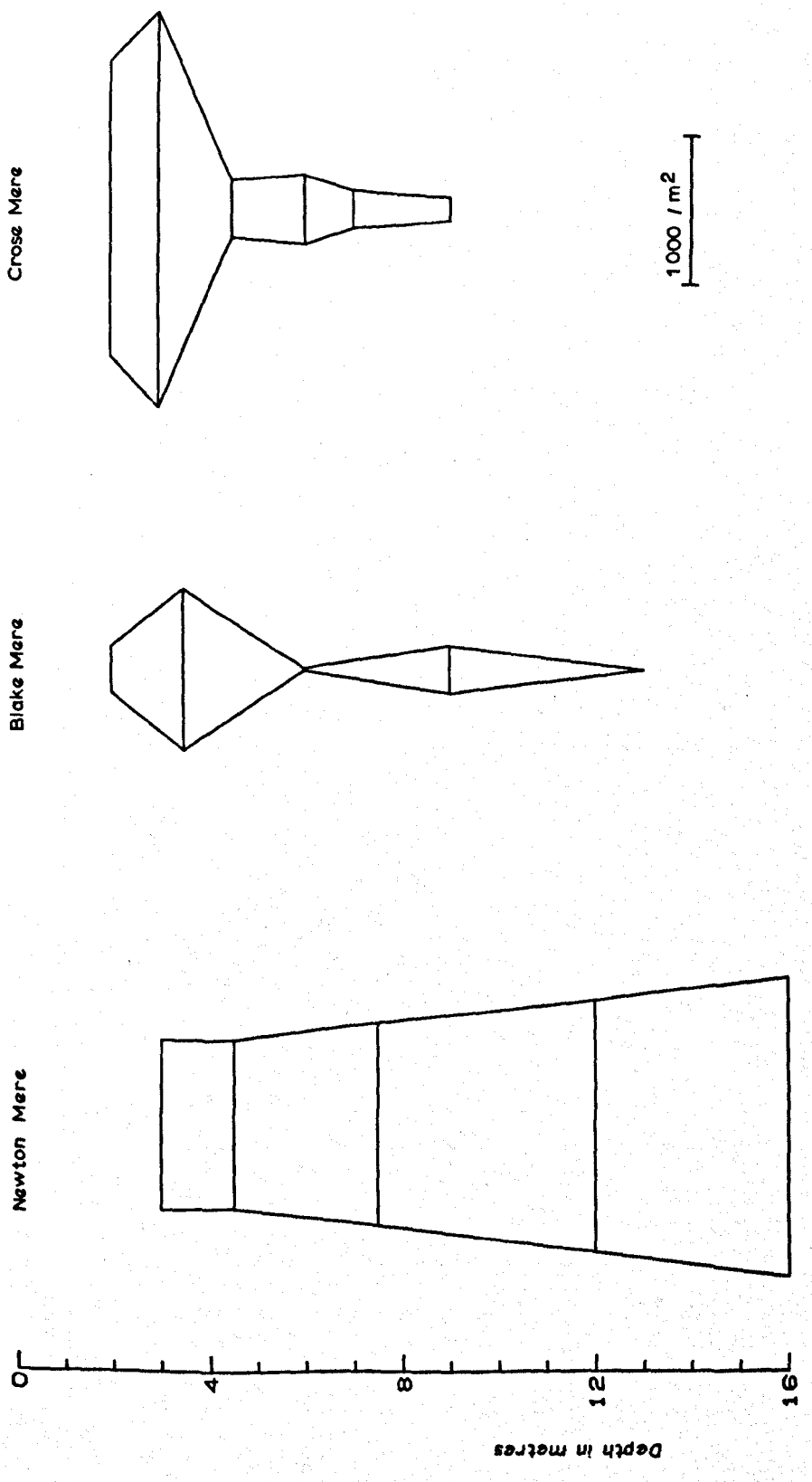


TABLE 5.2 Species list compiled from larval and adult records of the more numerous and widespread chironomids for Newton Mere, Blake Mere and Crose Mere. Numbers to left of species' names indicate ranked order of predominance

Species	Newton Mere	Blake Mere	Crose Mere
1. Chironomus anthracinus Zett.	xxxx	xxxx	xxxx
2. Procladius choreus Mg.	xxx	xxxx	xxxx
3. Microtendipes chloris Mg.	x	xxx	xxxx
4. Limnochironomus pulsus Walk.	xxx	xxx	xxx
5. Tanytarsus sp.	xxx	xxx	xxx
6. Chironomus riparius Mg.	xxx	xxx	xxx
7. Glyptotendipes glaucus Mg.	xx	xxx	xxx
8. Chironomus plumosus L.	xxx	xx	xxx
9. Endochironomus albipennis Mg.	x	xx	xxx
10. Chironomus dorsalis Mg.	x	xxx	x
Pentapedilum tritus Walk.	x	x	xx
Psilotanypus rufovittatus v.d.W.	x	x	x
Glyptotendipes gripekoveni Kieff.	x	x	x
11. Chironomus lugubris Zett.	xx	-	x
12. Phaenospectra flavipes Mg.	xx	x	-
13. Cricotopus sylvestris Fab.	-	xxx	x
14. Cricotopus trifasciatus Panz.	-	xxx	x
Polypedilum nubeculosus Mg.	x	x	-
Paratanytarsus tenellulus Goet.	x	-	x
Pentaneura monilis L.	x	x	-
Glyptotendipes paripes Edw.	x	x	-
Limnochironomus nervosus Staeg.	x	x	-
Eutanytarsus lestagei Goet.	x	x	-
Tanytarsus eminulus Walk.	x	x	-
Tanytarsus sylvaticus v.d.W.	-	x	x
Hydrobaenus apicalis Kieff.	-	x	x

Legend:

regular and abundant	xxxx
regular and few	xxx
regular and sparse	xx
occasional and sparse	x
absent	-

TABLE 5.3 Species list compiled from larval and adult records applying exclusively to Newton Mere and to Blake Mere

Species	Newton Mere	Blake Mere
Cryptochironomus "defectus" grp.	xx	-
Harnischia viridulus L.	x	-
Harnischia atriforceps Goet.	x	-
Endochironomus impar Walk.	x	-
Tanytarsus nemorosus Edw.	x	-
Eutanytarsus curticornis Kieff.	x	-
Calospectra lugens Kieff.	x	-
Camptochironomus pallidivittatus Mall.	-	x
Cricotopus obnixus Walk.	-	x
Cricotopus festivus Mg.	-	x
Psilotanypus rufovittatus van der Wulp	-	x
Psectrocladius platypus Edw.	-	x
Metriocnemus hygropetricus Kieff.	-	x
Parachironomus falcatus Kieff.	-	x
Glyptotendipes imbecillis Walk.	-	x
Limnochironomus lobiger Kieff.	-	x
Limnochironomus notatus Mg.	-	x
Paratanytarsus tenuis Mg.	-	x

Legend:

regular and sparse	xx
occasional and sparse	x
absent	-

TABLE 5.4 Species List compiled from larval and adult records applying to Crose Mere

Species	Crose Mere
Procladius choreus	
var. culiciformis L.	x
Procladius sagittalis Kieff.	x
Chironomus plumosus	
var. prasinatus Mg.	x
Chironomus dorsalis	
var. venustus Staeg.	x
var. viridicollis v.d.W.	x
Camptochironomus tentans Fab.	x
Chironomus annularius Deg.	x
Cricotopus sylvestris	
var. ornatus Mg.	x
Cricotopus tibialis Mg.	x
Cricotopus tricinctus Mg.	x
Anatopynia nebulosa Mg.	x
Psectrocladius calcaratus Edw.	x
Psectrocladius sordidellus Zett.	x
Psectrocladius stratiotes Kieff.	x
Trichocladius sp. (=?rufiventris) Mg.	x
Metriocnemus sp.	x
Prodiamesa olivacea Mg.	x
Microtendipes diffinis Edw.	x
Microtendipes pedellus Deg.	x
Eutanytarsus holochlorus Edw.	x
Stempellina bausei Kieff.	x

Legend: occasional and sparse x

TABLE 5.5 Depth distribution of chironomid larvae collected by Ekman grab from Newton Mere; values expressed as mean density/m^2/sampling depth

Species	3.0 m	4.5 m	7.5 m	12.0 m	16.0 m
Limnochiromonus pulsus	147	1	0	0	0
Phaenospectra flavipes	91	0	0	0	0
Glyptotendipes glaucus	37	0	0	0	0
Psilotanypus rufovittatus	3	0	0	0	0
Endochironomus albipennis	1	0	0	0	0
Microtendipes chloris	2	1	0	0	0
Pentaneura monilis	2	1	0	0	0
Pentapedilum tritus	0	1	0	0	0
Cryptochironomus "defectus"	30	28	0	0	0
Polypedilum nubeculosus	0	0	1	0	0
Chironomus dorsalis	0	0	1	0	0
Tanytarsus sp.	157	34	5	3	0
Procladius choreus	311	104	73	62	82
Chironomus plumosus	44	127	39	12	12
C. anthracinus	279	782	1187	1409	1749
C. riparius	2	17	12	75	44
C. lugubris	0	1	11	86	94
Total/m^2/sampling depth	1106	1097	1329	1647	1981

TABLE 5.6 Depth distribution of chironomid larvae collected by Ekman grab from Blake Mere; values expressed as mean density/m^2/sampling depth

Species	2.0 m	3.5 m	6.0 m	9.0 m	13.0 m
Glyptotendipes glaucus	95	14	0	0	0
Limnochiromonus pulsus	64	4	0	0	0
Microtendipes chloris	24	5	0	0	0
Endochironomus albipennis	14	0	0	0	0
Pentapedilum tritus	1	2	0	0	0
Pentaneura monilis	4	0	0	0	0
Parachironomus falcatus	4	0	0	0	0
Hydrobaenus sp.	1	0	0	0	0
Chironomus plumosus	0	8	0	0	0
Cryptochironomus "defectus" gp.	0	10	0	0	0
Tanytarsus sp.	1	54	0	0	0
Chironomus riparius	0	21	7	5	0
Procladius choreus	81	635	0	11	0
Chironomus anthracinus	0	284	5	259	0
C. dorsalis	0	0	0	29	0
Total/m^2/sampling depth	289	1037	12	304	0

TABLE 5.7 Depth distribution of chironomid larvae collected by Ekman grab from Crose Mere, values expressed as mean density/m^2/sampling depth

Species	2.0 m	3.0 m	4.5 m	6.0 m	7.0 m	9.0 m
Glyptotendipes glaucus	139	25	0	0	0	0
Limnochironomus pulsus	75	100	0	0	0	0
Chironomus tentans	20	0	0	0	0	0
Pentapedilum tritus	2	20	0	0	0	0
Cricotopus sylvestris	0	11	0	0	0	0
Hydrobaenus apicalis	0	5	0	0	0	0
Polypedilum nubeculosus	0	7	0	0	0	0
Trichocladius sp.	0	1	0	0	0	0
Chironomus lugubris	2	2	2	0	0	0
Psectrocladius sp.	0	0	0	6	0	0
Microtendipes chloris	1134	63	0	2	0	0
Tanytarsus sp.	6	240	11	0	0	0
Phaenospectra flavipes	6	1	0	0	0	0
Chironomus dorsalis	1	3	1	1	0	0
Endochironomus albipennis	62	63	1	6	0	0
Chironomus annularius	0	2	3	26	0	0
C. plumosus	3	44	33	6	28	1
Procladius choreus	380	902	189	174	86	44
Chironomus anthracinus	62	1000	126	169	113	90
C. riparius	0	67	7	47	12	19
Chironomus s.s.	41	39	6	14	8	2
Total/m^2/sampling depth	1933	2595	379	457	247	156

SECTION 2 DISTRIBUTION AND ABUNDANCE OF THE MOST WIDESPREAD AND ABUNDANT SPECIES

5.2.1 Chironomus anthracinus Zett.

Of all the chironomid larvae which were collected and identified, 52% were C. anthracinus, but, as shown in Fig. 5.5, the bulk of this value originated with the massive population of Newton Mere which accounted for 74% of all the chironomids taken from that mere. The relative abundance of anthracinus in each mere appears to be negatively related to eutrophication, ie. as the ionic concentration of the meres increases, so the proportion of anthracinus present in the population falls (Table 5.8).

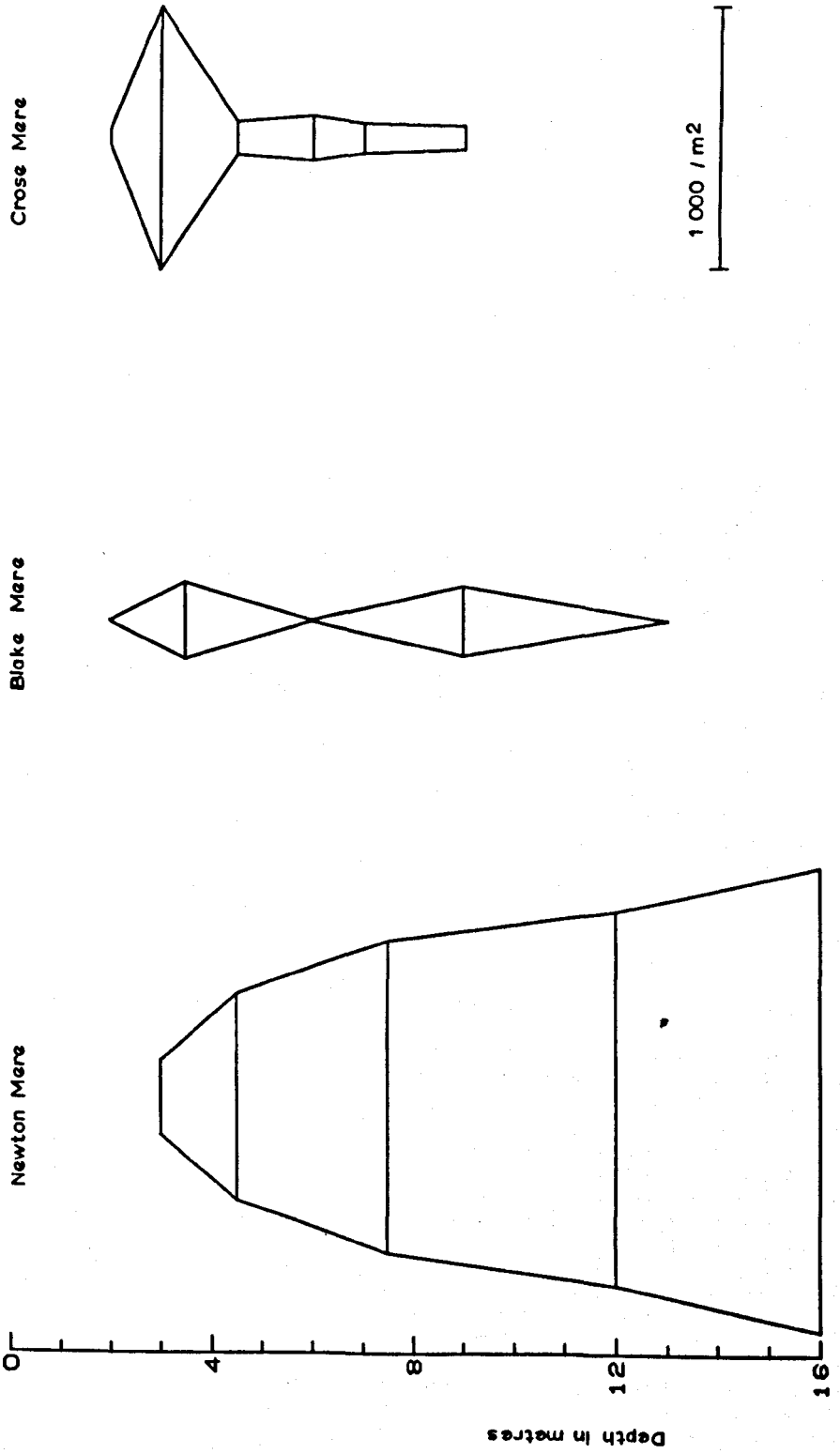
TABLE 5.8 Proportion of Chironomus anthracinus in total chironomid populations from three meres

	% values in population of C. anthracinus		
Species	Newton Mere	Blake Mere	Crose Mere
Chironomus anthracinus	74%	33%	26%

From this brief comparison, it can be seen that the conditions prevailing in Newton Mere appear to be optimal for anthracinus and lead one to suppose that the distribution of this species in Newton Mere must be more typical than has been found in either Blake Mere or Crose Mere. Comparison with these two other meres is valuable because it offers an explanation for the problem why anthracinus may not be found at a certain depth, or in a particular habitat.

Chironomus anthracinus has been found throughout Newton Mere below 3 m and its specific depth distribution is positively related to increasing depth (Fig. 5.5; Table 5.5). The mean density/m^2 (over 2

Figure 5.5 Depth distribution of Chironomus anthracinus (mean number of larvae / m^2 / sampling depth) in Newton Mere, Blake Mere and Crose Mere.



years sampling) increases at each sampling depth from 279/m^2 at 3 m, to 1187/m^2 at 7.5 m and 1749/m^2 at 16 m. Comparison with Crose Mere reveals that anthracinus is found at 2 m off the Phragmites fringe. Hand sampling from 0 - 1 m indicates that 2 m is probably the minimum depth for this species in the Shropshire meres, as the lists for the upper littoral zones do not contain anthracinus (Appendix 2).

This indicates strongly that anthracinus is intolerant of the sandy gravel conditions of the upper littoral in Newton Mere and at 2 m in Blake Mere (Fig. 5.2) or of a habitat which includes decomposing vegetation, either of reeds, as at 2 m on Crose Mere (Fig. 5.3) or of leaves, as found around the shores of Blake Mere.

Simple habitat selection experiments have been carried out in which anthracinus larvae were offered a choice of 3 habitats: sand, lake mud or leaves. The majority of the larvae burrowed into the mud. Credland (1973b) and Edgar & Meadows (1969) both describe similar behaviour in Chironomus riparius larvae.

Generally therefore, it can be stated that in Newton Mere, anthracinus larvae are widespread and increasingly abundant below 2 - 3 m where there is a mud substratum suitable for tube construction. However, Fig. 5.5 shows clearly that this generalisation is obviously not applicable to either Blake Mere or Crose Mere.

Concerning Blake Mere, Table 5.6 shows that no anthracinus larvae were ever recorded for 2 m or 13 m and occur at an average of 5/m^2 only, at 6 m. It is not surprising that anthracinus was not recorded at 2 m, for reasons which have been described above. As will be recalled, 6 m and 13 m refer to the deepest points of the two basins comprising Blake Mere and that the substrata are similar in being composed of fine black silt containing little coarse organic matter except slightly decomposed leaves. It is considered that probably there is not enough "substance"

in this silt for the larvae to construct tubes, but the major factor involved in their absence at 13 m and virtual absence at 6 m, is believed to be the early onset of stratification and resulting low oxygen levels. Fig. 5.6 shows the development throughout the season, of stratification compared against the monthly anthracinus population figures. The population fluctuations show that emergence was complete by May, when the water temperature in the profundal was 5.6°C and oxygen levels at 3%. These low temperatures would mean that any eggs which had been carried down to 13 m and similarly to 6 m, would take about three weeks to hatch, if indeed they did hatch, by which time anoxic conditions would be well developed. The significance of this is probably that as the 1st instars do not have haemoglobin, they cannot survive the low oxygen conditions.

There seems to be some indecision (Townes, 1945) whether C. anthracinus or Chironomus plumosus is the more tolerant of anoxia; in these meres it is evident that anthracinus is the better adapted species, as can be seen in Tables 5.5, 5.6 and 5.7 and from comparing Fig. 5.5 with 5.17. The absence of all other macroscopic fauna at 6 m and 13 m in Blake Mere supports this: if anthracinus cannot survive in the profundal of Blake Mere, then very little else will.

Brinkhurst and Walsh (1967) attributed the lifeless, deep water zone in Rostherne Mere to deoxygenated conditions in the sediments, caused by an abnormal quantity of faecal matter from water birds. Conditions in Blake Mere are not so extreme as in Rostherne; isothermal conditions return for three months in winter, whereas deoxygenation persisted in the deep water zone of Rostherne Mere, accompanied by hydrogen sulphide. In her search to find a similar lifeless zone in another mere, Walsh did not visit Blake Mere.

However, compared with the mean values/m^2 for anthracinus larvae in

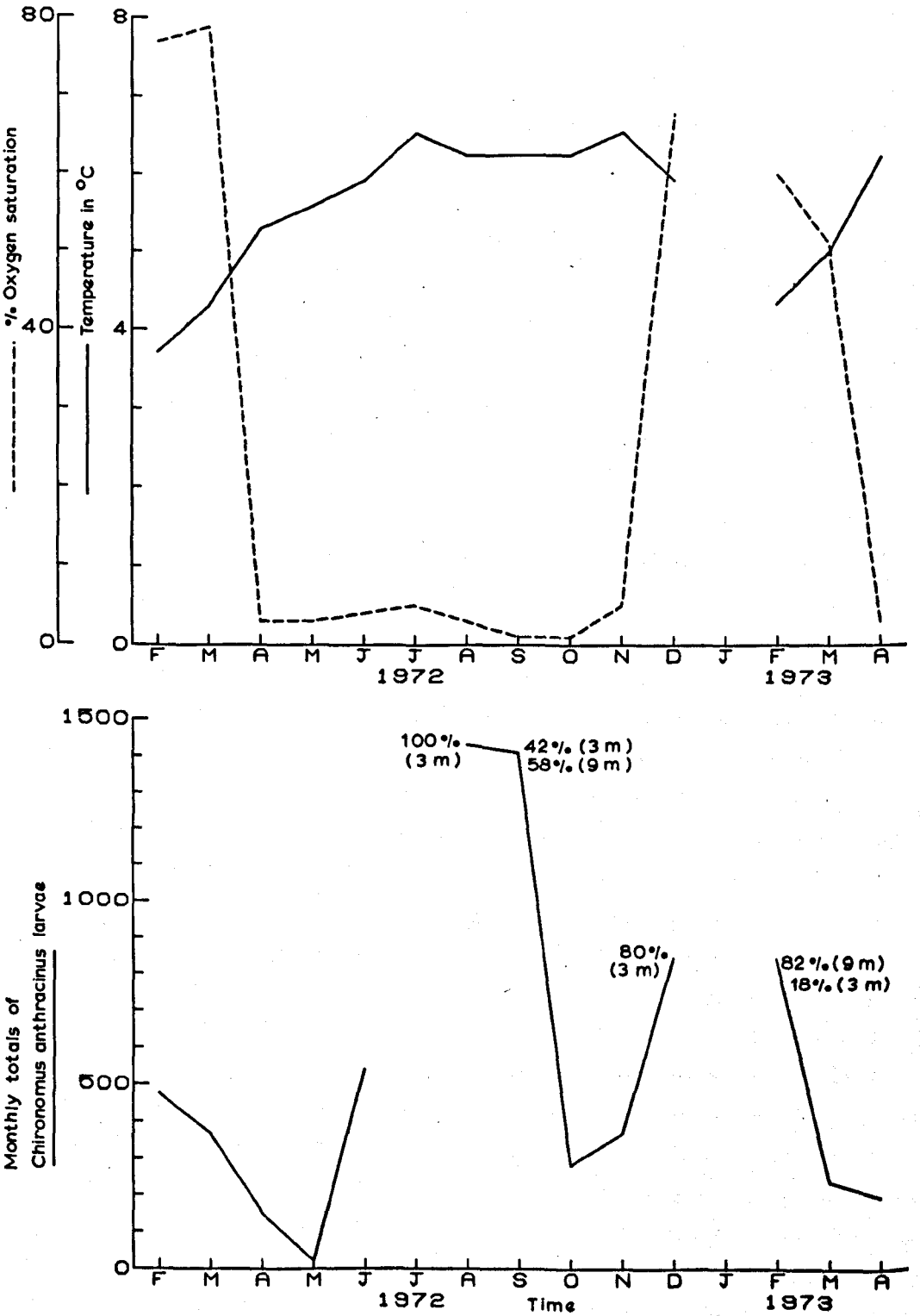


Figure 5.6 Monthly fluctuations of the density of Chironomus anthracinus larvae in Blake Mere in relation to profundal temperature and % oxygen saturation.

Newton Mere, the population levels for this species in Blake Mere, even where they have been recorded, are still low, reaching 284/m^2 at 3.5 m and 259/m^2 at 9 m (Table 5.6), suggesting that there are additional factors involved in the ecology of anthracinus in Blake Mere.

The depth distribution of anthracinus in Crose Mere (Fig. 5.5) indicates virtually the opposite to that which has been observed for Newton Mere, ie. maximum density in the fen zone at 3 m with 1000 larvae/m^2 (Table 5.7) and thereafter a rapid decline followed by similarly sized, small populations at other stations, showing a slight decrease in numbers with depth. The small population off the Phragmites fringe at 2 m, of 62/m^2, constituted only 3% of the population, (Fig. 5.3). The pattern of anthracinus distribution in Crose Mere illustrates the close connection between the factors of habitat selection and availability of food.

The bottom material in Crose Mere ranges from stones and coarse gravel through shelly, silty sand smelling strongly of hydrogen sulphide, to black organic, shelly mud. The four deepest stations (4.5, 6, 7.5 and 9 m) all have this silty sand which produces hydrogen sulphide during summer stratification. The monthly figures for numbers of anthracinus/m^2 (Appendix 2) illustrate the adverse effect this environment has upon, not only anthracinus larvae, but also Procladius choreus larvae. From April/June, depending on when the mere stratifies, to October/November, chironomid larvae are virtually absent below 6 m, and even when the mere is isothermal, population figures are quite small, the highest recorded density being 390/m^2 at 4.5 m in January 1973. The bottom deposits found at these four stations have only a small amount of detritus mixed with and overlying the sand, which - even without the adverse effects of the sandy substratum and the hydrogen sulphide - would be insufficient to support large populations.

The only station to support a fairly large population of anthracinus larvae is at 3 m in the fen zone, which had thick black mud mixed with bleached gastropod shells and coarsely shredded organic matter. The station is shallow enough not to be under the influence of the thermocline in summer, but consideration of Table 5.7 reveals that with a mean population of 2595/m^2, competition for space must be very high when all the other fauna characteristic of such rich littoral zones are included.

It is inevitable that predation will be high, specifically from diving ducks, fish and carnivorous insect larvae, such as Phryganea varia Fab. which was seen to take chironomids in dishes in the laboratory.

How heavy the predation was on the chironomid population and specifically anthracinus is not known but certain similarities with the monthly population figures for Blake Mere, and the contrast with those for Newton Mere, give some indication how anthracinus can change its life-cycle in adapting to the environment, as discussed below.

Emergence of the overwintering population of anthracinus larvae was complete by June 1972 in Blake Mere, 6 weeks after the onset of thermal stratification (Fig. 5.6) and was followed by a summer generation of larvae which first reached its peak at 3 m in August and a month later at 9 m. The percentage values on the graph refer to the proportion within the population of the larvae from any one station. The value for August of 100% in Fig. 5.6, came exclusively from 3 m and was followed a month later by another peak which was mainly from 9 m. This generation had emerged by October and gave rise to the overwintering generation at 3 and 9 m which was much smaller than the summer generation. A similar pattern has been observed in the generation at 3 m reaching a peak first (80% of the total population in December 1972) followed by a peak at 9 m which accounted for 82% of the total population. It appears that anthracinus is bivoltine in Blake Mere. The time differential

between peaks at 3 and 9 m would not be affected and the larvae would grow faster in the more favourable conditions. The 9 m station was very close to the steeply shelving shore of Blake Mere and may not have been so affected by stratification as its depth implies.

A similar situation has been observed at 3 m in Crose Mere (Fig. 5.7), which does not stratify so early as Blake Mere. Emergence of the overwintering generation was complete by June 1972, a month before thermal stratification developed, which that year only lasted just over a month before being destroyed by storms. All the percentage values on this graph refer to 3 m and it can be seen that both high summer peaks in August 1972 and June 1973 were due to the population at this depth. It would appear that the life cycle can be completed in about 2 months in shallow water probably due to a combination of factors including high temperature, high oxygen and plentiful food resulting in a high sustained growth rate. Predators would still be plentiful, as the fen reeds bordering the eastern alder carr would be a prime habitat for fish fry. Emergence of the summer generation gives rise to a small winter population which appears to migrate to deeper waters. In November 1972, 85% of the total anthracinus population was at 3 m; by January, only 43% remained there, while numbers at all other stations except 2 m increased. Migration of larvae is not unexpected: before anoxic conditions develop in the profundal, the larvae move towards shallower water before emergence, as can be seen from the monthly figures for each station in Appendix 2. The larvae are also distributed passively over the surface of the mud (Barthelmess, 1963) by water currents. The 1972/1973 winter generation decreased in number after January 1973 and emergence was complete in May, when the mere stratified.

In comparison, the anthracinus population in Newton Mere appears not to be bivoltine but perhaps not strictly univoltine, (Fig. 5.8). There

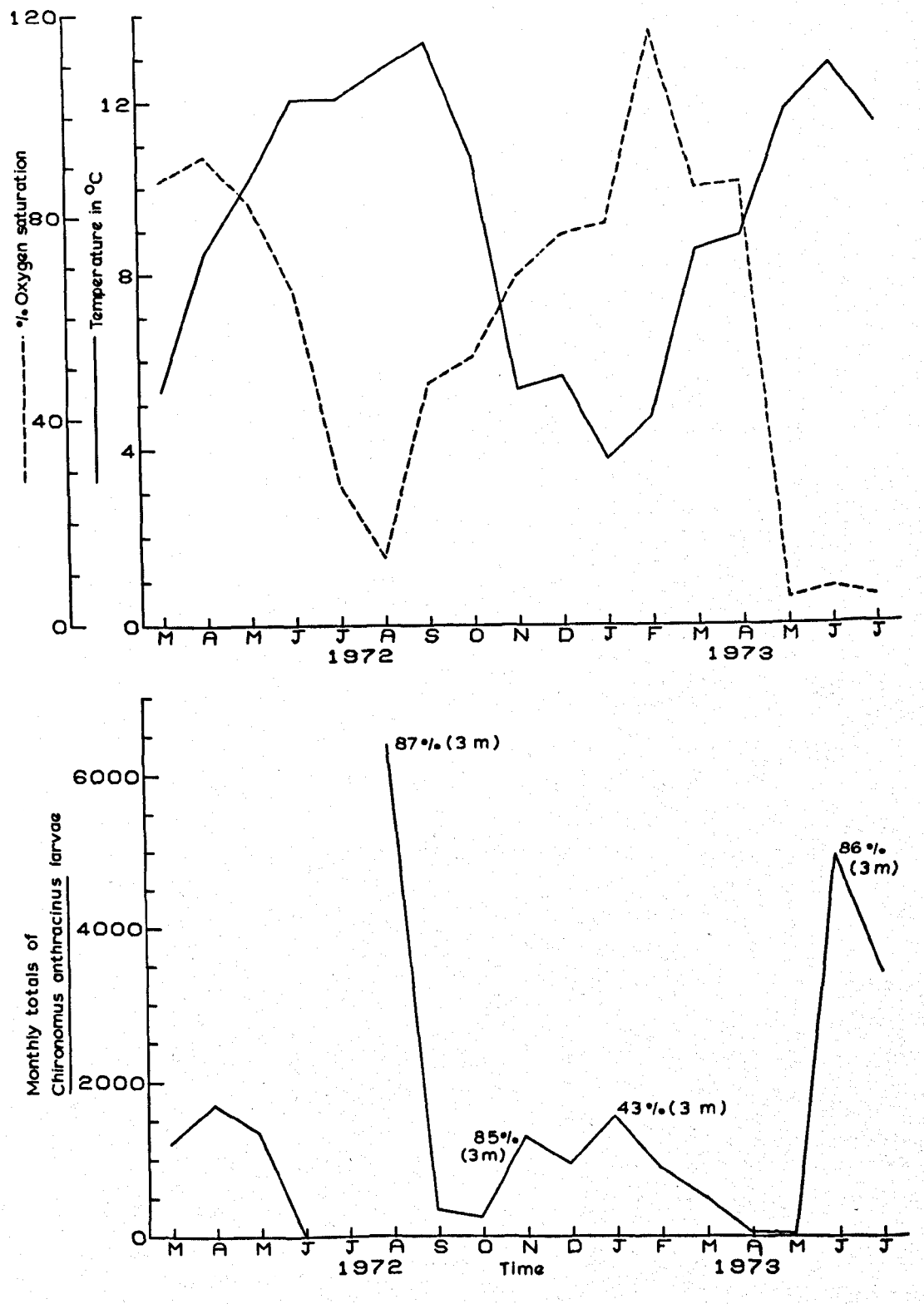


Figure 5.7 Monthly fluctuations of the density of Chironomus anthracinus larvae in Crose Mere in relation to profundal temperature and % oxygen saturation.

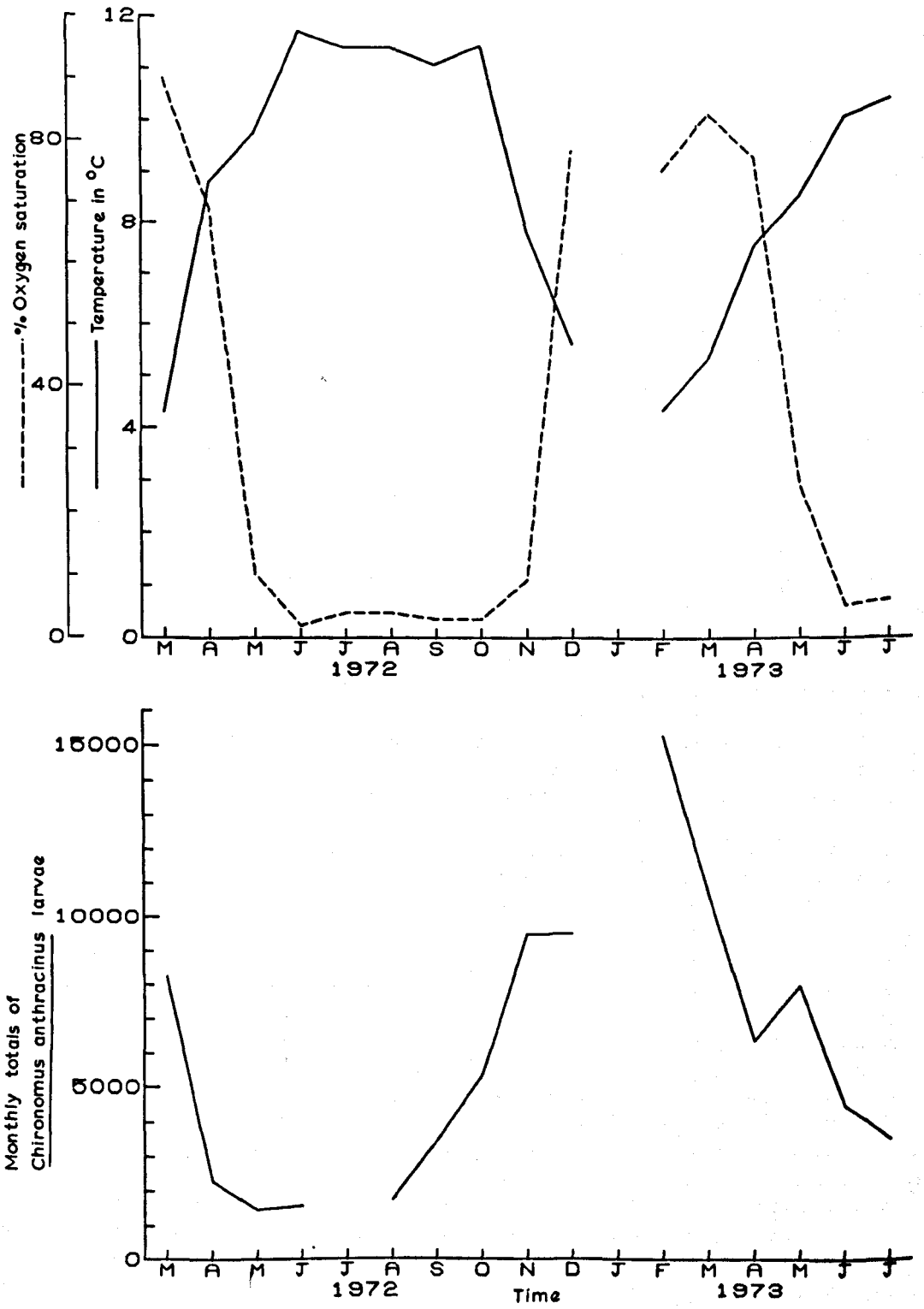


Figure 5.8 Monthly fluctuations of the density of Chironomus anthracinus larvae in Newton Mere in relation to profundal temperature and % oxygen saturation.

seems to be evidence that one generation of anthracinus is "staggered". The numbers increased after August but the growth rate levelled off between November and December, to be followed by a rapid increase in February at 16 m from 4177 to 7281/m^2 and from 108 to 2207/m^2 at 3 m before declining prior to emergence. The stabilisation of growth between November and December represents the maturation of one group, and the peak following in February, represents the second group.

A point of comparison between Figs. 5.6, 5.7 and 5.8, lies in the decline in population density immediately the lake water showed an increase in temperature following the January minimum temperature. It is not known whether this decline is due to increased predation by fish, low level emergence in the population or migration of the larvae (or even their death), but the former would appear to offer the most reasonable explanation. Chironomus s.s. pupae did not appear in benthic samples in Newton Mere until 19.4.72 and 11.4.73, when they were present at all depths beyond 7.5 m, so emergence would seem not to account for the late winter fall in numbers. Similarly, although chironomid larvae are known to be transported passively by water currents (Barthelmess, 1963; Davies, 1974), there is no reason to believe the larvae moved away from, or died on, the transect line only.

Allen (1935) and Craig (1974) both describe perch as feeding more actively in spring and summer than in winter, and also during their migration to shallow water from deep water to spawn from April to June (Bagenal, 1973). Varley (1967) lists benthic chironomids as comprising a major part in the diet of most freshwater fish, including perch, which form large populations in the Shropshire meres and it is possible that the decline is due to fish predation. Other fish common to all three meres include roach, pike and bream, with eels living only in Blake Mere and Crose Mere. Some tench and rudd are also found in Crose Mere,

(Pratt, pers. comm.).

In those populations where anthracinus is bivoltine, the winter generation is lower in number than the summer generation. This could be related to the effect of weather conditions on parental fecundity and survival. Jónasson (1970) describes how anthracinus will swarm only in "dead calm":

"....If the weather is rough, fewer imagines will hatch and the resultant number of juvenile larvae is small."

Weerekoon (1956) also inferred that windy weather had an unfavourable influence by reducing not only the amount of time spent swarming and thereby the number of successful copulations, but also the number of ovipositing flights. The summer generations of anthracinus were emerging by the end of September in Shropshire when autumn gales were influencing turn-over of the meres and therefore it is assumed that the lower winter generations were a result of reduced survival in the adult stage of the summer generation.

5.2.2 Procladius choreus Mg.

Procladius choreus is a predatory benthic chironomid of the sub-family Tanypodinae, the distribution and abundance of which is largely determined by the oxygen content of the water and the availability of food. Analysis of the gut contents of some larvae revealed a large number of oligochaete spicules, as well as fragments of Daphnia and nauplii from Cyclops. Morgan (1949) observed P. choreus larvae feeding on 1st instar chironomid larvae which were emerging from an egg mass, as well as earthworm pieces and even members of their own species when starvation threatened. These findings are largely supported by Kajak and Dusoge (1970) who listed Chironominae larvae under 5 mm, Crustacea and algae, which apparently supplement the diet, as being the food of Procladius. These authors also found that P. choreus fed on

the 1st instars of other chironomids, thus culling the population to some degree. It is unlikely that choreus feeds on larger, healthy Chironominae larvae, although Morgan (1949) found that a closely related Tanypodinid, Anatopynia nebulosa Mg. attacked wounded Chironomus larvae of 10 mm. Loden (1974) found that a species of Procladius fed on Dero digitata Mull. and Stylaria fossularis Leidy when kept in experimental ponds.

Procladius larvae are highly mobile, having a lateral fringe of swimming hairs and can therefore move away from adverse conditions and congregate where food is most plentiful. Because their distribution is closely related to the availability of food, Tanypodinids are not considered to be an important feature in lake classification (Humphries, 1936).

P. choreus is a fairly ubiquitous species, seemingly tolerant of a wide variety of conditions, having been found not only in typical freshwater habitats but also in a pool in Brown Moss, Cheshire, which had a pH of 4 and also highly saline pools and canal stretches in Cheshire (Buckley, pers. comm.). The one condition of which P. choreus seems to be intolerant, is low oxygen. Stagnant field pools rarely contain Procladius larvae and support instead another Tanypodinid, Anatopynia varia Fab. Fig. 5.9 gives no indication of the absence during summer of choreus from areas below the thermocline in Newton Mere and Crose Mere. No choreus larvae were ever obtained from 6 or 13 m in Blake Mere and a total of 13 larvae only were taken in 14 months from 9 m. Fig. 5.10 shows how, with the advent of stratification in Crose Mere and Newton Mere, the numbers of choreus larvae fall to $0/m^2$. This reduction is considered to be due principally to emergence of the adults, ie. the life-cycle of choreus is synchronised with the seasonal variations in oxygen. Evidence that migration to shallow waters also

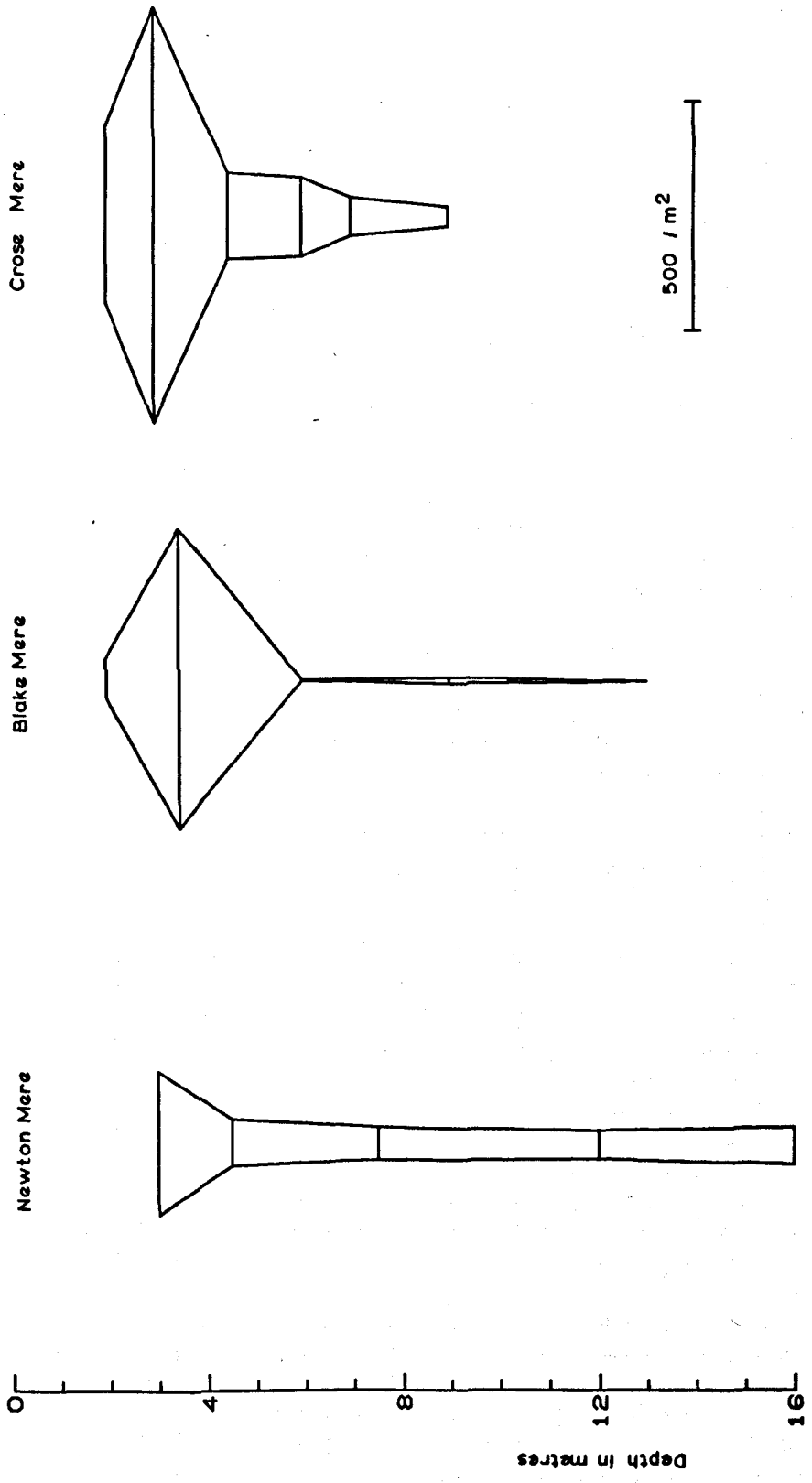


Figure 5.9 Depth distribution of Procladius choreus (mean number of larvae / m^2 / sampling depth) in Newton Mere, Blake Mere and Crose Mere.

occurs, can be found in the monthly figures for each station (Appendix 2) in Newton Mere for April and May 1972, when numbers fell in the profundal and increased temporarily in the littoral and sublittoral prior to emergence.

The maximum density of this species occurs between 2 and 4 m in all three meres (Fig. 5.9) and can reach over 2000 larvae/m^2 (Crose Mere, 3 m, Dec. 1972). At 3 - 3.5 m in Newton Mere and Blake Mere, choreus is the predominant form, comprising 28% and 61% respectively of the chironomid population (Figs. 5.1 and 5.2). At 3 m in Crose Mere, P. choreus accounts for 35% of the population there, second only to Chironomus anthracinus. Weerekoon (1956) found that a related species Procladius crassinervis Zett. was most abundant in the phytal zone of Loch Lomond at 4 m, although its general range was from 0 - 180 m. Similarly, P. choreus is found throughout the meres (except, of course, below 3 m in Blake Mere), although the population does decline with depth (Fig. 5.9).

Crose Mere supported the largest population of P. choreus, an observation which can be related to the wider variety and greater abundance of prey in Crose Mere, compared with the other two meres. Table 5.9 indicates the relative percentage values of choreus in the total chironomid catch/mere.

TABLE 5.9 Proportion of Procladius choreus in chironomid populations from three meres

Species	% values in population of P. choreus		
	Newton Mere	Blake Mere	Crose Mere
Procladius choreus	8%	40%	30%

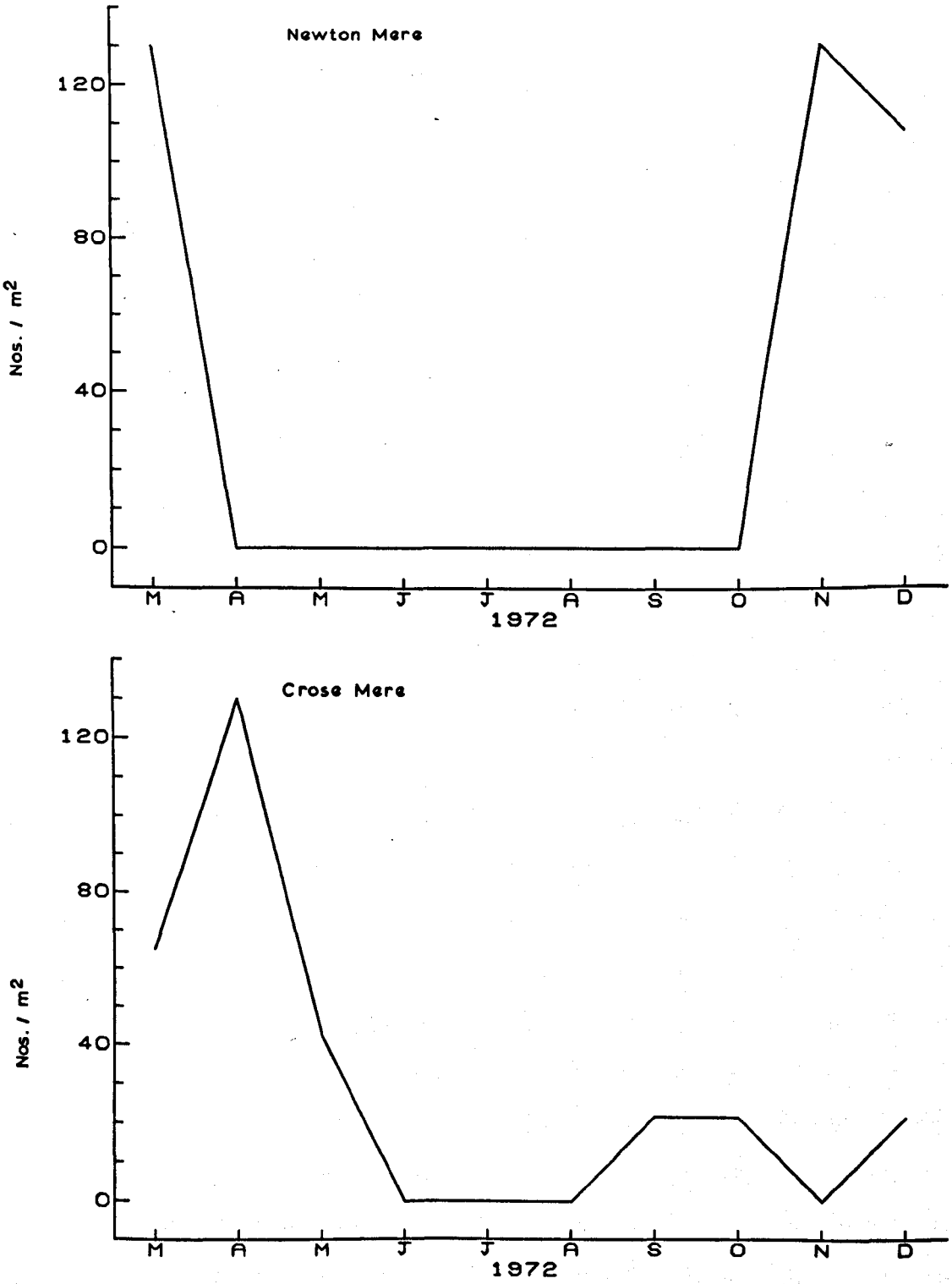


Figure 5.10 Abundance of Procladius choreus : monthly totals / m^2 at Newton Mere (16 m) and Crose Mere (9 m).

This table shows that although choreus was regularly sampled in each mere, it was abundant only in Blake Mere and Crose Mere, as was also shown in Table 5.2.

The mean values/m^2 for each sampling depth (Tables 5.5, 5.6 and 5.7) indicate further that at the depth of maximum density in each mere (3.0 - 3.5 m), there were 311 choreus/m^2 in Newton Mere, 635/m^2 in Blake Mere and 902/m^2 in Crose Mere. The higher value of 40% for Blake Mere in Table 5.9 shows only that there were low numbers of species other than C. anthracinus and P. choreus.

Although P. choreus is a very mobile animal whose pattern of distribution varies frequently, the monthly abundance figures for each mere, computed by totalling the number/m^2 at each sampling depth, give an indication of developments within each population. Fig. 5.11 shows the fluctuations in the numbers sampled each month. The depths marked on the graphs refer to those sampling stations at which peak populations occurred. The most obvious feature of the three graphs is that choreus appears to be bivoltine in Newton Mere and Blake Mere and multivoltine in Crose Mere. This is supported by the appearance, after the population peaks, of larvae which were about to pupate. A second feature is that, with one exception (Crose Mere, 6 m, Sept. 1972), the population peaks all occur at 2 - 3 m, the zone of maximum density for this species. Mundie (1957) found choreus was bivoltine in Kempton Park East Resevoir (KPER), Staines, with a bimodal emergence suggesting two generations.

The overwintering generation of P. choreus (Oct. 1972 - March 1973) in Crose Mere has the longest duration compared with the two short summer generations which reach their peaks in May and September, before and after, respectively, thermal stratification. An explanation for the third late summer generation at Crose Mere must be found in relation to stratification, which, in 1972, lasted for only two months, although

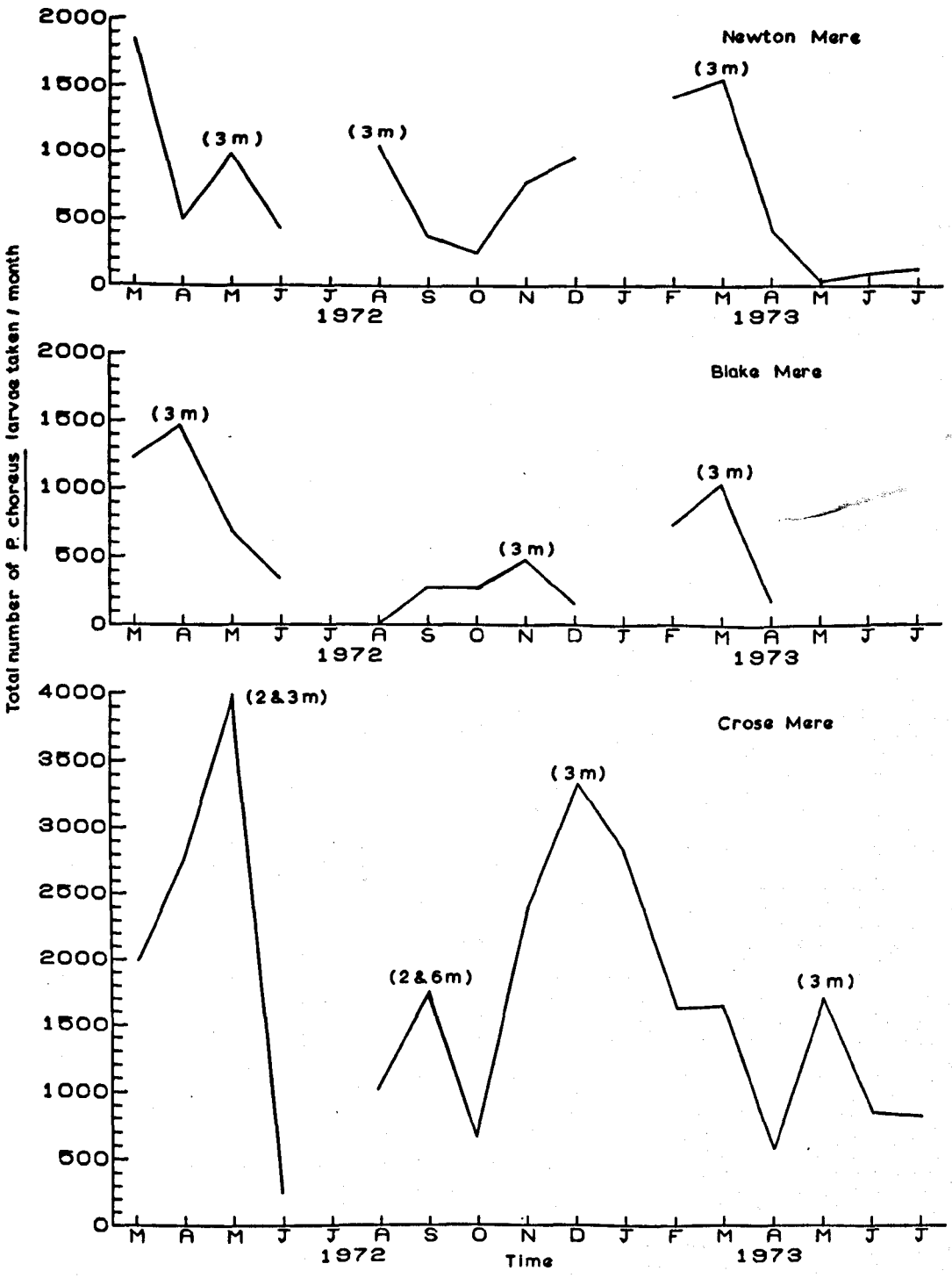


Figure 5.11 Abundance of Procladius choreus : total larval numbers / month for Newton Mere, Blake Mere and Crose Mere.

the choreus population increased during this time (July and August), Fig. 5.11). The peak populations occurred at 3 m which, although unaffected by stratification, would be affected by one of the causes of stratification - high temperatures. During this time the temperature reached 17.3°C and oxygen levels were high. The benthic fauna at 3 m on Crose Mere was very varied and abundant and would provide P. choreus with all the necessary food for rapid growth.

It cannot be stated with any real certainty that P. choreus was not multivoltine in Newton Mere and Blake Mere because the January 1973 data are missing. An interesting feature which does emerge, however, and which complements the Crose Mere data, is that the peak summer populations in 1972 occurred at the start of stratification and at the overturn, thus indicating that emergence and growth of the early instars is temperature dependent. The increases in population at 3 m in Blake Mere and Newton Mere were not under the thermocline, which developed during April and May in Newton Mere and was immediately followed by a peak population in May. Stratification broke down in September/October in Newton Mere following the August peak population. Thermal stratification lasted from March/April in Blake Mere to November/December, with peak choreus populations in April and November.

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SECTION 3

DISTRIBUTION AND ABUNDANCE OF THE LESS WIDESPREAD AND ABUNDANT SPECIES

5.3.1 Glyptotendipes glaucus Mg.

This red-blooded Chironomus s.l. Mg. larva is confined to the upper littoral zone down to 3.5 m in all the meres, and is most abundant in Crose Mere at 2 m off the Phragmites fringe, where the mean density was found to be 139/m^2 (Fig. 5.12). G. glaucus is the dominant chironomid at 2 m in Blake Mere (Fig. 5.2) where it comprises 32% of the population at a mean density of 95/m^2. Glyptotendipes larvae were collected by hand netting at 1 - 2 m from the gravelly shore at Newton Mere on 18.11.71, when 7 were found in the sample.

The substratum at 1 - 2 m in Newton Mere is comparable with 2 m at Blake Mere, except that mats of Cladophora, attached to stones and chunks of rotting wood, litter the surface of the ridge at the latter station. This seems to indicate that Glyptotendipes favours a substratum which offers places in which the larvae can shelter. The fall-off in the numbers with increase in water depth (14/m^2 at 3 m in Blake Mere; 25/m^2 at 3 m in Crose Mere) may be due to a reduction in places to live because of the smothering action of the lake silt.

The favourite place for G. glaucus larvae to live was found to be in chunks of rotting, water-logged wood, where they inhabited silk-lined channels. A small piece of wood about 2 x 1" could easily contain 20 - 30 glaucus larvae. Sokolova (1959) recorded that Glyptotendipes larvae accounted for 80% of the total biomass of all chironomid larvae among the submerged trees of the Rybinskoye reservoir.

Other habitats where G. glaucus larvae were found, included empty Gastropod shells and mats of Cladophora in which the larvae would build a rather flattened sand-coated tube of sturdy construction. Humphries (1937) described glaucus larvae as living "...between growths of

Cladophora" in the Grosser Plöner See. The larvae collected from 1 - 2 m in Newton Mere also constructed sandy tubes held together with salivary silk.

Maitland and Hudspith (1974), working on Loch Leven, Scotland, indicated from their data that Glyptotendipes larvae were preferred sand dwellers, having found 4515/m^2 in sand and 2310/m^2 in mud. Smith and Young (1973) collected Glyptotendipes from the zoöbenthos of Wood Park Pond, a naturalised marl pit on Merseyside. These two records, when compared with Berg (1950), who included G. glaucus among the net-spinning plankton eaters of those chironomids reared from Potamogeton, seem to indicate that Glyptotendipes larvae are very tolerant in their choice of habitat, and if no ready-made shelter can be found, the larvae construct their own.

An analysis of the gut contents of G. glaucus revealed detritus and bits of plankton, and thus supports Berg's (1950) findings. Loden (1974) described how a species of Glyptotendipes fed on the oligochaetes Stylaria fossularis Leidy and Limnodrilus hoffmeisteri Claparede when kept in an experimental pond, with no other food available.

An interesting morphological observation has been made concerning the very large head capsules of glaucus larvae. The frontal edge of the frontoclypeus is concave and the whole head capsule is very strong and thick. The hypochilum is typical for the Chironominae but the mandibles are stronger than usual. Although staining for lignin in the gut contents revealed no wood particles, it is assumed that at some stage the larvae must construct their tunnels in the chunks of wood and that the gross head capsule is an adaptation to burrowing in wood.

Glyptotendipes glaucus Mg. larvae were identified using Kalugina's (1963) key for separating glaucus and gripekoveni Kieff. A few

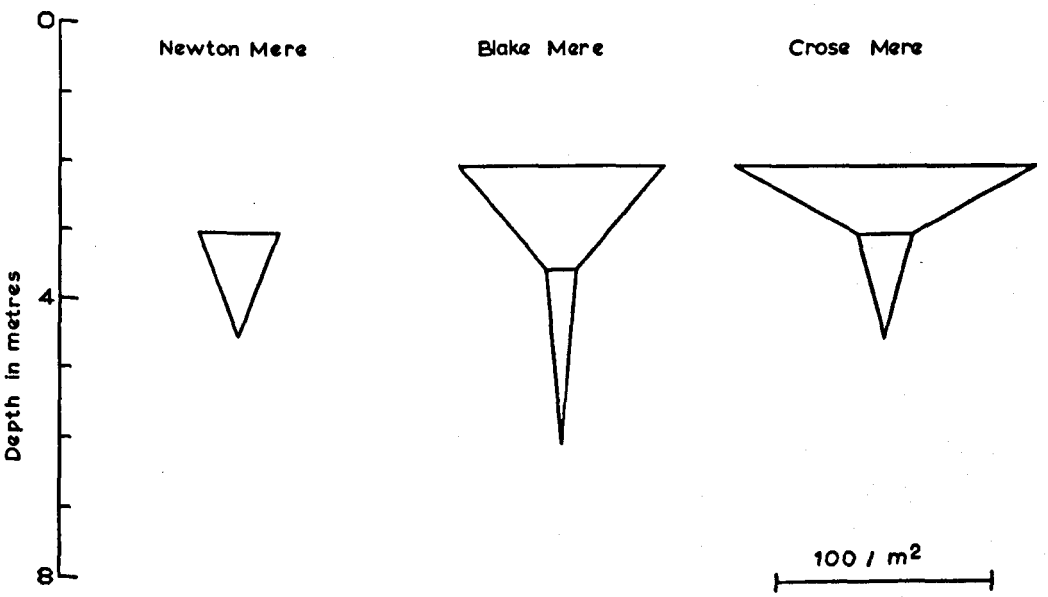

Figure 5.12 Glyptotendipes glaucus

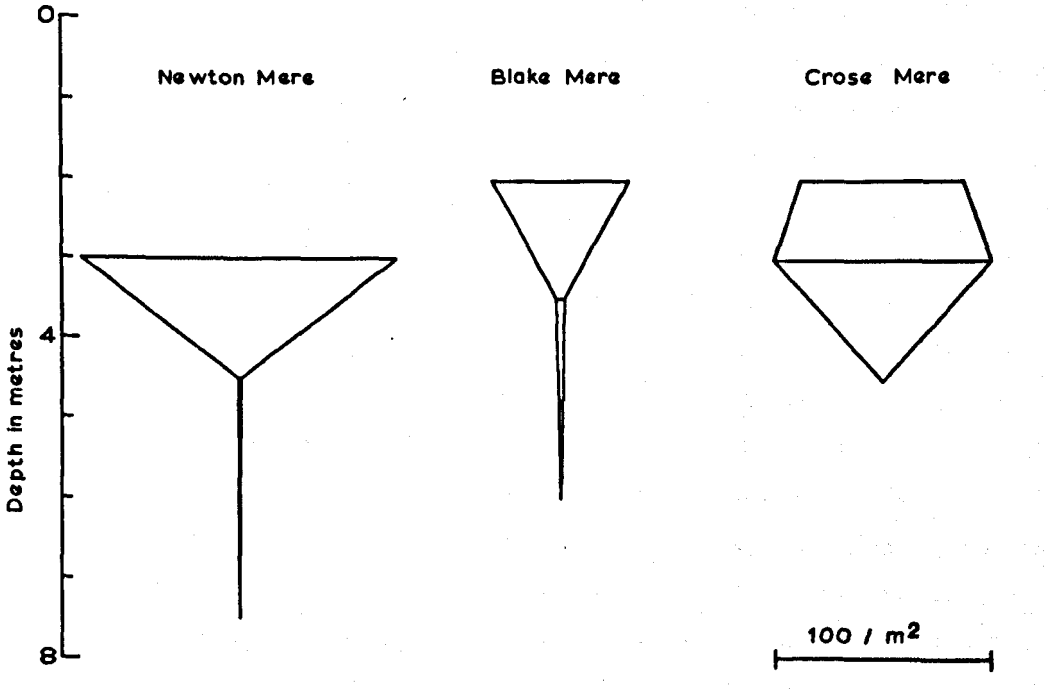

Figure 5.13 Limnochironomus pulsus

Figures 5.12 & 5.13 Depth distributions of Glyptotendipes glaucus and Limnochironomus pulsus (mean number of larvae / m^2 / sampling depth) in Newton Mere, Blake Mere and Crose Mere.

gripekoveni and imbecillis Walk. adults were reared from Blake Mere material.

5.3.2 Limnochironomus (= Dicrotendipes) pulsus Walk.

This rather small, red Chironomus s.l. larva with its characteristic black fronto-clypeus, is confined to the littoral zone from 1 - 4.5 m in the Shropshire meres, where it constructs messy tubes from sand grains and mud, and is most abundant at 3 m in Newton Mere (mean density 147/m^2). L. pulsus has been found regularly at 2 and 3 m in Crose Mere (75/m^2 and 100/m^2 respectively) and at 2 m (64/m^2) in Blake Mere (Fig. 5.13).

The first factor common to these four, otherwise dissimilar, sampling stations is that, in varying degrees, the substrata contain sand. L. pulsus larvae were also collected by hand netting around the shores of Newton Mere. Mundie (1957) found exactly the same distribution in Kempton Park East Reservoir (KPER) and recorded that pulsus lived in algal mats, littoral muds, reed beds and stony substrata and that its optimal site was between 3 and 5 m. Maitland and Hudspith (1974) recorded that Limnochironomus larvae were equally abundant in mud and sand.

The depth distribution of L. pulsus seems to depend much on the ionic concentration of each lake. All four stations in the Shropshire meres are shallow, indicating that pulsus could be an upper littoral species in eutrophic lakes. In less productive lakes, such as Llyn Tegid (Hunt and Jones, 1972), Esrom in the 1930s (Berg, 1938) and the Grosser Plöner See, (Humphries, 1937), the maximum depth for pulsus is about 20 m, although maximum density occurs between 6 and 8 m. Dunn (1954), sampling in Frederiksborg Sløtts, a highly eutrophic and polluted lake in Denmark, found Limnochironomus larvae around the edge.

5.3.3 Microtendipes chloris Mg.

M. chloris is a littoral species in the Shropshire meres although in Esrom Lake, Berg (1938) described Microtendipes sp. (which he called "The Chironomus connectans Group") as being littoral and sublittoral with a range from 0 - 15 m. M. chloris was found at very low densities at Newton Mere in sand, and in Cladophora mats in Blake Mere but the station at which chloris was most abundant, and on average formed 59% of the population there, was 2 m in Crose Mere, off the Phragmites/Carex fringe (Fig. 5.14). The mean density over the sampling period was 1134/m^2 which reflects a massive June 1973 population of 12005/m^2. M. chloris was the third most abundant chironomid in Crose Mere, accounting for 22% of the total number collected.

The mean density at 3 m, in the fen zone, was 63/m^2. Although a thick bed of Phragmites and Carex also borders the mere at this station, the samples were taken 3 - 5 m off the edge of the vegetation. At 2 m, the samples were taken immediately at the edge of the Phragmites. This indicates that chloris favours close proximity with reeds and this was confirmed when chloris larvae were found inhabiting empty sections of reed stems just wide enough for the larva and about twice its length. The larvae, which lie undulating in a silk "harness", were also found immediately under the broken epidermis of decomposing chunks of Phragmites, as well as in empty Gastropod shells and occasionally swimming free.

Mundie (1955) found M. chloris in low numbers at KPER between 1 - 2 m. The species had one emergence period from April to May.

5.3.4 Endochironomus albipennis Mg.

Unlike the red-blooded M. chloris, Endochironomus albipennis is a large yellow larva also belonging to the Chironomus s.l. and according to

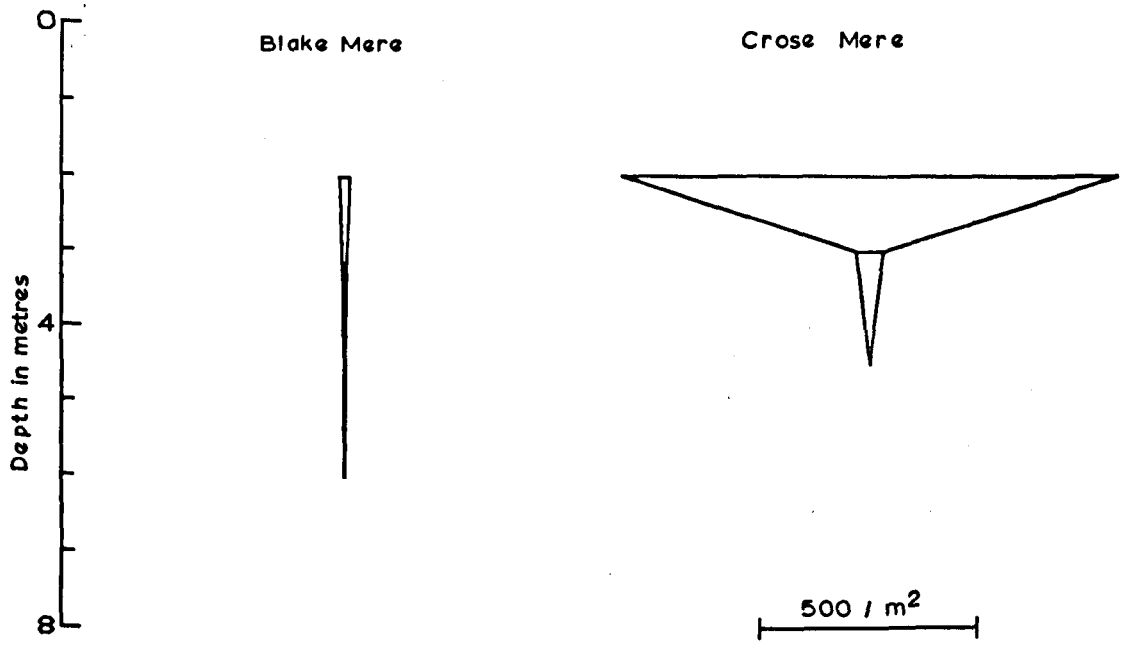

Figure 5.14 Microtendipes chloris

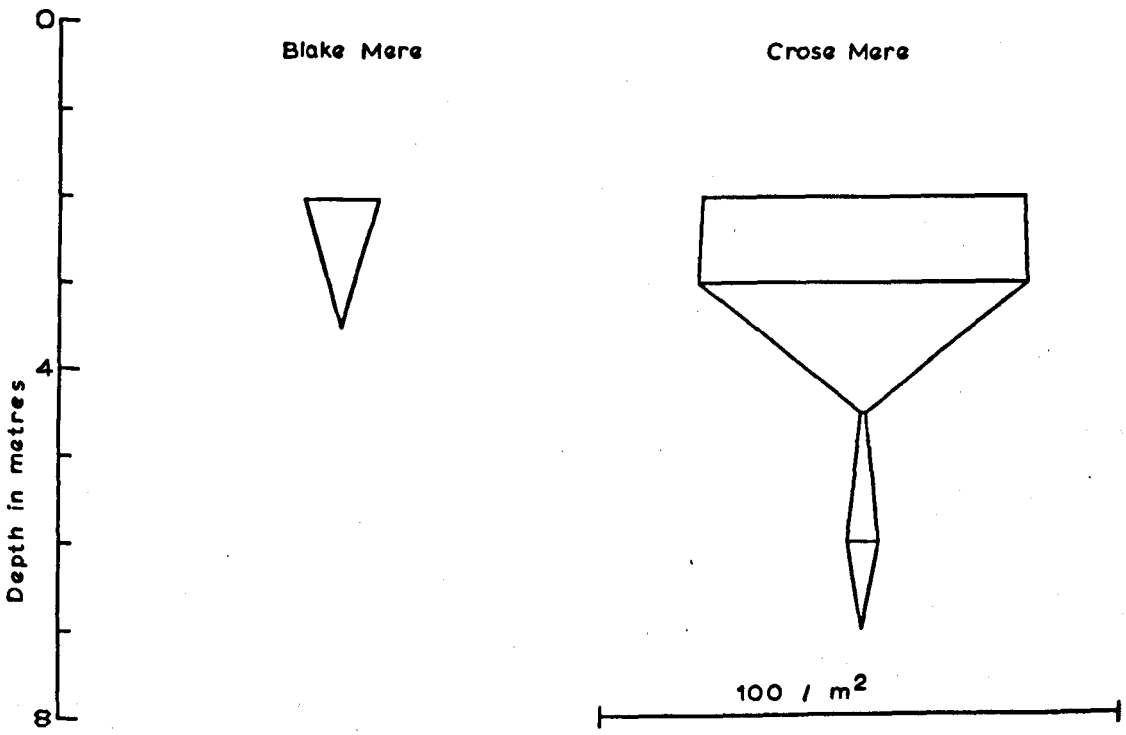

Figure 5.15 Endochironomus albipennis

Figures 5.14 & 5.15 Depth distributions of Microtendipes chloris and Endochironomus albipennis (mean number of larvae / m^2 / sampling depth) in Blake Mere and Crose Mere.

Lenz (1955) and Kalugina (1961), a species included in the 'nymphoides' group of this genus.

E. albipennis was abundant only in Crose Mere (Fig. 5.15), particularly at 2 and 3 m ($62/m^2$) and was collected down to 6 m in low numbers. Although only a small population was found at 2 m in Blake Mere, hand netting amongst the banks of leaves at the edge of the mere showed that albipennis was very numerous here, living in sparse nets spun between two leaves. The larvae were living amongst Cladophora at 2 m and on any firm surface, eg. reed stalks, in Crose Mere. Its virtual absence from Newton Mere seems to indicate that albipennis requires shelter and a firm surface on which to spin its net. The net is vital to this larva and within it, albipennis can withstand the most anoxic conditions, as was discovered in the laboratory when larvae were occasionally overlooked and found later, when everything but albipennis and anthracinus had died.

Most of the literature states that E. albipennis is a littoral form, although Hunt and Jones (1972) described it as being "more common in the deep littoral zone" of Llyn Tegid. Mundie (1955) found its optimum was 1 - 2 m in KPER; Humphries (1937) called it "an algal dweller", littoral in the Grosser Plöner See; Meuche (1939) found albipennis in algal mats in eutrophic lakes. Dunn (1954) found albipennis only in the more eutrophic Danish lakes she was surveying, eg. Esrom, Almind, Aum and Børres, and not in the oligotrophic lakes which were tending towards dystrophy. Berg (1938), also working on Esrom, did not take nymphoides larvae from his deep-water transect but only from amongst vegetation in shallow water. However, Humphries (1936) found albipennis frequently down to 12 m in Windermere, and Hunt and Jones (1972) recorded it at 6, 12, 20 and 30 m in Llyn Tegid.

As regards feeding, Walshe (1951) found albipennis was a filter-feeder, feeding on plankton and organic matter. Loden (1974), however, described how Endochironomus larvae would feed from their tubes on the oligochaetes L. hoffmeisteri and S. fossularis.

On 13.12.72, cysts or capsules as described by Lenz (1955) were found at 3 m in Crose Mere. These capsules contain a dormant Endochironomus larva and are presumably a protective device for surviving the winter, although no other species was found to use such a device. Larvae removed from these capsules did not survive more than a couple of days and were not at all active.

5.3.5 Tanytarsus sp.

The optimal site for larvae of Tanytarsus s.s. was at 3 m in each mere (Fig. 5.16), although larvae were found down to 12 m in the less eutrophic Newton Mere. Beyond the site of maximum density, the numbers rapidly declined. Tanytarsus larvae were most abundant in Crose Mere at 3 m where the mean density in the mud was found to be 240/m^2; and in Newton Mere at 3 m (157/m^2), where they accounted for 13% of the chironomid population.

No larvae were collected by hand netting from the mere shores. All the larvae collected were tube dwellers which were more attracted to a muddy substratum. In Loch Leven, Maitland and Hudspith (1974) found that the Tanytarsini there were preferred sand dwellers, with 11333/m^2 in sand and only 1668/m^2 in the mud.

Several of the species in the Shropshire meres were Eutanytarsus spp. (lestagei Goet., holochlorus Edw. and curticornis Kieff.) which according to Berg (1938) are the true inhabitants of the bottom ooze of lakes but which are confined in these meres to the littoral and sublittoral because of their high oxygen requirement.

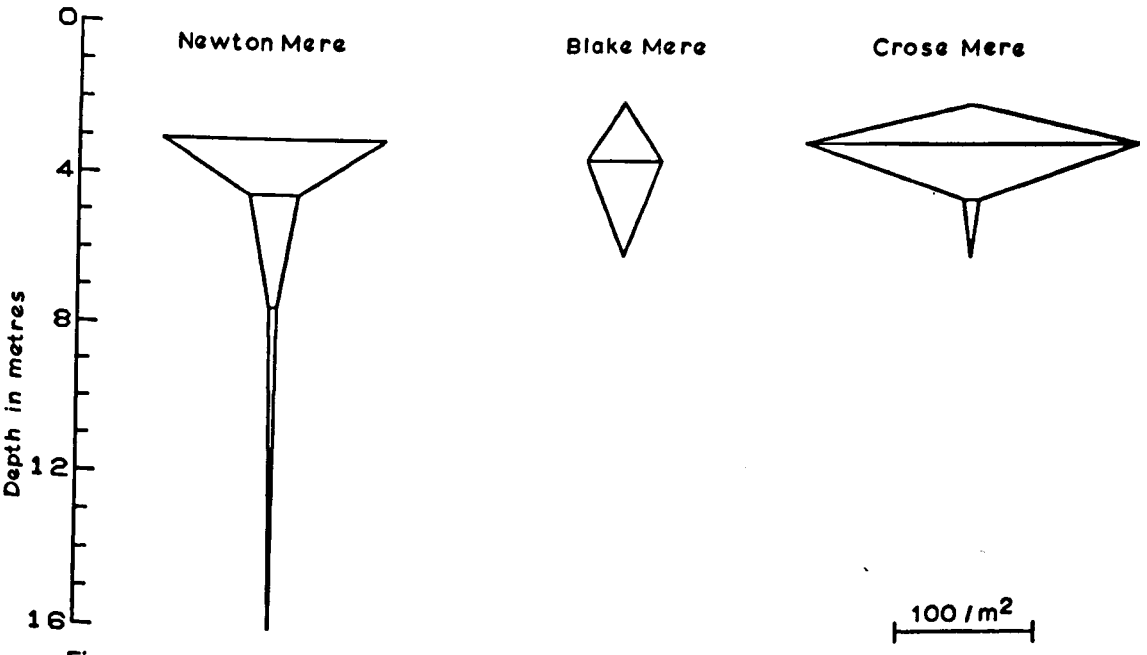

Figure 5.16 Tanytarsus sp.

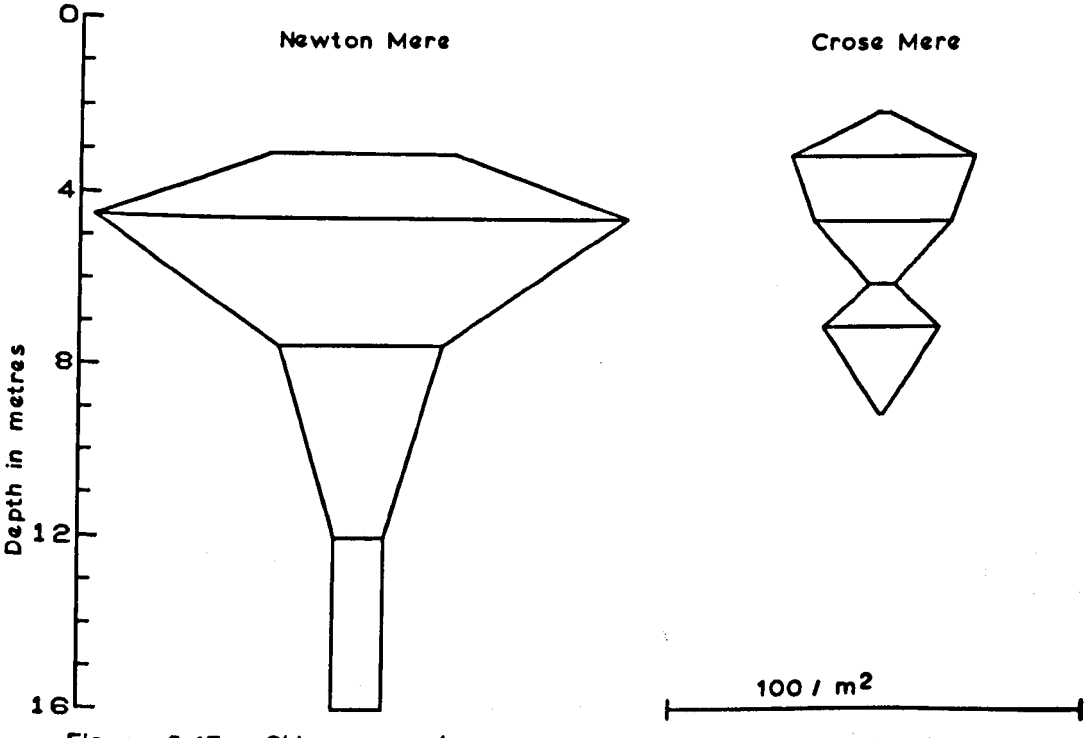

Figure 5.17 Chironomus plumosus

Figures 5.16 & 5.17 Depth distributions of Tanytarsus sp. and Chironomus plumosus (mean number of larvae / m^2 / sampling depth) in Blake Mere, Newton Mere and Crose Mere.

Tanytarsini larvae have a far wider range in oligotrophic lakes and are the predominant chironomids there (Thienemann, 1915). Humphries (1936), working on a less eutrophic Windermere, frequently found Tanytarsus larvae down to 60 m.

The majority of Tanytarsus larvae remain unidentified because the keys available are unreliable and incomplete. The species which are listed in Tables 5.2, 5.3 and 5.4 were reared and identified using Coe (1950) and Reiss and Fittkau (1971).

Paratanytarsus tenellulus Goet. (=Microspectra tenellula (Reiss 1968)) is a littoral species and was found in Newton Mere and Crose Mere amongst the mud and decaying reed stalks.

Eutanytarsus lestagei Goet. was collected between 2 and 3 m in Newton Mere and Blake Mere amongst coarse detritus. Reiss and Fittkau (1971) describe it as littoral although Mundie (1957) found it abundant at 7 m in KPER where it tolerated the low oxygen conditions of the resevoir during summer.

Tanytarsus eminulus Walk. was found only in Newton Mere and Blake Mere. Hall (1951) described it as being amongst fine gravel and silt with a covering of mud and organic debris such as leaves and twigs.

Tanytarsus sylvaticus v.d.W. prefers a more eutrophic habitat having been found only in littoral sediments of productive lakes as well as ponds and puddles. Mundie (1957) found it was univoltine in KPER with its optimal density between 3 and 5 m.

Tanytarsus nemorosus Edw., Eutanytarsus curticornis Kieff., and Calopsectra lugens Kieff. were collected from Newton Mere only amongst littoral sand and sediments. Reiss and Fittkau (1971) described the distribution of curticornis as being from 0 to 6 m but Humphries (1937) found it in the Grosser Plöner See from only 50 cm to 1 m in sand. Mundie (1957) found C. lugens down to 7 m but this species did not appear to have a marked optimum depth zone. It is a cold stenotherm of N. Europe which can

inhabit the profundal.

Eutanytarsus holochlorus Edw. and Stempellina bausei Kieff. were found only in Crose Mere. E. holochlorus is an inhabitant of littoral sediments in puddles, ponds, meres and lakes. Humphries (1937) found it at 2 - 3 m in coarse detritus, 3 - 5 m in the dead shell zone and at 20 m in mud in the Grosser Plöner See.

5.3.6 Chironomus plumosus s.s.L.

The 4th instar of this Chironomus s.l. larva can reach 24 mm and is recognisable by its clear red abdomen and green mottling on the thoracic segments. It is generally regarded as being the profundal species of distinctly eutrophic lakes but nowhere in these meres did it reach the abundance and widespread distribution of C. anthracinus, being virtually absent from Blake Mere (Table 5.6).

Fig. 5.17 shows the depth distribution of this species in Newton Mere and Crose Mere. C. plumosus is abundant only in Newton Mere where its optimal density lies at 4.5 m ($127/m^2$), although it is found throughout the mere beyond 3 m. The figure shows that there is a gradual decrease in numbers with depth to a mean density of $12/m^2$ at both 12 m and 16 m.

In Crose Mere, three stations have rather similar densities: 3 m, 4.5 m and 7 m where mean values of 44, 33 and $28/m^2$ respectively are found. Although there were fewer larvae at 7 m, plumosus accounted for 11% of the population there and 9% at 4.5 m.

Mundie (1957) found plumosus throughout KPER with its optimum density at 7 m. Shallow mud prevented tube building. C. plumosus is a solitary tube dweller which prefers a muddy substratum. Because of its larger size, it is thought not to fare well when in competition with C. anthracinus.

Lindeman (1942) described how plumosus and anthracinus can withstand

lengthy periods of anaerobiosis. Berg (1938) established that anthracinus and plumosus penetrated oxygen-free mud 30 - 40 cm below the surface and lay still in the tunnels when conditions became bad.

A report by Johnson and Munger (1930) on the excessive abundance of plumosus in Lake Pepin on the Mississippi River, highlights the effect of increasing eutrophication caused by organic pollution and sewage. The lake water was not in fact badly polluted but plumosus adults became serious pests and the larvae reached densities of 7000/m^2 in the lake mud.

5.3.7 Chironomus riparius Mg.

The distribution of riparius in Newton Mere, where it is most abundant, is quite different from that of plumosus. Density increases with depth down to 12 m and reaches levels of 75/m^2 (Fig. 5.18). Table 5.5 shows the mean densities at each sampling depth.

C. riparius is present at low levels in Blake Mere (Table 5.6) and is one of the few species found at 6 m. There seem to be two peaks of optimal density in Crose Mere at 3 and 6 m where mean values are 67 and 47/m^2 respectively.

No riparius larvae were found in hand netting samples. It is a tubiculous larva preferring a muddy substratum. This larva was identified from keys as 'riparius' but it is quite possible that the data may include some early instars of C. anthracinus which have not developed the black ventral plates of the mature 4th instar. The only visible difference other than size, between anthracinus and riparius is the degree of darkening of the ventral plates. In the 4th instar this difference is quite apparent when comparing the two species but earlier instars are paler in colour and the difference may not be so apparent.

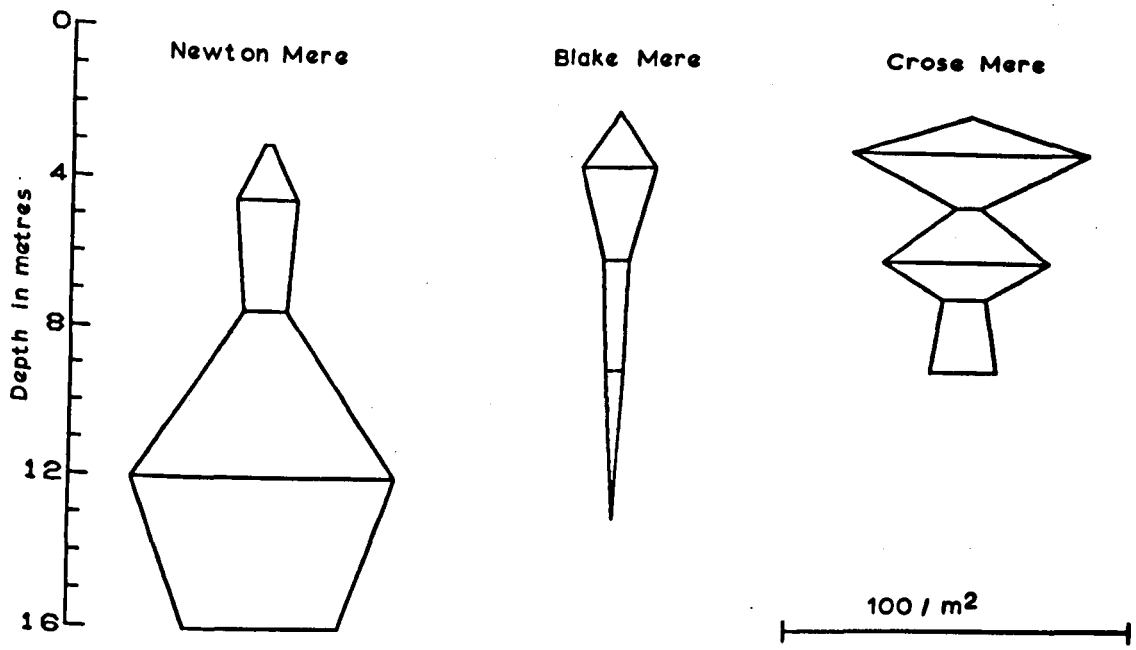

Figure 5.18 Chironomus riparius

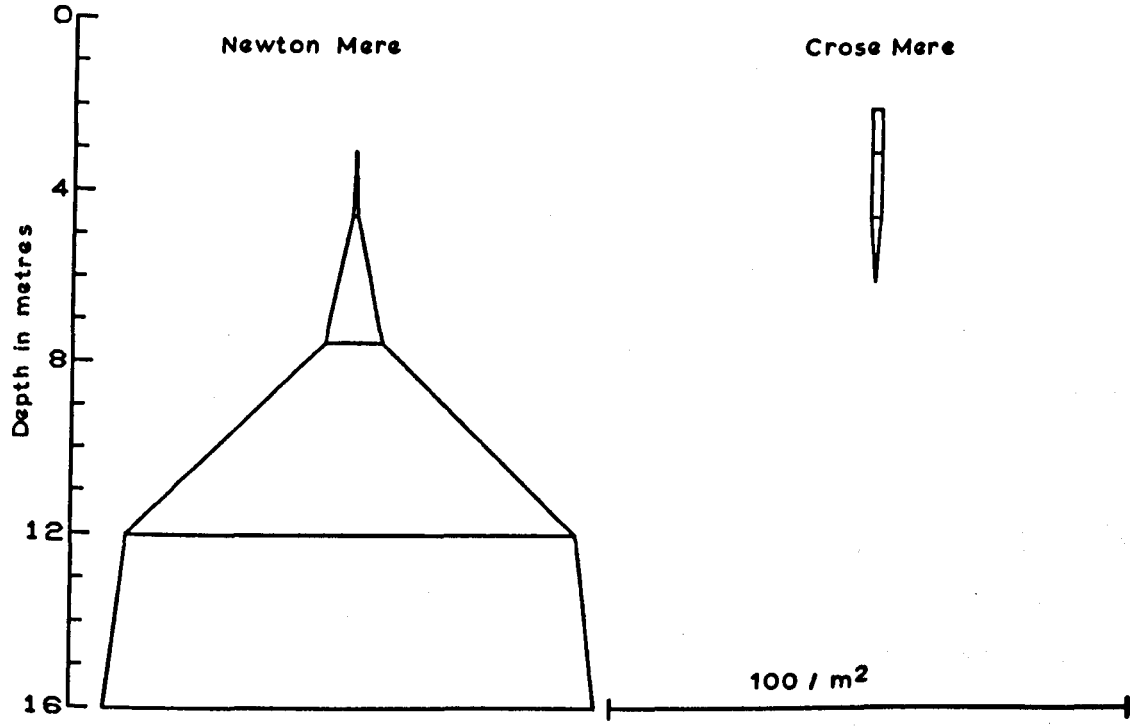

Figure 5.19 Chironomus lugubris

Figures 5.18 & 5.19 Depth distributions of Chironomus riparius and C. lugubris (mean number of larvae / m^2 / sampling depth) in Newton Mere, Blake Mere and Crose Mere.

5.3.8 Chironomus lugubris Zett.

This is a "thummi"-type larva as described in Chapter 3 with no colouring on the ventral plates at all. Fig. 5.19 shows that its presence in Crose Mere was negligible and it was never found in Blake Mere.

C. lugubris is abundant and widespread only in Newton Mere where its distribution compliments that of anthracinus. Table 5.5 shows that lugubris is a profundal species, increasing in density from 11/m^2 at 7.5 m to 86/m^2 at 12 m and 94/m^2 at 16 m. It accounts for 5% of the population at both 12 m and 16 m. Its habitat and behaviour are similar to the other Chironomus s.s. Group B, Series 1 species (Coe 1950) in that it is a sedentary tube dweller living in the mud of eutrophic ponds and lakes.

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SECTION 4

DISTRIBUTION AND ABUNDANCE OF THE LEAST WIDESPREAD AND ABUNDANT SPECIES

5.4.1 Phaenospectra flavipes Mg. is a small dark red Chironomus s.l. species which was found in Newton Mere and Crose Mere in the littoral zone. Mean densities reached 91/m^2 at 3 m in Newton Mere (Table 5.5) and accounted for 1.4% of the total number of larvae taken from there. There was a mean density of 6/m^2 at 2 m in Crose Mere, (Table 5.7).

5.4.2 Cryptochironomus 'defectus' is the group name given to those species which have 6 - 7 pale lateral teeth either side of a membranous hypochilum, (Fig. 3.9). Larvae were found in the littoral zones of Newton Mere and Blake Mere but were more numerous and widespread in Newton Mere where mean densities of 30/m^2 at 3 m and 28/m^2 at 4.5 m were found, (Table 5.5). 10/m^2 were found at 3 m in Blake Mere, (Table 5.6). Hunt and Jones (1972) found Cryptochironomus 'defectus' from 6 - 40 m and regularly at 6, 12 and 20 m. 'Defectus' may be a semi-carnivorous group; Loden (1974) found that Cryptochironomus larvae ate oligochaetes L. hoffmeisteri and Nais elinguis in a polluted stream and quotes Wirth and Stone (1956) and Darby (1962) as also having described Cryptochironomus as carnivorous.

5.4.3 Pentapedilum tritus Walk. was found irregularly and in low numbers in the littoral of all three meres, (Tables 5.5, 5.6 and 5.7). It was most abundant (20/m^2) at 3 m in Crose Mere.

5.4.4 Polypedilum nubeculosus Mg. is a littoral species in eutrophic lakes and was found at 3 m in Crose Mere, and at 7.5 m in Newton Mere, (Tables 5.5 and 5.7).

5.4.5 Chironomus dorsalis Mg. is a species indicative of organic pollution such as sewage. It was found in a trickle flowing into Crose Mere from some farms and cow byres, in such huge numbers that the mud heaved with their movement, (Table 5.7).

5.4.6 Chironomus annularius Deg. is recorded for Crose Mere only, Table 5.7), occasionally in the littoral zone but more abundantly at 6 m where the mean density was $26/m^2$.

5.4.7 Chironomus tentans Fab. has been described very fully by Sadler (1935) and lives in "pools, ponds, shallow warm-water lakes and sluggish streams" occurring in greatest abundance where the water has been treated with fertilizer. C. tentans was found at 2 m in Crose Mere (Table 5.7) at an average density of $20/m^2$. The only other site where tentans was found was Copmere, Staffs. where the larvae were living in sand overlain with silt and detritus.

5.4.8 Pentaneura monilis L. was found irregularly and in low numbers at 3 m and 4.5 m in Newton Mere and at 2 m in Blake Mere, (Tables 5.5 and 5.6). This species was very numerous in the profundal of Oakmere, Cheshire which is an oligotrophic mere. Hunt and Jones (1972) found monilis irregularly at 6, 12 and 20 m in Llyn Tegid where its maximum density reached $48/m^2$ at 20 m. Humphries (1937) described the habitats in the Grosser Plöner See where monilis was found as being in fine detritus, coarse sand and algae on stones at 1 m and amongst algae in the dead shell zone at 2 m.

5.4.9 Psilotanypus rufovittatus v.d.W. is a benthic predator and was found in very low numbers at 3 m in Newton Mere, (Table 5.5). This was

the most abundant form in KPER (Mundie, 1957) whose greatest abundance occurred at 1 - 3 m and at 7 m.

5.4.10 Hydrobaenus sp. (= ?apicalis) Kieff. was recorded at very low densities in Blake Mere and Crose Mere from shallow water, (Tables 5.6 and 5.7). This species was also caught flying in swarms over the outlet from the sewage works at the University of Keele.

5.4.11 Trichocladius sp. (= ?rufiventris) Mg. was found once in Crose Mere at 3 m, (Table 5.7). Humphries (1938) described this genus as littoral dwellers.

5.4.12 Psectrocladius sp. is recorded only for Crose Mere at 6 m at a mean density of $6/m^2$ (Table 5.7). Humphries (1937) found representatives of this genus in the Grosser Plöner See in the littoral zone in fine detritus and coarse sand.

5.4.13 Cricotopus sylvestris Fab. Included under this heading are varieties of sylvestris, such as ornatus, and another species, trifasciatus. The larval forms of Cricotopus are not easily distinguished, although the adult forms can be identified. Larvae were found in algae and fresh vegetation at 3 m in Crose Mere (Table 5.7) but were most numerous on the undersides of Nuphar pumila in Blake Mere. Each leaf could be covered with dozens of nets which the larvae quickly vacated when disturbed. Cricotopus larvae were only found when the lily pads had come to the surface. Berg (1950) quotes Kettisch (1936-1937) who described how the winter is passed as eggs attached to stems. Plankton nets samples during spring in 1974 failed to find any larvae swimming at the surface. Berg also notes that trifasciatus channels through the leaves of aquatic

plants between the epidermal layers. Mundie (1957) described sylvestris as a cosmopolitan species found in lakes and streams under leaves, in mud and in mats of Cladophora.

* *

The most obvious general feature of the data presented in this chapter is that as eutrophication increases, so does the number of chironomid species found in each mere, and also the number of species unique to each mere.

29 species were recorded for the less eutrophic Newton Mere, but only seven as shown in Table 5.3 were unique to it. Of the forms confined to Newton Mere, Tanytarsus sp. and Cryptochironomus sp. are both, according to Maitland and Hudspith (1974) preferred sand dwellers, while Endochironomus sp. lives in sand or mud. It is considered that the uniformity of the littoral zone of Newton Mere which is predominantly sand and gravel and therefore inhospitable to many chironomids, is a major factor accounting for the low numbers of species. The virtual absence of Microtendipes sp. and Glyptotendipes sp., indicators of, respectively, reed beds and trees with their roots in water, supports this contention. Of less importance as a factor perhaps, could be the annual spring treatment with copper sulphate crystals, which were thrown into the water around the shore and lay dissolving on the sand for at least several hours. The toxic effect of the copper could well have killed most of the fauna living around where the crystals lay.

In constrast, Crose Mere, the most eutrophic of the three meres, had the highest number of species recorded (40), half of which (21) were unique to the mere and had representatives from the four subfamilies (Table 5.1). The littoral zone of Crose Mere has been described in excellent detail by Sinker (1962) and ranges from a stony shore, alder carr, Phragmites reedswamp and a fringe of Carex paniculata, to fen, thereby offering a variety of habitats with different substrata and vegetation. The success of Microtendipes chloris in Crose Mere is directly related to there being a Phragmites and Carex fringe, as this species lives in the narrow, empty stems of these reeds.

TABLE 5.10 Depth distribution of chironomid larvae collected by Ekman grab from Newton Mere (NM), Blake Mere (BM) and Crose Mere (CM). Values expressed as mean density/m^2/zone

Species	Littoral zone 0 - 4 m			S'littoral zone 5 - 6 m			Profundal zone 7- deepest pt.		
	NM	BM	CM	NM	BM	CM	NM	BM	CM
Glyptotendipes glaucus	9	24	41	0	5	0	0	0	0
Limnochironomus pulsus	37	16	44	<1	1	0	0	0	0
Phaenospectra flavipes	23	-	2	0	-	0	0	-	0
Microtendipes chloris	<1	6	299	<1	2	<1	0	0	0
Chironomus tentans	-	-	5	-	-	0	-	-	0
Endochironomus albipennis	<1	4	31	0	0	2	0	0	0
Pentapedilum tritus	0	<1	5	<1	<1	0	0	0	0
Psilotanypus rufovittatus	<1	-	-	0	-	-	0	-	-
Cricotopus sylvestris	-	-	3	-	-	0	-	-	0
Pentaneura monilis	<1	1	-	<1	0	-	0	0	-
Hydrobaenus apicalis	-	<1	1	-	0	0	-	0	0
Parachironomus falcatus	-	1	-	-	0	-	-	0	-
Polypedilum nubeculosus	0	-	2	0	-	0	<1	-	0
Trichocladius sp.	-	-	<1	-	-	0	-	-	0
Cryptochironomus "defectus"	8	0	-	9	3	-	0	0	-
Chironomus plumosus	11	0	12	42	3	13	6	0	7
Chironomus lugubris	0	-	1	<1	-	<1	64	-	0
Psectrocladius sp.	-	-	0	-	-	2	-	-	0
Chironomus dorsalis	0	0	1	0	0	<1	<1	3	0
Tanytarsus sp.	39	<1	62	11	18	4	<1	0	0
Chironomus riparius	<1	0	17	6	9	18	12	<1	8
Procladius choreus	78	20	321	35	212	121	20	1	33
Chironomus anthracinus	70	0	265	260	96	98	395	29	51
Chironomus annularius	-	-	<1	-	-	10	-	-	0
Chironomus s.s.	-	-	20	-	-	7	-	-	2

Legend

absent from mere -

none collected at that site 0

Blake Mere again occupies an intermediate position between the dilute Newton Mere and the eutrophic Crose Mere, this time in both number of species recorded (34) and the species restricted to it (11). The presence of Orthocladiinae larvae, which were absent from Newton Mere, is associated with the increase in emergent vegetation, in particular, the Nuphar pumila and a small pocket of Iris.

The overriding predominance of C. anthracinus (Figs. 5.1, 5.2, 5.3 and 5.5) distinguishes all three meres as Chironomus lakes, indicative of the true eutrophic condition according to Lenz's (1925) adaptation of Thienemann's (1915) classification of lakes. However, examination of a summary of the depth distributions for each mere (Table 5.10) shows that, as might have been expected, this description is an oversimplification.

Microtendipes and Polypedilum spp. are considered to be the chief accompanying forms in Chironomus lakes, and on this basis, only Crose Mere is truly eutrophic. Newton Mere has Limnochironomus and Tanytarsus as the major accompanying species to C. anthracinus and in Blake Mere, Glyptotendipes accompanies anthracinus.

Therefore Newton Mere and Blake Mere show some features rather more typical of the last stages of a Sergentia-type lake in which the accompanying forms are Tanytarsus sp. and other "gill-less" forms of Chironominae, apart from Microtendipes. Glyptotendipes sp. (except for polytomus Kieff.) and Limnochironomus sp. are "gill-less", ie. without ventral tubules.

The distribution of Tanypodinae is of no especial interest in this context, being found in great numbers wherever food is plentiful.

* * * *

6.

RESPIRATORY MECHANISMS

SECTION 1 EXTRACELLULAR RESPIRATION: STUDIES OF TRACHEAL PATTERNS

INTRODUCTION

A comparative morphological study of the tracheal patterns in larval chironomids from Newton Mere, Blake Mere and Crose Mere has shown considerable variation between the subfamilies Orthocladiinae, Tanypodinae and Chironominae, as well as within the Chironominae. Stuart (1941) was the first to recognise a relationship between the apneustic tracheal systems of chironomid larvae (from the Millport shore pools) and their environment. He described the patterns found in several Cricotopus species, Spaniotoma rubicunda Mg. (now: Orthocladius rubicundus Mg.), Corynoneura scutellata Winn., Anatopynia varia (sic: varius) Fab., Pentaneura barbitarsis Zett., Chironomus dorsalis Mg., C. longistylus Goet. and Polypedilum nubeculosus Mg. It was already well known that Chironomus s.s. species had a rudimentary thoracic tracheal system (Miall, 1895; Miall and Harmond, 1900; Keilin, 1924; Thorpe, 1932) but no records had been published before of tracheal patterns in other aquatic chironomid species.

Since Stuart's (1941) paper, Whitten (1960) and Faucheux (1974) have described, respectively, the tracheal patterns in Chironomus dorsalis larvae and Chironomus tendens Fab. adults. This latter species is better known as Endochironomus tendens Fab.

It was apparent from this brief review of the literature available, that a more detailed study of the tracheal patterns in chironomid larvae was required, primarily to examine if Stuart's original premise, that a relationship exists between morphology and environment, would apply to freshwater chironomids from the Shropshire meres. Also, Stuart's drawings and descriptions are rather slight and in some cases

inaccurate, as will be described later.

6.1.1 The Basic Plan of the Larval Dipteran Tracheal System

Keilin (1944), in his comparative study of larval Dipteran respiratory systems listed seven characteristic features:

1. two main longitudinal latero-dorsal tracheal trunks,
2. two secondary longitudinal latero-ventral tracheal trunks,
3. lateral transverse branches connecting (1) and (2), continuing as spiracular branches and terminating in spiracles,
4. transverse commissures in each segment connecting the longitudinal latero-dorsal trunks,
5. branches or tufts from the secondary longitudinal latero-ventral trunks which serve various organs,
6. branches arising from the transverse commissures, and
7. spiracles and their associated glands.

In addition to these components, Whitten (1955, 1960) included the dorsal and ventral cervical tracheae in the "basic plan", with the dorsal cervical anastomosis as a subsidiary feature. Following partly Whitten's terminology and partly Snodgrass (1935), the following parts can be distinguished in the Chironomidae:

1. two principal dorsal longitudinal tracheae (d.l.t.),
2. two lateral longitudinal tracheae (l.l.t.), from which all but one of the ventral ganglionic tracheae (g.t.) arise,
3. transverse tracheal commissures (t.t.c.) connecting (1) and (2),
4. dorsal tracheal commissures (d.t.c.) connecting the dorsal longitudinal tracheae,
5. visceral tracheae (vs. t.),
6. branches arising from (4),
7. dorsal cervical tracheae (d.c.t.) from which arise the supraoesophageal

Table 6.1 A Comparison of Terminology used in Studies of Dipteran larval tracheal patterns

	Keilin (1944)	Whitten (1955, 1960)	The present study
1.	Longitudinal latero-dorsal trunks	Dorsal longitudinal trunks	Dorsal longitudinal tracheae
2.	Longitudinal latero-ventral trunks	Lateral longitudinal trunks	Lateral longitudinal trachea and ganglionic tracheae
3.	Transverse branches which give rise to spiracular branches	Transverse connectives and spiracular tracheae	Transverse tracheal commissures
4.	Transverse commissures to latero-dorsal trunks	Dorsal anastomoses	Dorsal tracheal commissures
5.	Tracheal branches (tufts) to organs	Visceral tracheae	Visceral tracheae
6.	Branches from transverse commissures	-	Branches from dorsal tracheal commissures
7.	Spiracles	Spiracles	Larvae apneustic - no spiracles
8.	-	Dorsal cervical tracheae	Dorsal cervical tracheae
9.	-	Dorsal cervical anastomosis	Dorsal cervical commissure
10.	-	Ventral cervical tracheae	Ventral cervical tracheae

ganglionic tracheae (spo.) and the suboesophageal ganglionic tracheae (sbo.), the latter giving off the dorsal cervical commissure (d.c.c.), and

8. ventral cervical tracheae (v.c.t.), from which arise the 1st ventral ganglionic tracheae and the proleg tracheae (p.t.).

The term 'commissure' has been used instead of Whitten's 'anastomosis' and 'connective', following Leftwich's (1973) definition of a commissure as a band of tissue linking two parts or organs, and of an anastomosis as an intercommunication or network (Plates 6.1, 6.2). Table 6.1 has been compiled to show where terms used in this study have deviated or been derived from those in previous works.

The tracheal system in the Chironomidae is apneustic which Snodgrass (1935) defines as being "without specific external breathing organs, either spiracles or gills; the tracheal system is usually absent or rudimentary." Because of the lack of spiracles, the dorsal longitudinal tracheae have become the principal tracheal trunks and the lateral longitudinal tracheae are reduced and appear as a series of short connectives. Gaseous exchange is effected through the skin which is densely tracheated. The characteristic subcutaneous ramifications have been termed tracheal fans, (Plate 6.3), as a shorter alternative to Keilin's (1944) description of "...peripheral tracheoles forming numerous radiating plexuses".

Four basic tracheal patterns have been found which show the sequential development of the tracheal systems in chironomid larvae from the Shropshire meres. These have been called the tricommissural thoracic pattern, the bicommissural thoracic pattern, the anterior/posterior pattern and the rudimentary thoracic pattern. The tracheal systems are progressively reduced coincidental with the increase in the concentration of haemoglobin within those groups which possess the pigment.

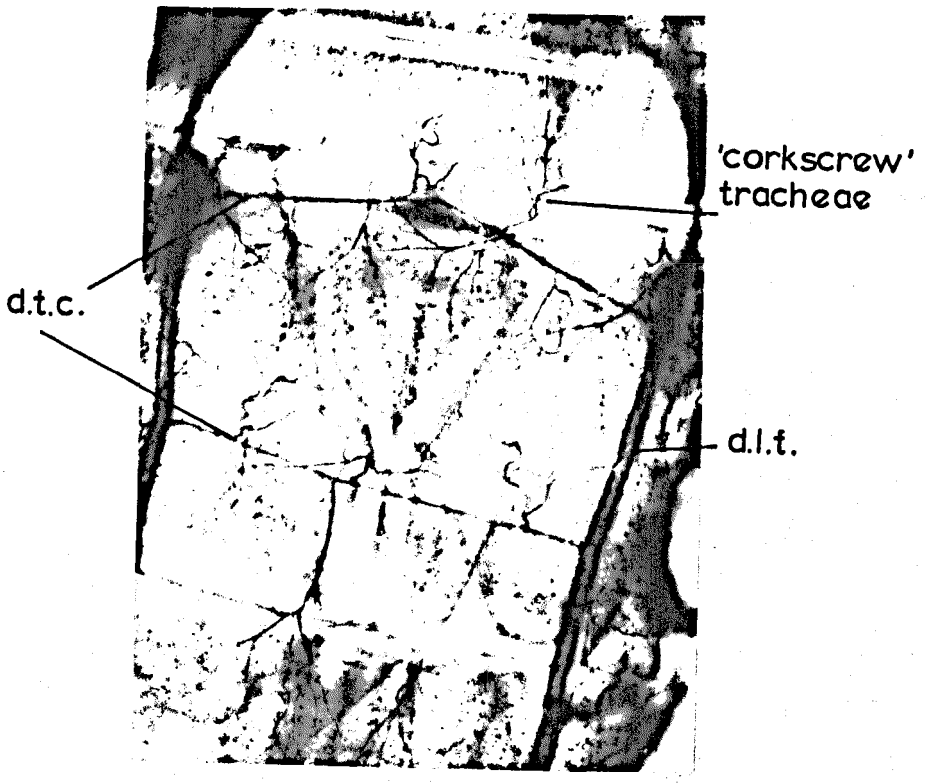


Plate 6.1 Dorsal tracheal commissures in Cricotopus sylvestris Fab., segments 2 and 3

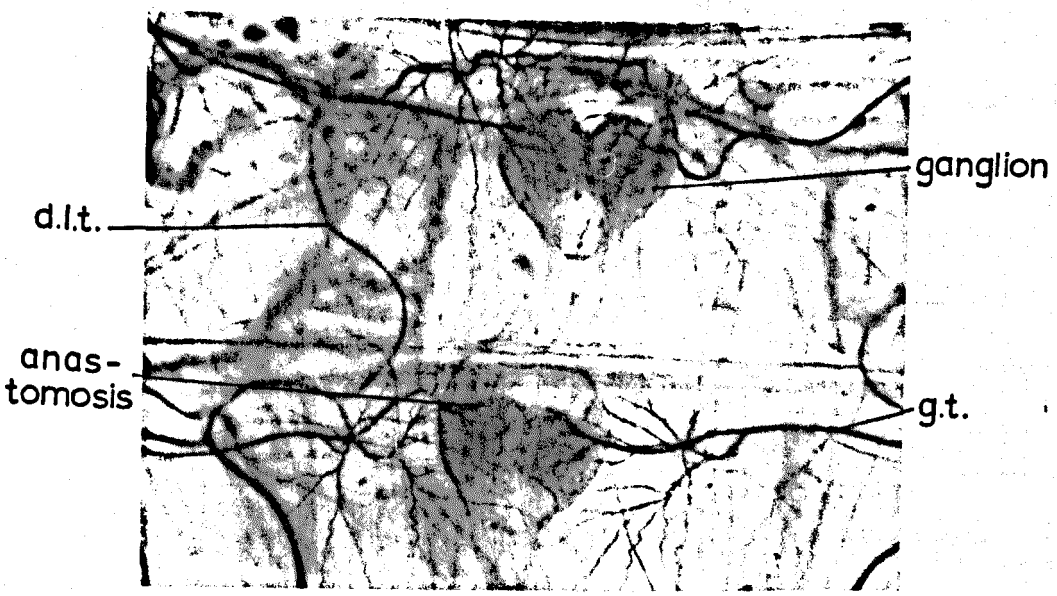


Plate 6.2 Ventral ganglionic anastomoses in Procladius choreus Mg., segments 2 and 3

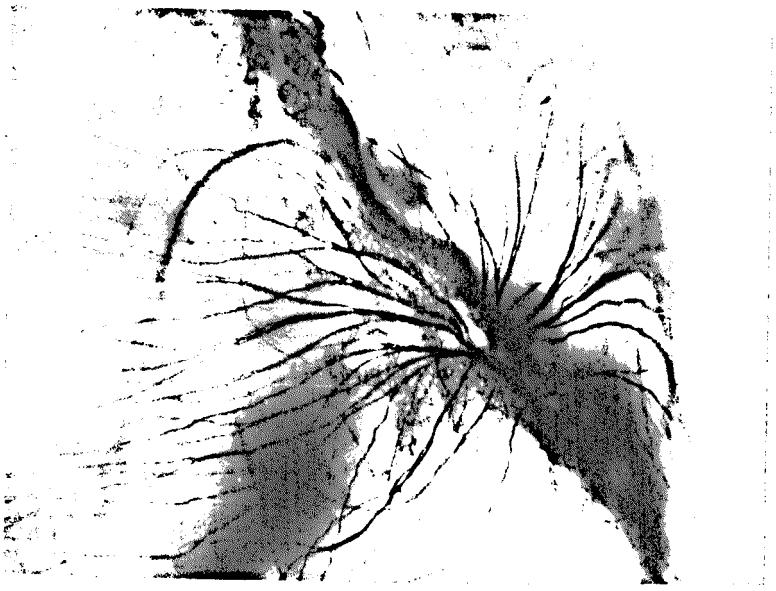


Plate 6.3 Ventral tracheal fan in Cryptochironomus 'defectus'

6.1.2 The Tricommissural Thoracic Tracheal Pattern

This is the most fully developed of the systems which has been found within the Chironomidae, although compared with the "complete" tracheal systems of other Nematocerous families such as the Bibionidae, Psychodidae, Anisopidae, Trichoceridae and Scatopsidae (Whitten, 1960), the tricommissural pattern is very reduced. It is characteristic of the orthocladinid larvae, a large number of which are surface dwelling species which do not possess haemoglobin. This tracheal pattern has been called "tricommissural" because there are three dorsal commissures in the thoracic segments. Stuart (1941) showed typical orthocladinid larvae with only two dorsal commissures in the 2nd and 3rd postcephalic segments.

The tricommissural thoracic pattern as seen in larvae in Cricotopus sylvestris Fab.

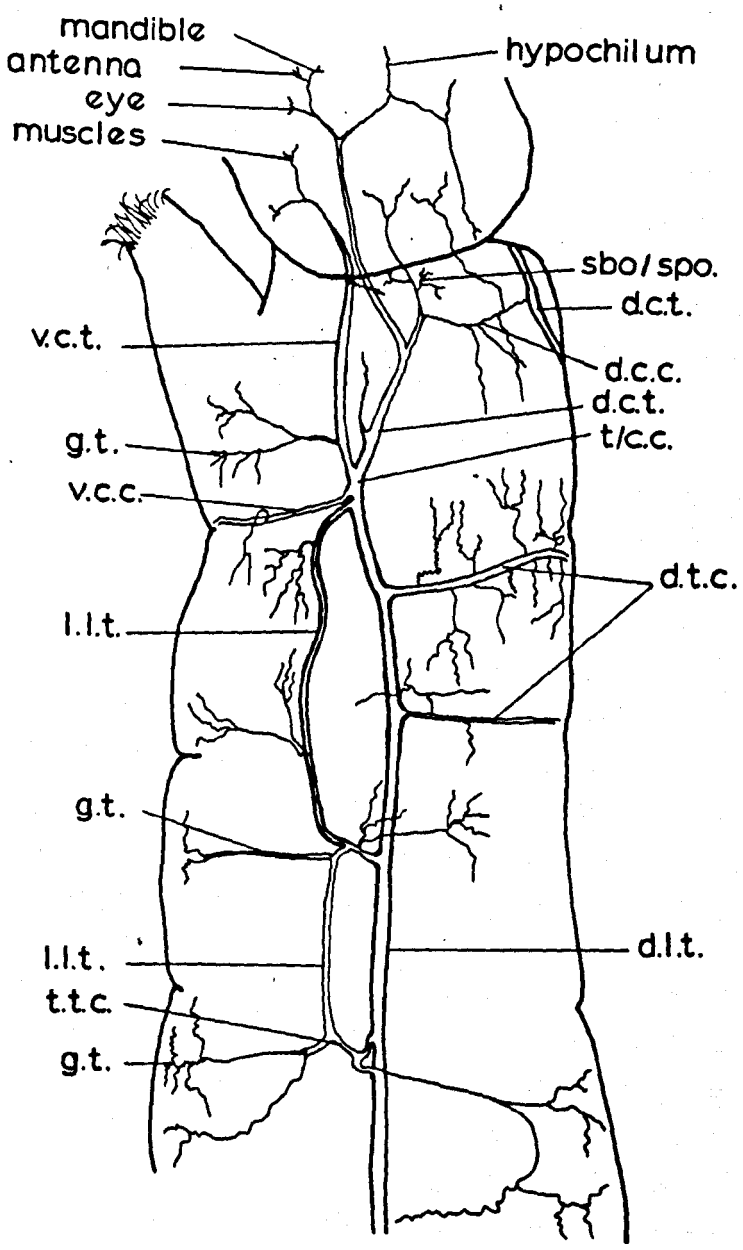
The larva of Cricotopus sylvestris is a filter feeder which lives in tubular nets, spun from salivary secretions, on the underside of floating leaves, on stalks of emergent vegetation and amongst algal mats. It is 5 - 8 mm long and very active, vacating its tube readily when touched and swimming towards the surface in a vigorous manner.

The two dorsal longitudinal tracheae, (Fig. 6.1) which are the principal tracheal trunks, arise within the 1st body segment and terminate as tracheal fans in the anal papillae and anal pseudopods. These dorsal longitudinal tracheae (d.l.t.) vary in width being widest (132 μ) in the 4th body segment (ie. the first abdominal segment) and narrowest (16 μ) in the 12th body segment. The most conspicuous feature about the d.l.t. is their sinuous passage through the body when the larva is relaxed. This allows greater flexibility for the tracheae when the animal is swimming and irrigating its tube.

Figure 6.1 Cricotopus sylvestris Fab. larva, lateral aspect of tricommissural thoracic tracheal system; segments 1 - 4, left side only.

LEGEND

d.a., dorsal anastomosis; d.c.c., dorsal cervical commissure; d.c.t., dorsal cervical tracheae; d.l.t., dorsal longitudinal tracheae; d.t.c., dorsal tracheal commissure; d - v.c., dorsal - ventral commissure; g.t., ganglionic tracheae; l.l.t., lateral longitudinal tracheae; p.t., proleg tracheae; sbo., suboesophageal tracheae; spo., supraoesophageal tracheae; t/c.c., thoracic/cervical commissure; t.t.c., transverse tracheal commissure; t.t/g.t.c., transverse thoracic/ganglionic tracheal commissure; v.c.c., ventral cervical commissure; v.c.t., ventral cervical tracheae; vs.t., visceral tracheae

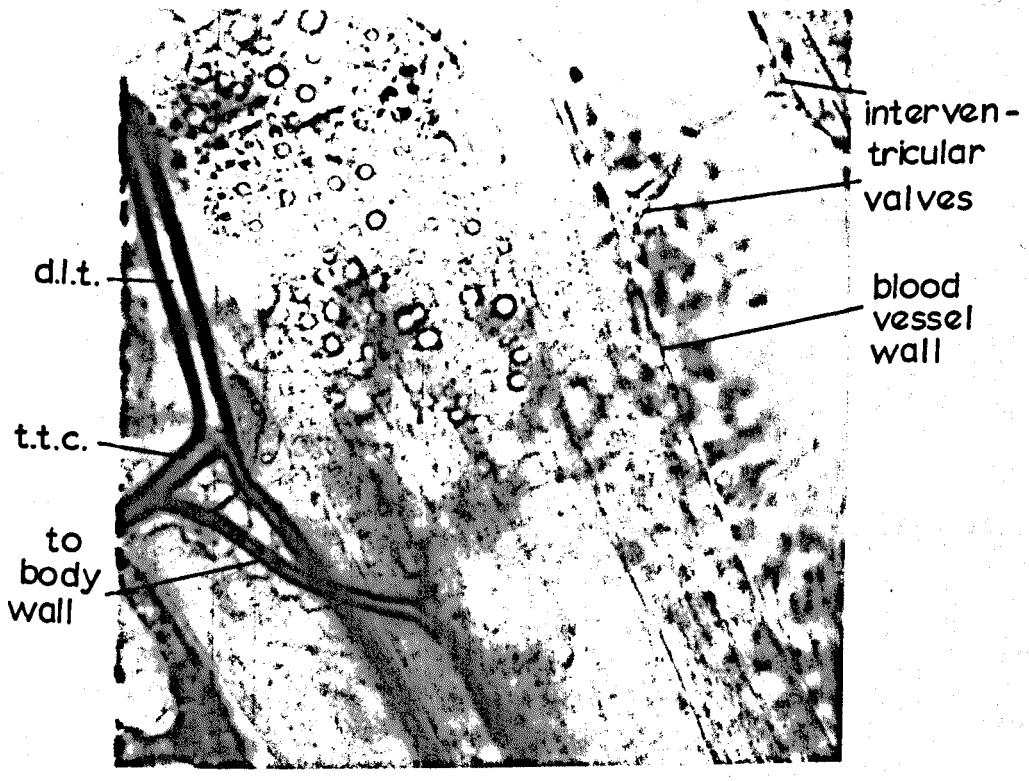

mandible
antenna
eye
muscles
hypochilum
sbo/spo.
d.c.t.
v.c.t.
d.c.c.
d.c.t.
g.t.
t/c.c.
v.c.c.
d.t.c.
l.l.t.
g.t.
l.l.t.
d.l.t.
t.t.c.
g.t.

Beyond the 4th segment the sequential tracheal branching is repeated in every segment. At the anterior end of every segment (Plate 6.4) a transverse branch arises which curves around to the ventral surface and divides - one branch tracheating the midventral ganglion and the other ramifying as tracheal fans over the body wall and ventral muscles (Plate 6.5). As this transverse branch leaves the d.l.t., there arises a secondary trachea which crosses over the d.l.t. and divides several times. These tracheae serve the dorsal musculature and subcutaneous fat bodies. As a point of interest, to the right of the d.l.t. in the enlargement of part of Plate 6.4, three interventricular valves can be seen within the dorsal aorta. These are sites of contraction which pump the blood anteriorally.

The arrangement of tracheae in the first four postcephalic segments of the body is the most "complete" which has been found in the Shropshire chironomid larvae (Fig. 6.1). The "pivot" of the whole body system is the thoracic/cervical commissure (t/c.c.) in segment 1, a short trachea where, in holopneustic larvae, the 1st spiracle would be situated.

Posteriorally to this "pivot" are the main d.l.t. and the reduced lateral longitudinal tracheae (l.l.t.)(Fig. 6.1 and Plate 6.6). Both continue into the 2nd body segment, the d.l.t. giving off two dorsal commissures with their characteristic "corkscrew" tracheae (Plate 6.1), which come off at right angles to the commissures and run anteriorally and posteriorally. There is no connection between the d.l.t. and the l.l.t. in the 2nd segment. In the 3rd segment, the first transverse commissure connects the d.l.t. and the l.l.t., the latter giving off the ventral ganglionic tracheae and a small branch which doubles back and tracheates the dorsal body wall. This sequence is repeated in the 4th segment, although the l.l.t. terminate in this segment and the branch which runs dorsally is more robust.

Plate 6.4 Dorsal body wall of Cricotopus sylvestris Fab. showing tracheal arrangement, segment 6



Enlargement of circled area in Plate 6.4

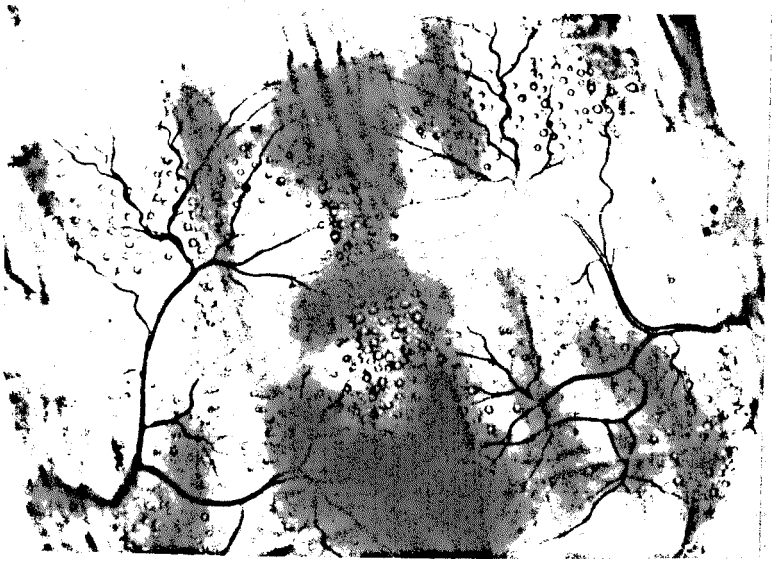


Plate 6.5 Ventral body wall of Cricotopus sylvestris Fab. showing tracheal arrangement in an abdominal segment

Plate 6.6 Lateral aspect of segments 2 - 4 in Cricotopus sylvestris Fab. showing connections between l.l.t. and d.l.t.

Plate 6.7 Dorsal cervical commissure in Cricotopus sylvestris Fab., segment 1.

Anteriorally to the t/c.c., the ventral cervical commissure (v.c.c.) arises from, and connects, the ventral cervical tracheae (v.c.t.), which then enter the head capsule after giving off the 1st ganglionic tracheae and the proleg tracheae. Immediately before the junction of the v.c.t. and the 1st ganglionic tracheae, the dorsal cervical tracheae (d.c.t.) arise and run towards the head capsule. A transverse dorsal cervical commissure is present as are the suboesophageal and supraoesophageal ganglionic tracheae (Plate 6.7). As the d.c.t. enter the head capsule, there is an anastomosis with the v.c.t. Inside the head capsule, the v.c.t. terminate laterally in a series of tracheal fans. Beyond the dorso-ventral cervical anastomosis, the d.c.t. divides to send branches to the eyes and hypochilum. The two branches to the hypochilum join in a cephalic commissure. Branches from the eye tracheae serve the mandibles and antennae.

6.1.3 The Bicommissural Thoracic Tracheal Pattern

This tracheal pattern is similar to the tricommissural except there are only two dorsal thoracic commissures. In addition, there is an abdominal commissure situated (as in some Tipulidae) in the 10th body segment, a return to the primitive pattern in which each segment contained a dorsal commissure. This bicommissural pattern is typical of the Tanypodinae and has been observed in both Procladius choreus and Anatopynia varia.

The bicommissural thoracic pattern as seen in Procladius choreus Mg.

According to Scheer (1934), the subfamily Tanypodinae, of which P. choreus is a member, has only "recently" acquired haemoglobin, which accounted for the low amount of the pigment in the haemolymph when compared with two Chironomus species, C. genuinus and C. connectans.

Scheer estimated that the concentration of haemoglobin in Tanypodinae was 4 - 10% of human blood whereas in C. genuinus and C. connectans, the concentration was between 25 - 30%.

It must be assumed that haemoglobin was acquired because the extant tracheal system was inadequate for the respiratory requirements of the larva. Jones (1972) considers that the evolution of haemoglobin would be quite simple as the structure of haem is similar to the cytochromes, common to most aerobic cells. Also, the acquisition of this pigment might reasonably be expected to affect in some way the tracheal system in Tanypodinae. A preliminary observation which can be made is, that although the underlying structure of the tracheal pattern in Procladius follows the basic pattern for Dipterous larvae, some major features have been simplified and segmental tracheation is more complex.

The two principal tracheae, the dorsal longitudinal tracheae (d.l.t.), arise concurrently with the lateral longitudinal tracheae (l.l.t.) from the thoracic/cervical commissure (t/c.c.) in the 1st postcephalic segment (Fig. 6.2) and meander through the body terminating as tracheal fans in the papillae, pseudopods and brush pedestals of the anal segment (Fig. 6.3). Stuart (1941) followed by Whitten (1960), stated that the tracheal system in Tanypodinae larvae extended only to the 10th postcephalic segment but this has been found to be incorrect for both P. choreus and Anatopynia varia. However, beyond the 10th segment, at which the lateral fringe of hairs terminates, the d.l.t. are reduced in diameter and the tracheal fans are not so extensive.

Two dorsal thoracic tracheal commissures are present in segments 1 and 2 connecting the two d.l.t., but unlike the robust commissures in Cricotopus sylvestris, they are extremely narrow and can be seen with ease only under high magnification. In addition, there is an abdominal dorsal commissure in segment 10 connecting the two d.l.t.

Figure 6.2 Procladius choreus Mg. larva, ventral aspect of bicommissural thoracic tracheal system; segments 1 - 4, right side only.

LEGEND

d.a., dorsal anastomosis; d.c.c., dorsal cervical commissure; d.c.t., dorsal cervical tracheae; d.l.t., dorsal longitudinal tracheae; d.t.c., dorsal tracheal commissure; d - v.c., dorsal - ventral commissure; g.t., ganglionic tracheae; l.l.t., lateral longitudinal tracheae; p.t., proleg tracheae; sbo., suboesophageal tracheae; spo., supraoesophageal tracheae; t/c.c., thoracic/cervical commissure; t.t.c., transverse tracheal commissure; t.t/g.t.c., transverse thoracic/ganglionic tracheal commissure; v.c.c., ventral cervical commissure; v.c.t., ventral cervical tracheae; vs.t., visceral tracheae

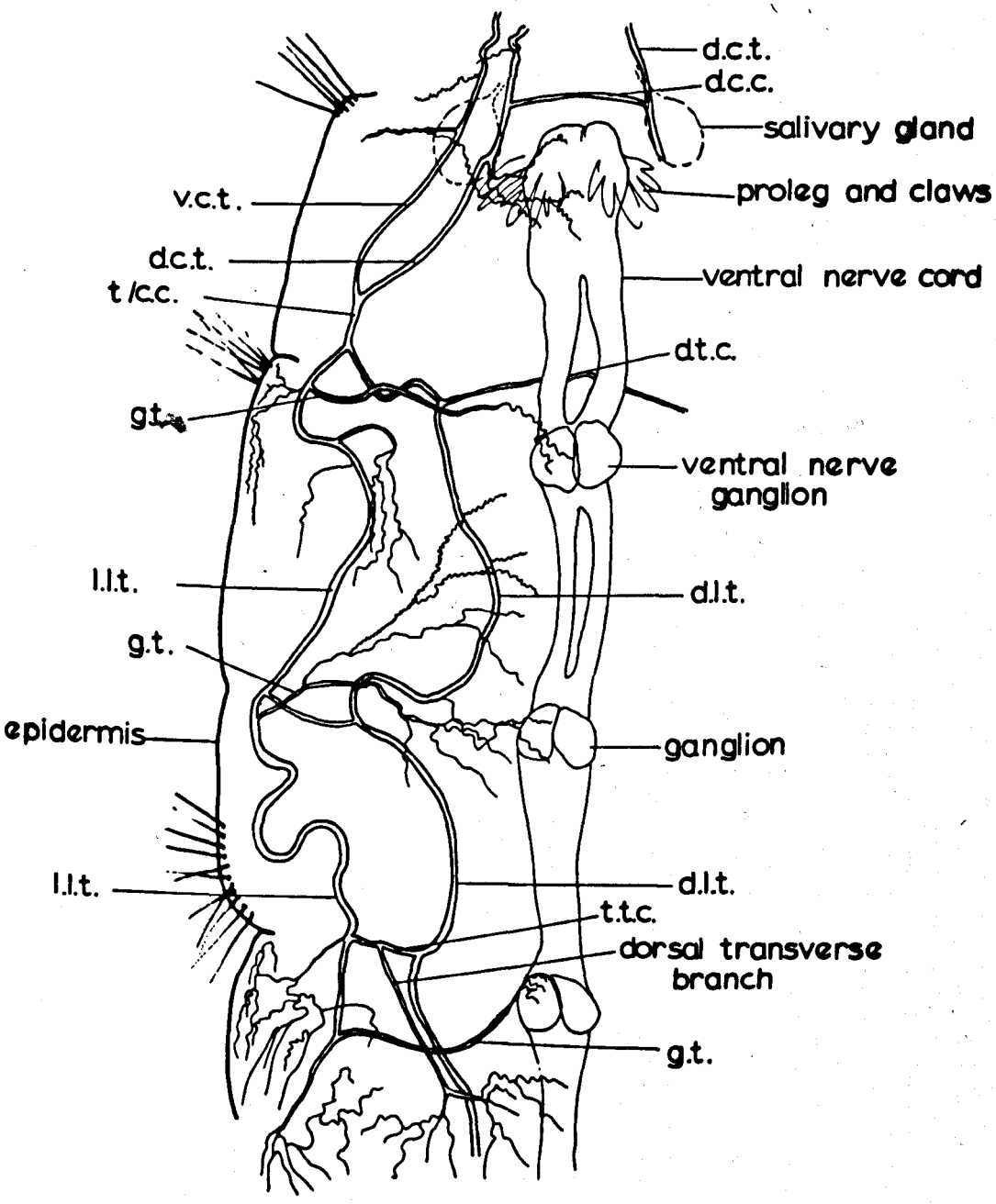
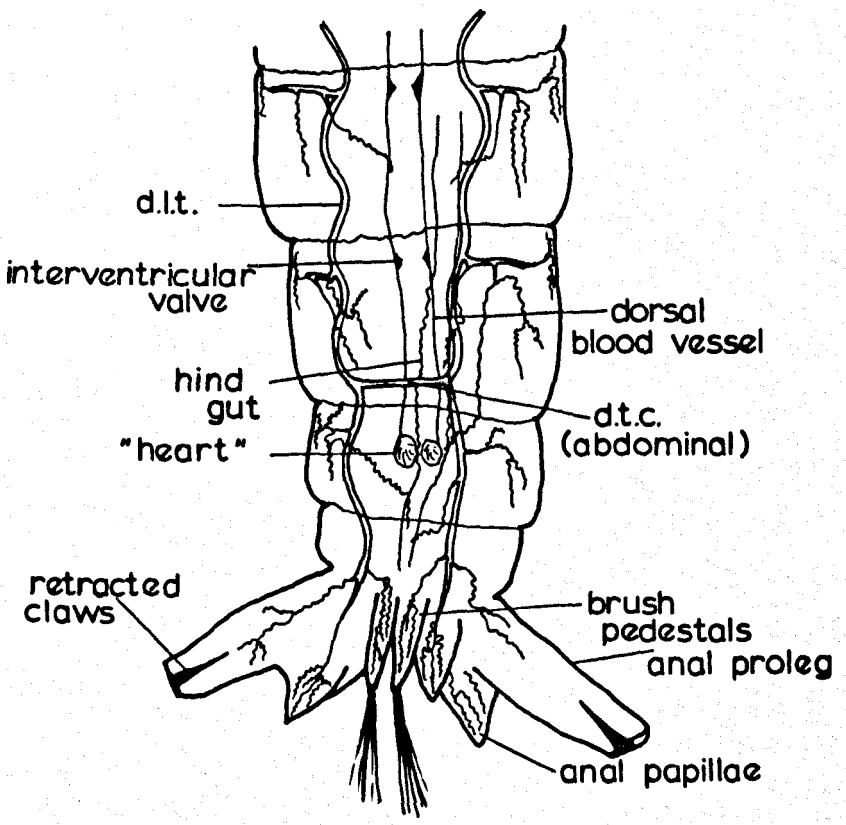

d.c.t.
d.c.c.
salivary gland
proleg and claws
v.c.t.
d.c.t.
t/c.c.
ventral nerve cord
d.t.c.
g.t.
ventral nerve ganglion
l.l.t.
d.l.t.
g.t.
epidermis
ganglion
l.l.t.
d.l.t.
t.t.c.
dorsal transverse branch
g.t.

Figure 6.3 Procladius choreus Mg. larva, dorsal aspect of tracheal arrangement in lower abdomen, segments 9 - 12.

LEGEND

d.a., dorsal anastomosis; d.c.c., dorsal cervical commissure; d.c.t., dorsal cervical tracheae; d.l.t., dorsal longitudinal tracheae; d.t.c., dorsal tracheal commissure; d - v.c., dorsal - ventral commissure; g.t., ganglionic tracheae; l.l.t., lateral longitudinal tracheae; p.t., proleg tracheae; sbo., suboesophageal tracheae; spo., supraoesophageal tracheae; t/c.c., thoracic/cervical commissure; t.t.c., transverse tracheal commissure; t.t/g.t.c., transverse thoracic/ganglionic tracheal commissure; v.c.c., ventral cervical commissure; v.c.t., ventral cervical tracheae; vs.t., visceral tracheae


d.l.t.
interventricular valve
dorsal blood vessel
hind gut
d.t.c. (abdominal)
"heart"
retracted claws
brush pedestals
anal proleg
anal papillae

This arrangement is similar in some Tipulidae and the limoniid, Pedicia (Whitten, 1960) but its significance is unclear. None of the commissures have the characteristic "corkscrew" tracheae of Cricotopus. In the middle of the second thoracic commissure, there are two small nodes close together which may be growth points, (Locke, 1958). Neither Whitten nor Stuart showed Tanypodinae larvae with any dorsal commissures.

The l.l.t. are present in each segment but complete only in segments 2 and 3. After arising from the t/c.c., the l.l.t. pass through segments 2 and 3, giving off the 2nd and 3rd ganglionic tracheae. Transverse commissures anteriorally in segments 3 and 4 connect the l.l.t. to the d.l.t.

From segment 4 onwards posteriorally, the segmental tracheation is repeated in every segment (Fig. 6.4 and Plate 6.8). The d.l.t. penetrate the segment anteriorally and branch giving off a transverse trachea (Plate 6.9). Arising from this branch are: a trachea which serves the dorsal musculature in a series of ramifications and tracheal fans; a truncated l.l.t. which divides, giving off a ganglionic trachea (g.t.) and a branch which terminates in tracheal fans over the ventral muscles. The transverse branch then ends in the body wall as tracheal fans immediately under the lateral fringe of swimming hairs. Snodgrass (1935) stated that it was probable that in the primitive stage of insect tracheal development, each segment was independently tracheated before the longitudinal tracheae were connected to provide more efficient aeration. The appearance of short lateral tracheae in each segment beyond segment 3 may be an adaptation to provide for the greater respiratory needs of the predatory Tanypodinae larvae.

In the 9th segment, a small modification of the general pattern has been found. Between the dorsal branch and the short lateral trachea,

Figure 6.4 Procladius choreus Mg. larva, ventral aspect of tracheal arrangement in segment 6, right side only.

LEGEND

d.a., dorsal anastomosis; d.c.c., dorsal cervical commissure; d.c.t., dorsal cervical tracheae; d.l.t., dorsal longitudinal tracheae; d.t.c., dorsal tracheal commissure; d - v.c., dorsal - ventral commissure; g.t., ganglionic tracheae; l.l.t., lateral longitudinal tracheae; p.t., proleg tracheae; sbo., suboesophageal tracheae; spo., supraoesophageal tracheae; t/c.c., thoracic/cervical commissure; t.t.c., transverse tracheal commissure; t.t/g.t.c., transverse thoracic/ganglionic tracheal commissure; v.c.c., ventral cervical commissure; v.c.t., ventral cervical tracheae; vs.t., visceral tracheae

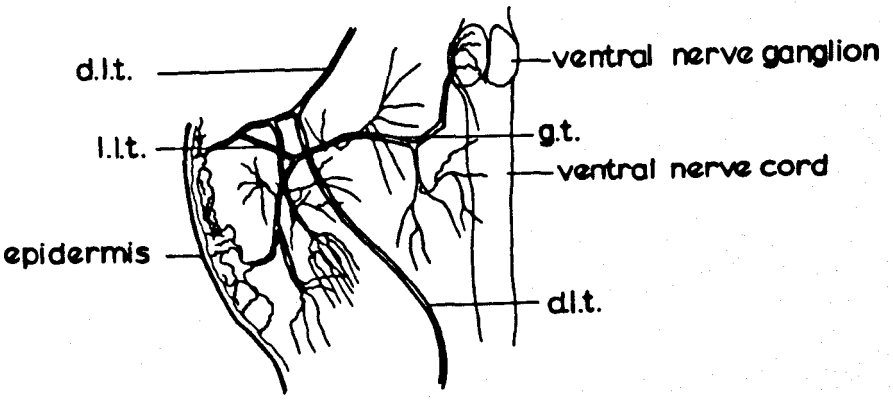


Figure 6.4

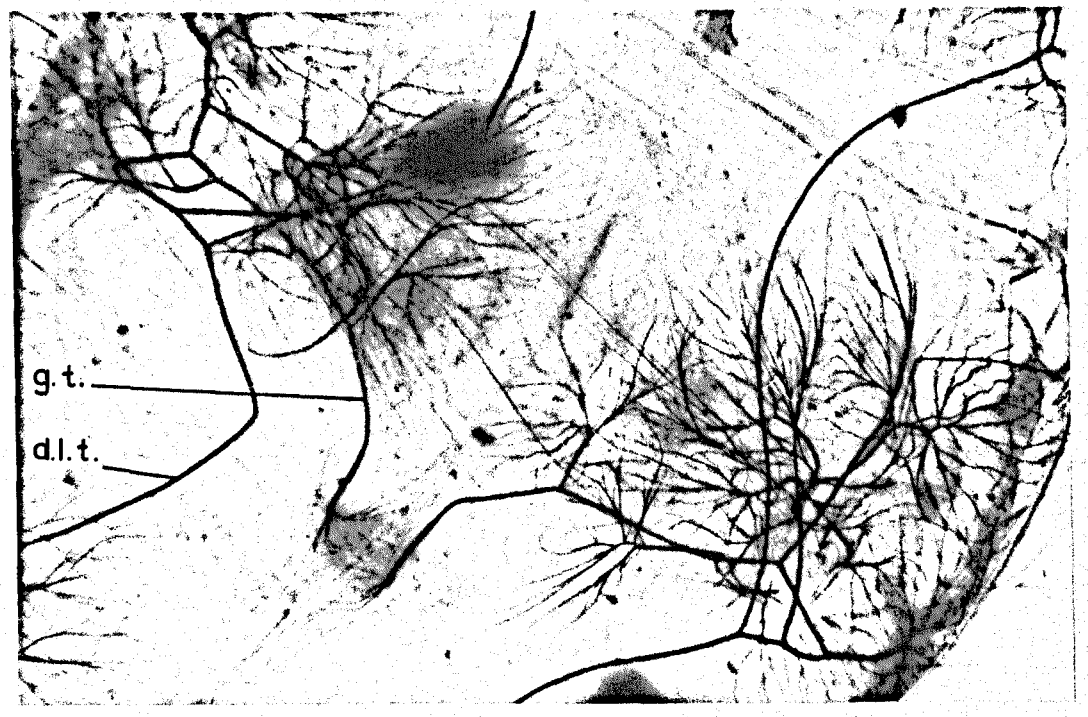


Plate 6.8 Segmental arrangement of ventral tracheae in Procladius choreus Mg. showing d.l.t. and g.t.; segment 5, seen from left side

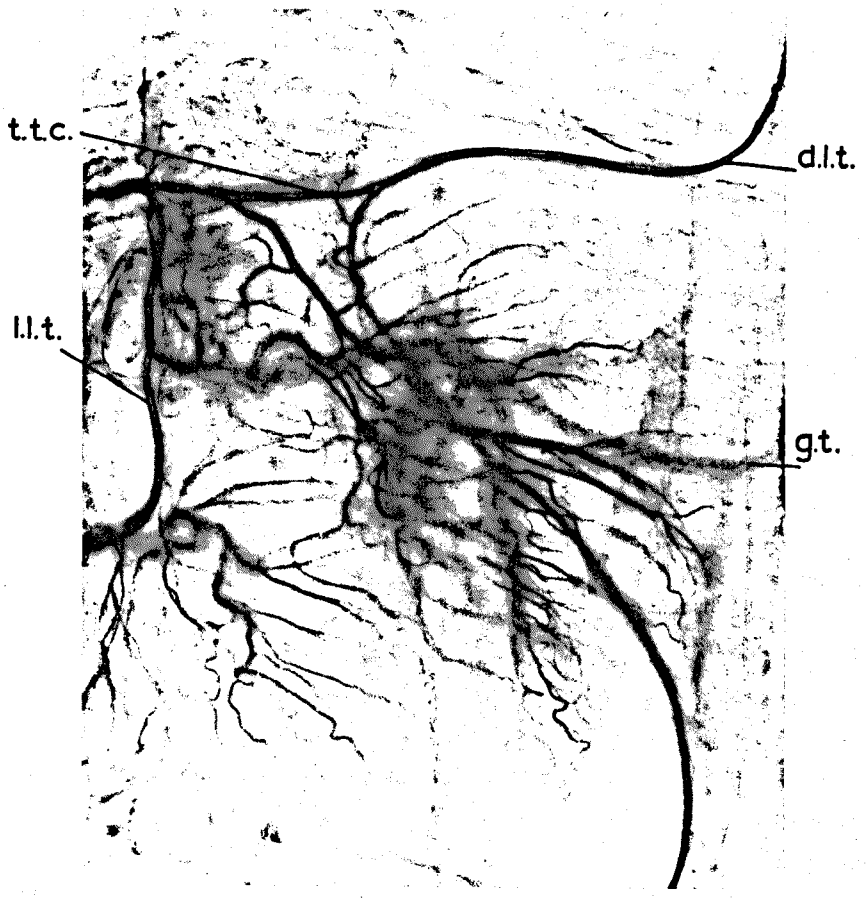


Plate 6.9 Dorsal longitudinal trachea and t.t.c.

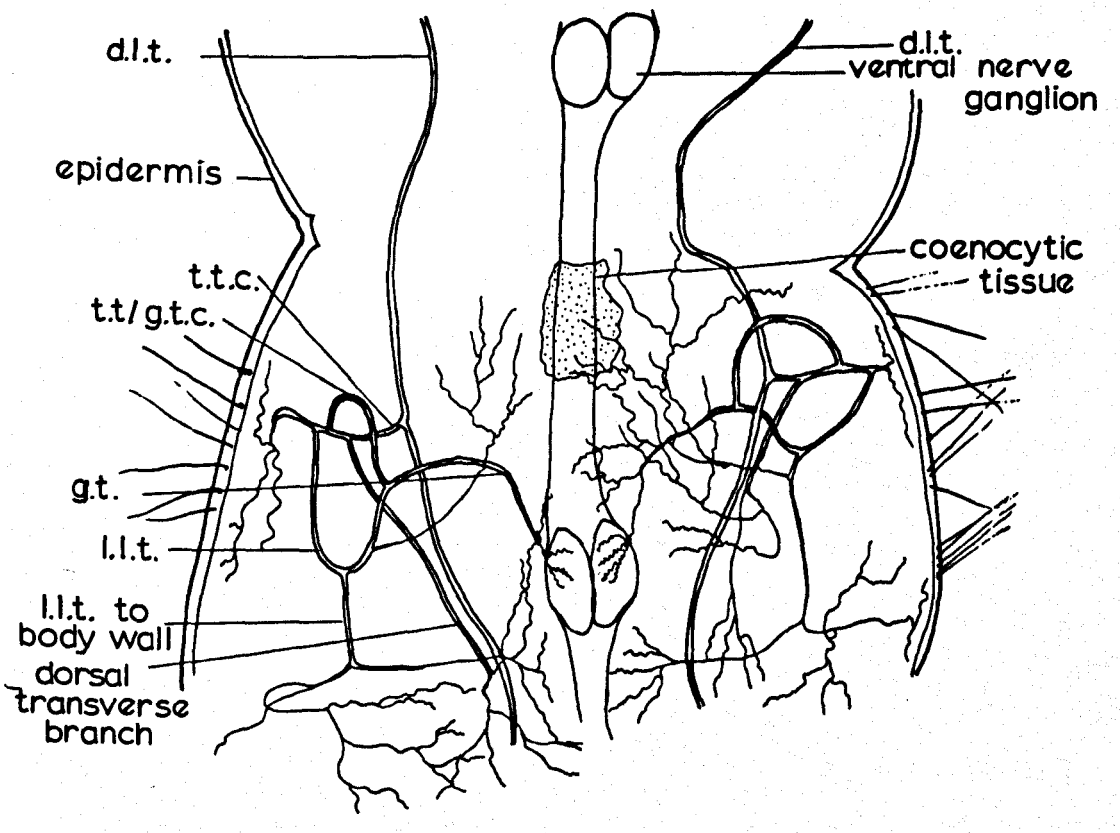
in Procladius choreus;

segment 5, seen from right side

Figure 6.5 Procladius choreus Mg. larva, ventral aspect showing details of the transverse tracheal/ganglionic tracheal commissure in segment 9.

LEGEND

d.a., dorsal anastomosis; d.c.c., dorsal cervical commissure; d.c.t., dorsal cervical tracheae; d.l.t., dorsal longitudinal tracheae; d.t.c., dorsal tracheal commissure; d - v.c., dorsal - ventral commissure; g.t., ganglionic tracheae; l.l.t., lateral longitudinal tracheae; p.t., proleg tracheae; sbo., suboesophageal tracheae; spo., supraoesophageal tracheae; t/c.c., thoracic/cervical commissure; t.t.c., transverse tracheal commissure; t.t/g.t.c., transverse thoracic/ganglionic tracheal commissure; v.c.c., ventral cervical commissure; v.c.t., ventral cervical tracheae; vs.t., visceral tracheae


d.l.t.
epidermis
t.t.c.
t.t/g.t.c.
g.t.
l.l.t.
l.l.t. to body wall
dorsal transverse branch
d.l.t.
ventral nerve ganglion
coenocytic tissue

a connecting branch arises which joins the transverse tracheae to the g.t. (Fig. 6.5). Its function is unclear but in this segment and segment 10, conspicuous tracheae serve the Malpighian tubules. A dorsal commissure is present in segment 10. Beyond this segment there are no ventral ganglionic tracheae.

All the tracheae passing into the head capsule arise from the t/c.c. and are branches from the two main tracheae in this area, the dorsal cervical tracheae.

6.1.4 The Anterior-Posterior Tracheal Pattern

Two types of tracheal system have been found in the Chironominae - the anterior-posterior type and the rudimentary thoracic type. The former pattern dealt with here, is more "complete" than the rudimentary thoracic pattern and therefore more primitive and has been found in Tanytarsus sp. and Polypedilum nubeculosus. The pattern seems to represent a transitional stage between the bicommissural and the rudimentary thoracic pattern.

As suggested by the title, the tracheae are present in the head capsule, the first three and the last three segments. There are apparently no tracheae in the mid-gut region. Tanytarsus sp. and Polypedilum both possess haemoglobin, although the deeper red colour of Polypedilum indicates that in this species the haemoglobin is more concentrated.

The tracheal pattern in both Tanytarsus and Polypedilum will be described.

The anterior-posterior tracheal pattern as seen in Polypedilum nubeculosus Mg.

Polypedilum nubeculosus has extensive subcutaneous deposits filled

with a green pigment, which is probably some bile pigment such as biliverdin, derived from the breakdown of haemoglobin. The fat deposits tend to mask the tracheae. Stuart (1941) described this species as differing little in its tracheal pattern from Chironomus dorsalis and C. longistylus. He apparently did not see the posterior tracheae.

Tracheae are present in the head capsule and in the postcephalic segments 1, 2, 3, 10, 11 and 12. There is apparently no connection between the two groups of tracheae. This sort of arrangement is not unique and has its precedent in the amphipneustic respiratory system typical of other larval Diptera, in which only the prothoracic and posterior abdominal spiracles are functional (Imms, 1951). Also, in Chaoborus, the two main longitudinal tracheal trunks are strongly dilated into two pairs of sacs, one pair being located in the thorax and the other in the abdomen.

The thoracic tracheal pattern follows the basic generalised pattern and is similar to all the other Chironominae which have been studied (Fig. 6.6 and Plate 6.10).

The dorsal longitudinal tracheae (d.l.t.) and the lateral longitudinal tracheae (l.l.t.) branch off in the 1st postcephalic segment from the thoracic/cervical commissure (t/c.c.) and give rise to, respectively, the dorsal tracheal commissure, a subsidiary branch and the 2nd ganglionic tracheae. The two main pairs of tracheae then travel parallel to each other through segment 2 and are connected at the anterior end of segment 3 by a transverse tracheal commissure (t.t.c.). Branches to the dorsal and lateral musculature arise from the t.t.c. as well as a short l.l.t. from which tracheae travel to the 3rd ventral ganglion and viscera. This is the extent of the thoracic tracheae.

Figure 6.6 Polypedilum nubeculosus Mg. larva, dorso-lateral aspect of anterior/posterior tracheal pattern; segments 1 - 3, left side only of thorax.

LEGEND

d.a., dorsal anastomosis; d.c.c., dorsal cervical commissure; d.c.t., dorsal cervical tracheae; d.l.t., dorsal longitudinal tracheae; d.t.c., dorsal tracheal commissure; d - v.c., dorsal - ventral commissure; g.t., ganglionic tracheae; l.l.t., lateral longitudinal tracheae; p.t., proleg tracheae; sbo., suboesophageal tracheae; spo., supraoesophageal tracheae; t/c.c., thoracic/cervical commissure; t.t.c., transverse tracheal commissure; t.t/g.t.c., transverse thoracic/ganglionic tracheal commissure; v.c.c., ventral cervical commissure; v.c.t., ventral cervical tracheae; vs.t., visceral tracheae

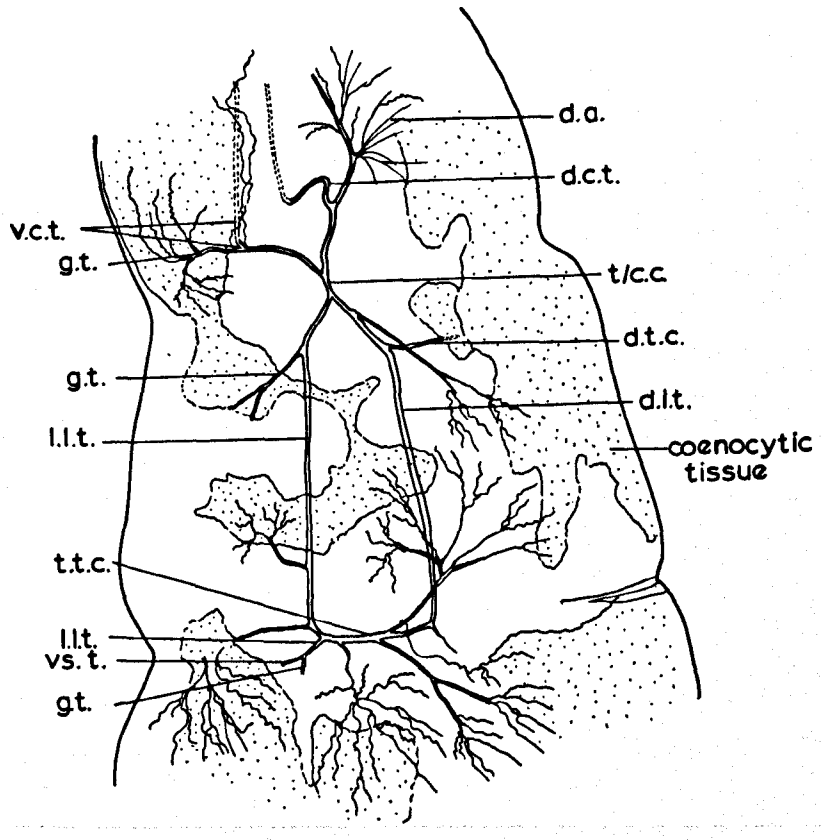


Figure 6.6.

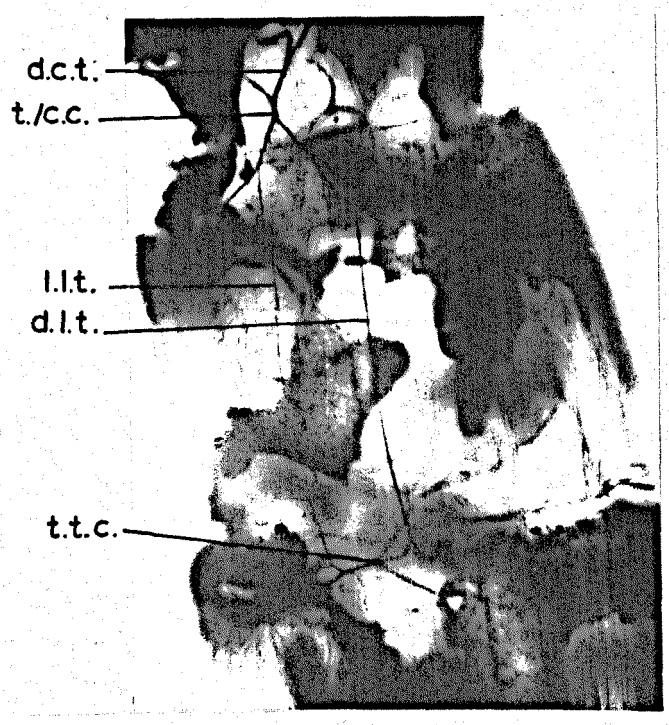


Plate 6.10 Arrangement of d.l.t. and l.l.t. in Polypedilum nubeculosus Mg.; segment 2, seen from left side

Figure 6.7 Polypedilum nubeculosus Mg. larva, lateral aspect of abdominal tracheae in the anterior/posterior tracheal pattern, segments 10 - 12.

LEGEND

d.a., dorsal anastomosis; d.c.c., dorsal cervical commissure; d.c.t., dorsal cervical tracheae; d.l.t., dorsal longitudinal tracheae; d.t.c., dorsal tracheal commissure; d - v.c., dorsal - ventral commissure; g.t., ganglionic tracheae; l.l.t., lateral longitudinal tracheae; p.t., proleg tracheae; sbo., suboesophageal tracheae; spo., supraoesophageal tracheae; t/c.c., thoracic/cervical commissure; t.t.c., transverse tracheal commissure; t.t/g.t.c., transverse thoracic/ganglionic tracheal commissure; v.c.c., ventral cervical commissure; v.c.t., ventral cervical tracheae; vs.t., visceral tracheae

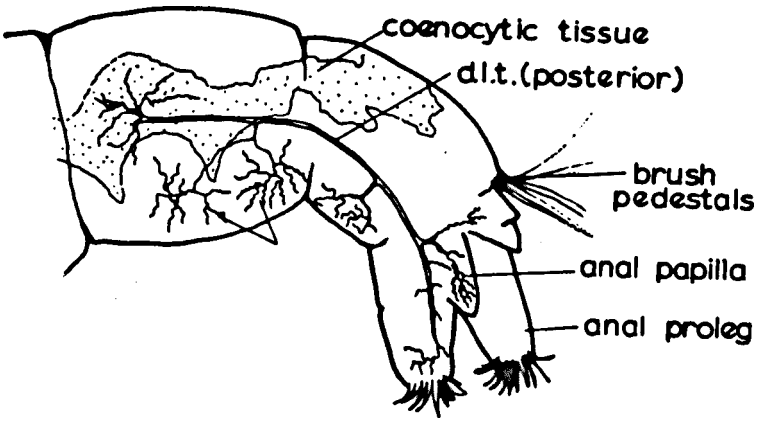


Figure 6.7

Plate 6.11 Anal end of Polypedilum nubeculosus Mg. showing abdominal tracheae; from left side

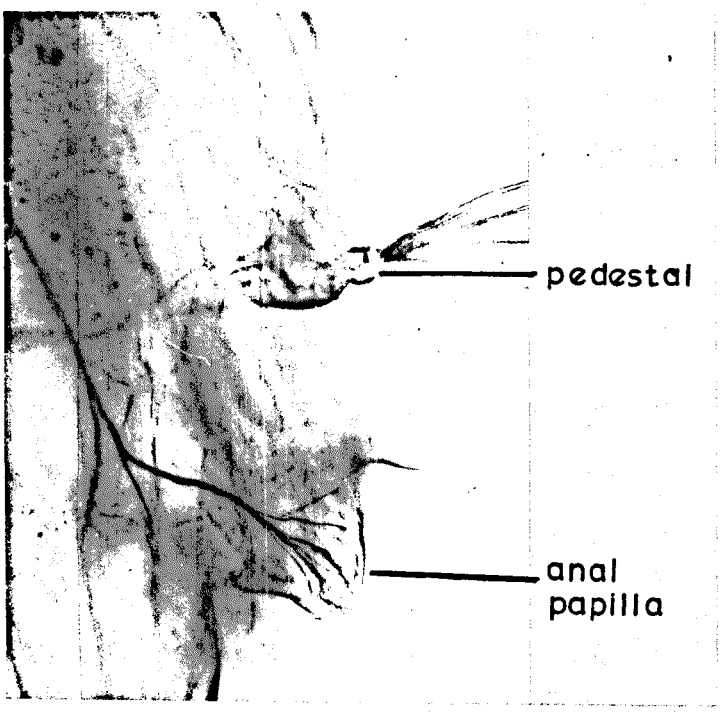


Plate 6.12 Anal papilla and anal brush pedestal in Polypedilum nubeculosus Mg. showing tracheal fan ending

Figure 6.8 Tanytarsus sp. larva, dorsal aspect of abdominal tracheae in the anterior/posterior tracheal pattern, segments 10 - 12.

LEGEND

d.a., dorsal anastomosis; d.c.c., dorsal cervical commissure; d.c.t., dorsal cervical tracheae; d.l.t., dorsal longitudinal tracheae; d.t.c., dorsal tracheal commissure; d - v.c., dorsal - ventral commissure; g.t., ganglionic tracheae; l.l.t., lateral longitudinal tracheae; p.t., proleg tracheae; sbo., suboesophageal tracheae; spo., supraoesophageal tracheae; t/c.c., thoracic/cervical commissure; t.t.c., transverse tracheal commissure; t.t/g.t.c., transverse thoracic/ganglionic tracheal commissure; v.c.c., ventral cervical commissure; v.c.t., ventral cervical tracheae; vs.t., visceral tracheae

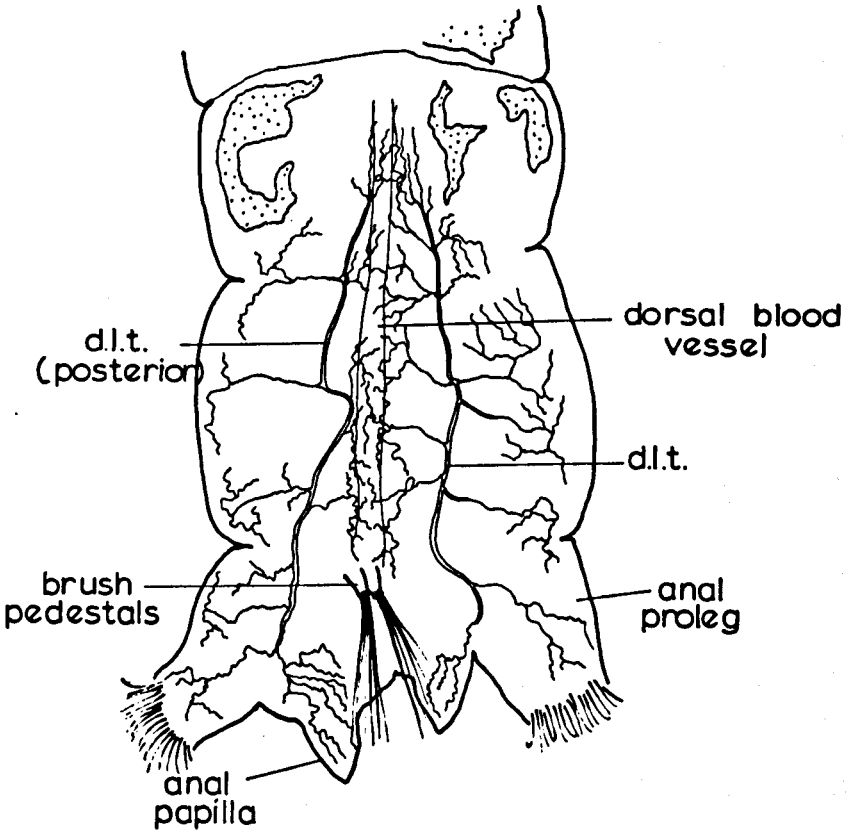


Figure 6.8

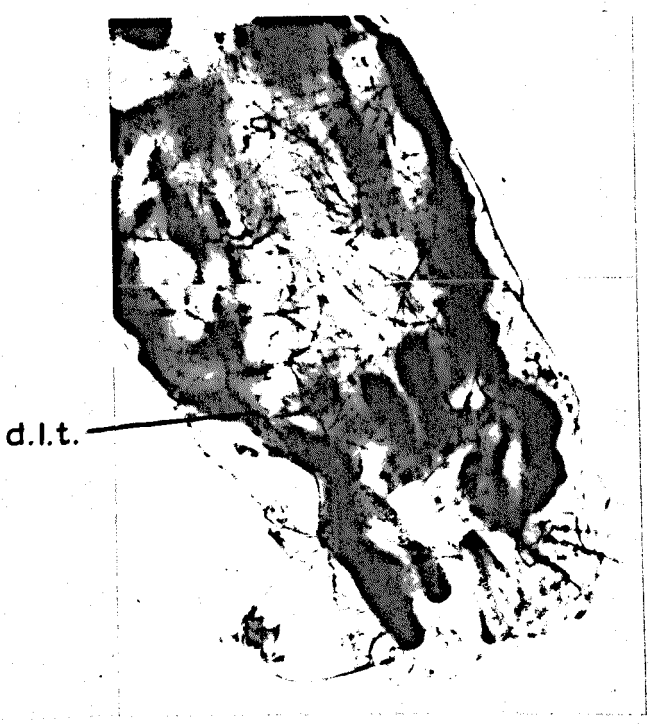


Plate 6.13 Anal end of Tanytarsus sp. showing dorsal tracheal fans radiating from abdominal d.l.t.

Anteriorally to the t/c.c., the dorsal and ventral cervical tracheae arise concurrently and pass into the head capsule, before giving rise to, respectively, the oesophageal ganglionic tracheae and the proleg tracheae and 1st ganglionic tracheae.

The posterior tracheae are very simple (Fig. 6.7 and Plate 6.11) and consist of two d.l.t. in segments 10, 11 and 12, which give rise to ventral ganglionic tracheae in segments 10 and 11 and branches to the brush pedestals, papillae (Plate 6.12) and pseudopods in the anal segment. There is apparently no dorsal commissure, which illustrates further reduction from the bicommissural pattern.

The anterior-posterior tracheal pattern as seen in Tanytarsus sp.

The tracheal pattern in the thorax is essentially the same as in Polypedilum nubeculosus. The posterior tracheae are, however, rather less simple, with more elaborate tracheal fans.

From the dorsal side, (Fig. 6.8 and Plate 6.13), the two d.l.t. can be seen arising in a series of branched tracheae, travelling through segment 11 and terminating in the anal papillae and anal pseudopods. The hind gut is very well supplied with tracheae and several branches travel around to the ventral surface. The lateral body wall is also well tracheated.

6.1.5 The Rudimentary Thoracic Tracheal Pattern

This pattern is typical of the majority of the Chironominae larvae which possess haemoglobin. There are no tracheae in the abdominal segments and those which are present are confined to the head capsule and thoracic segments. This rudimentary tracheal system has been observed in Chironomus anthracinus (Fig. 6.9 and Plates 6.14 and 6.15),

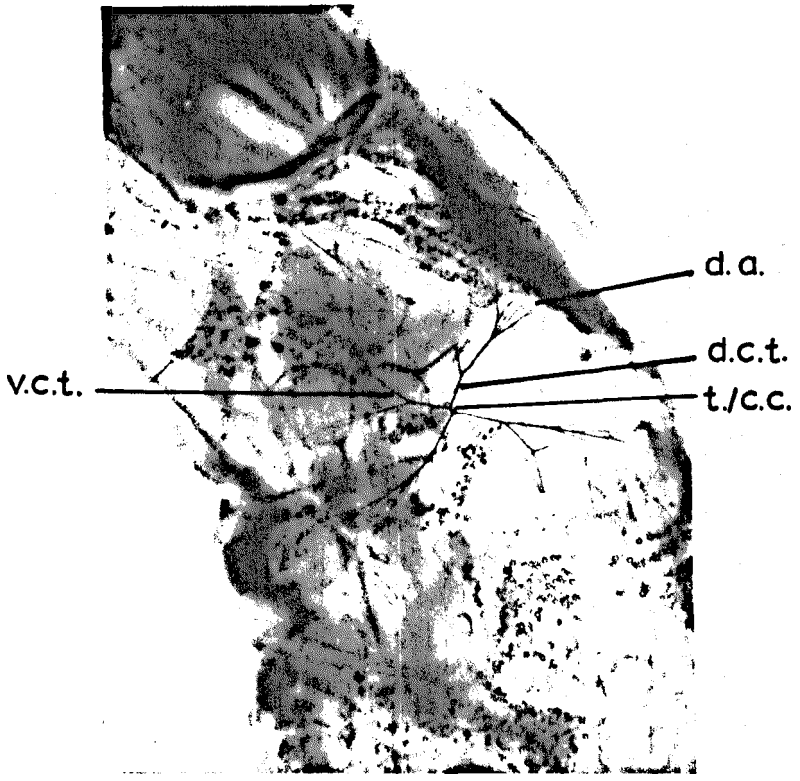


Plate 6.14 Thoracic tracheae in Chironomus anthracinus Zett.; dorso-lateral aspect, segments 1 and 2

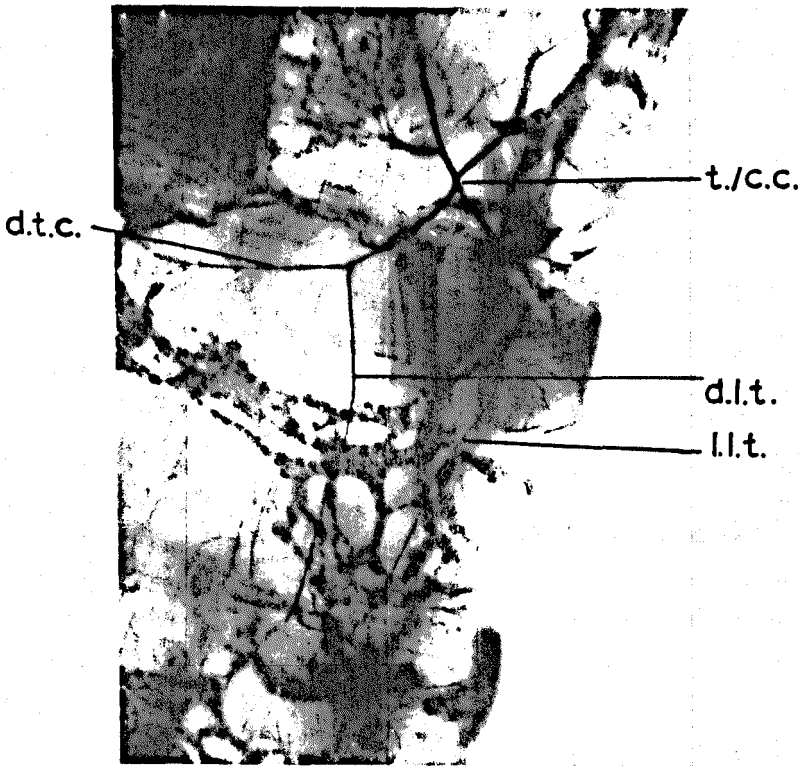


Plate 6.15 Thoracic tracheae in Chironomus anthracinus Zett.; segments 1 and 2, right side

Figure 6.9 Chironomus anthracinus Zett. larva, dorso-lateral aspect of rudimentary thoracic tracheal pattern, segments 1 - 3, right side only.

LEGEND

d.a., dorsal anastomosis; d.c.c., dorsal cervical commissure; d.c.t., dorsal cervical tracheae; d.l.t., dorsal longitudinal tracheae; d.t.c., dorsal tracheal commissure; d - v.c., dorsal - ventral commissure; g.t., ganglionic tracheae; l.l.t., lateral longitudinal tracheae; p.t., proleg tracheae; sbo., suboesophageal tracheae; spo., supraoesophageal tracheae; t/c.c., thoracic/cervical commissure; t.t.c., transverse tracheal commissure; t.t/g.t.c., transverse thoracic/ganglionic tracheal commissure; v.c.c., ventral cervical commissure; v.c.t., ventral cervical tracheae; vs.t., visceral tracheae

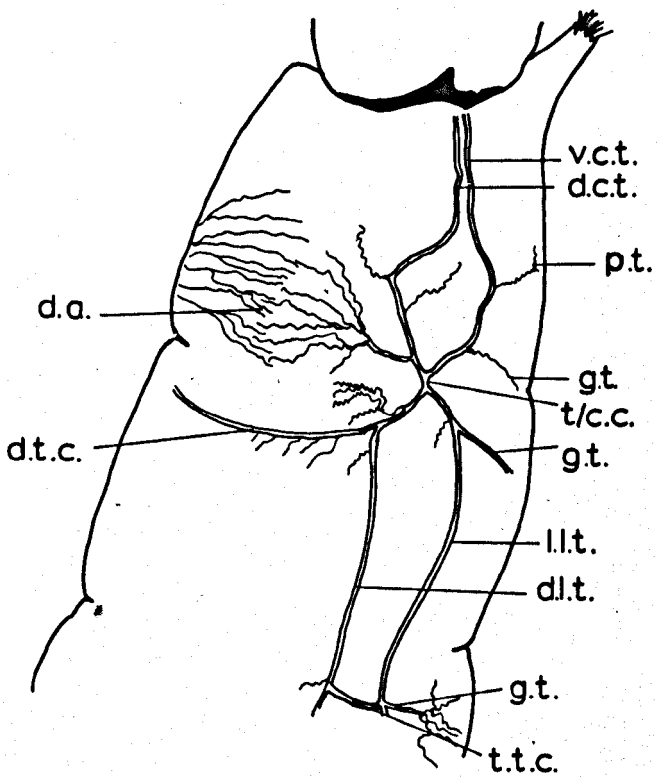

v.c.t.
d.c.t.
p.t.
d.a.
g.t.
t/c.c.
d.t.c.
g.t.
l.l.t.
d.l.t.
g.t.
t.t.c.

Figure 6.10 Chironomus tentans Fab. larva, dorso-lateral aspect of rudimentary thoracic tracheal pattern, segments 1 - 3, left side only.

LEGEND

d.a., dorsal anastomosis; d.c.c., dorsal cervical commissure; d.c.t., dorsal cervical tracheae; d.l.t., dorsal longitudinal tracheae; d.t.c., dorsal tracheal commissure; d - v.c., dorsal - ventral commissure; g.t., ganglionic tracheae; l.l.t., lateral longitudinal tracheae; p.t., proleg tracheae; sbo., suboesophageal tracheae; spo., supraoesophageal tracheae; t/c.c., thoracic/cervical commissure; t.t.c., transverse tracheal commissure; t.t/g.t.c., transverse thoracic/ganglionic tracheal commissure; v.c.c., ventral cervical commissure; v.c.t., ventral cervical tracheae; vs.t., visceral tracheae

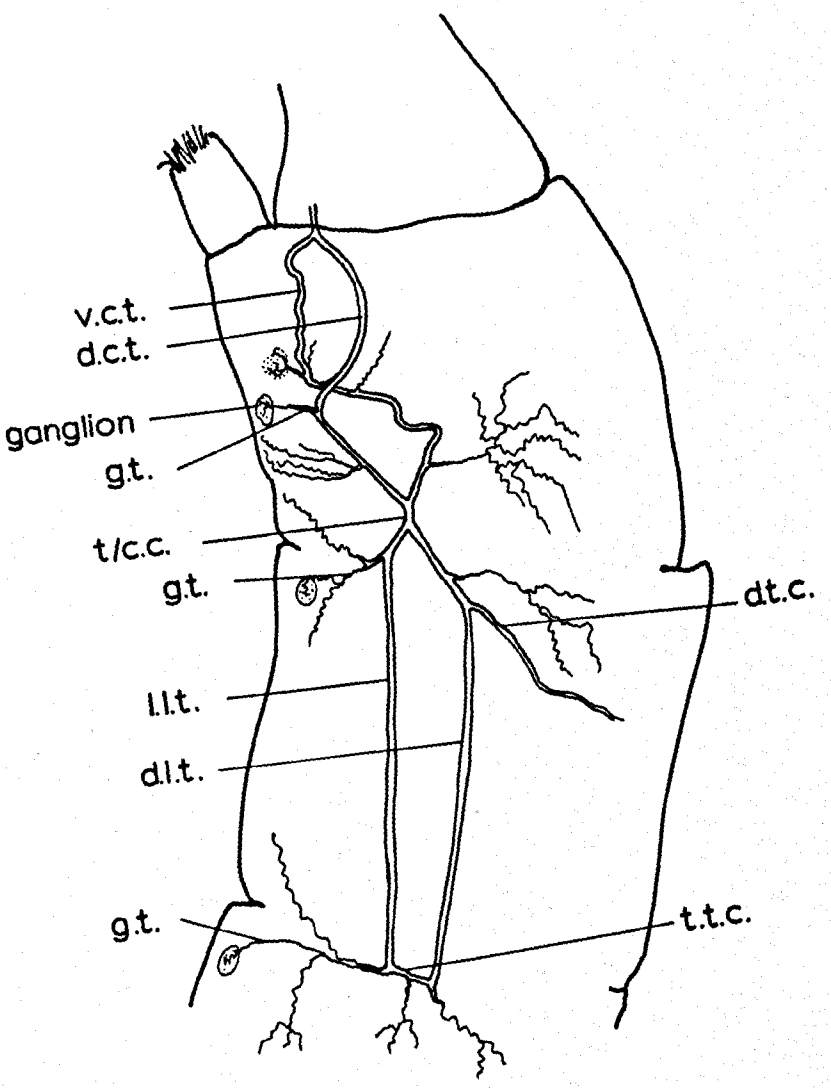

v.c.t.
d.c.t.
ganglion
g.t.
t/c.c.
g.t.
dt.c.
l.l.t.
d.l.t.
g.t.
t.t.c.

Figure 6.11 Chironomus lugubris Zett. larva, dorso-lateral aspect of rudimentary thoracic tracheal pattern, segments 1 - 3, left side only.

LEGEND

d.a., dorsal anastomosis; d.c.c., dorsal cervical commissure; d.c.t., dorsal cervical tracheae; d.l.t., dorsal longitudinal tracheae; d.t.c., dorsal tracheal commissure; d - v.c., dorsal - ventral commissure; g.t., ganglionic tracheae; l.l.t., lateral longitudinal tracheae; p.t., proleg tracheae; sbo., suboesophageal tracheae; spo., supraoesophageal tracheae; t/c.c., thoracic/cervical commissure; t.t.c., transverse tracheal commissure; t.t/g.t.c., transverse thoracic/ganglionic tracheal commissure; v.c.c., ventral cervical commissure; v.c.t., ventral cervical tracheae; vs.t., visceral tracheae

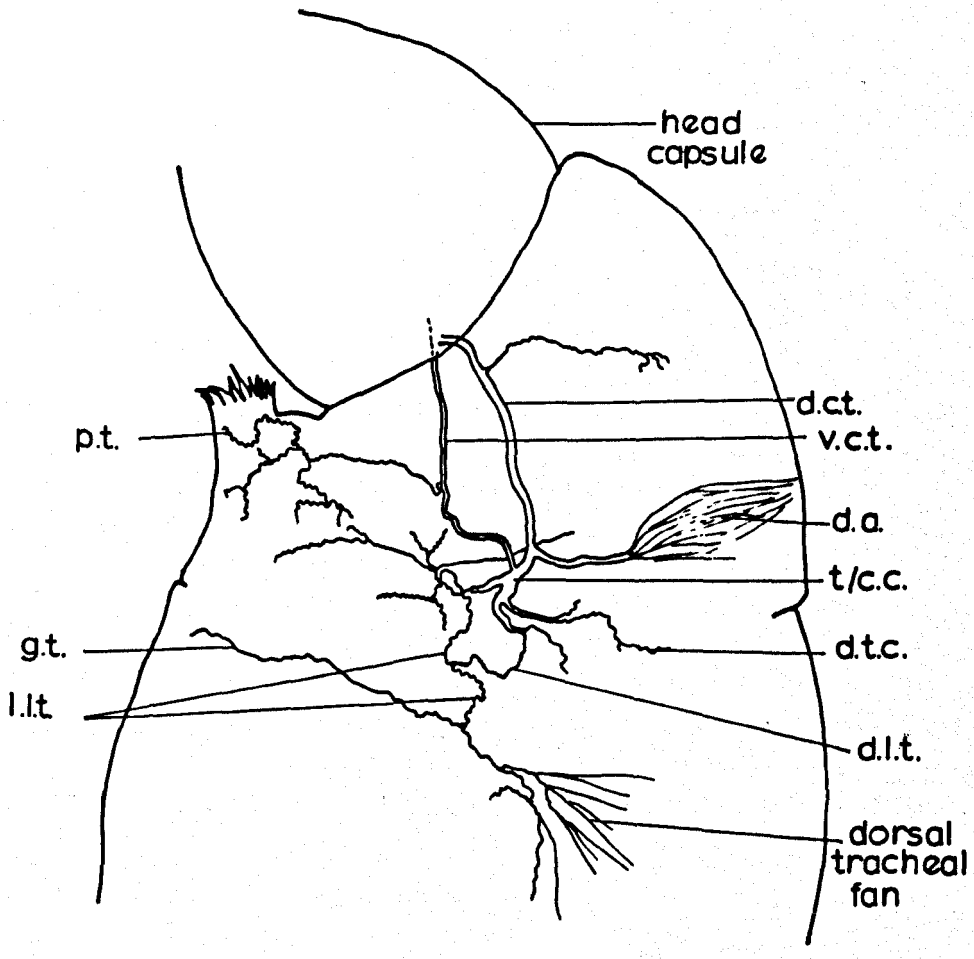

head
capsule
d.c.t.
v.c.t.
p.t.
d.a.
t/c.c.
g.t.
d.t.c.
l.l.t.
d.l.t.
dorsal
tracheal
fan

Figure 6.12 Glyptotendipes glaucus Mg. larva, dorso-lateral apsect of rudimentary thoracic tracheal pattern, segments 1 - 3, right side only.

LEGEND

d.a., dorsal anastomosis; d.c.c., dorsal cervical commissure; d.c.t., dorsal cervical tracheae; d.l.t., dorsal longitudinal tracheae; d.t.c., dorsal tracheal commissure; d - v.c., dorsal - ventral commissure; g.t., ganglionic tracheae; l.l.t., lateral longitudinal tracheae; p.t., proleg tracheae; sbo., suboesophageal tracheae; spo., supraoesophageal tracheae; t/c.c., thoracic/cervical commissure; t.t.c., transverse tracheal commissure; t.t/g.t.c., transverse thoracic/ganglionic tracheal commissure; v.c.c., ventral cervical commissure; v.c.t., ventral cervical tracheae; vs.t., visceral tracheae

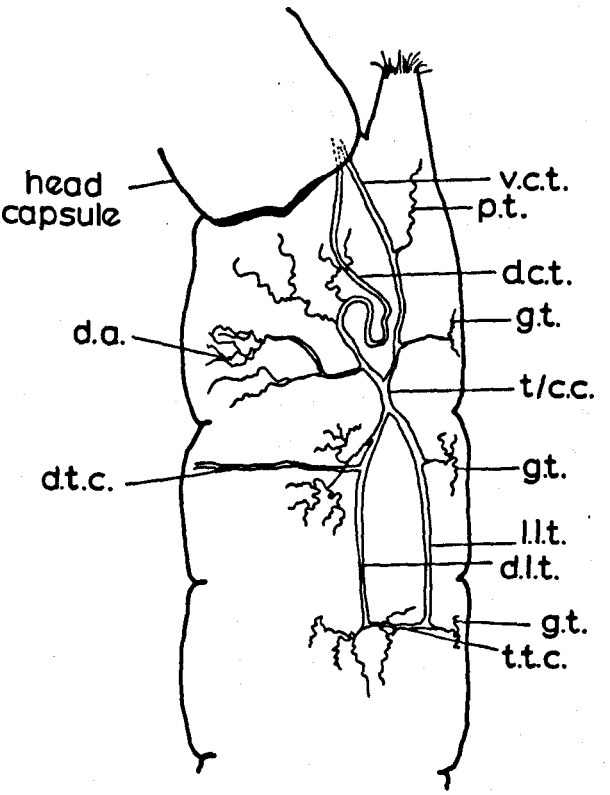
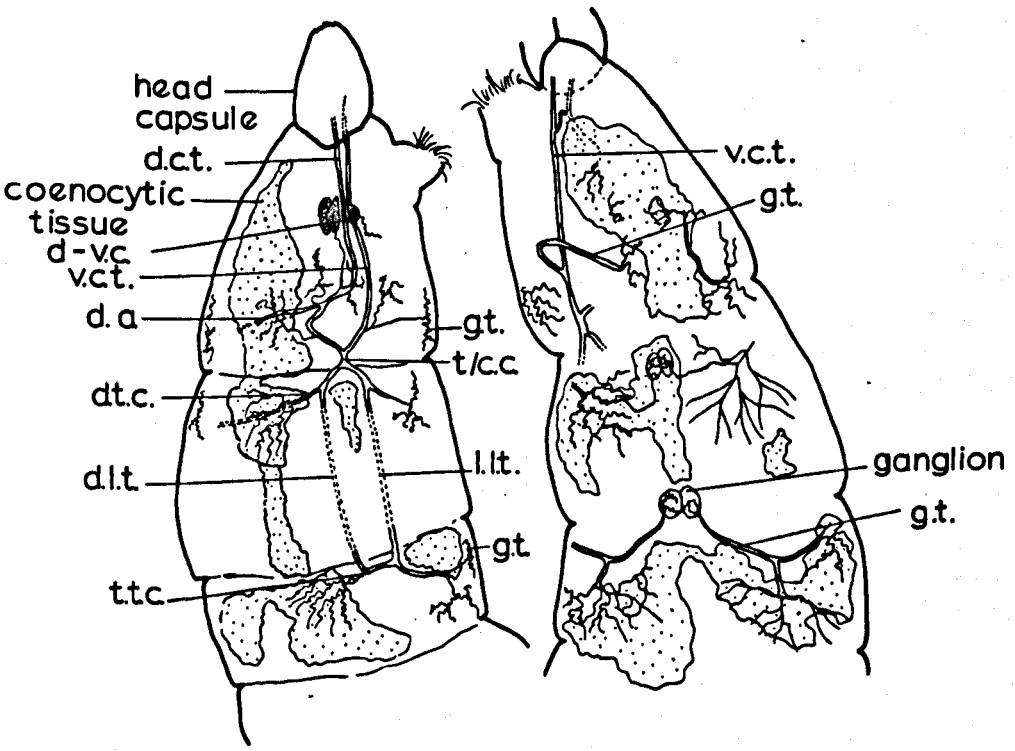

head capsule
v.c.t.
p.t.
d.c.t.
g.t.
d.a.
t/c.c.
g.t.
d.t.c.
l.l.t.
d.l.t.
g.t.
t.t.c.

Figure 6.13 Cryptochironomus 'defectus' larva, dorso-lateral (right side only) and ventral aspect of rudimentary thoracic tracheal pattern, segments 1 - 3.

LEGEND

d.a., dorsal anastomosis; d.c.c., dorsal cervical commissure; d.c.t., dorsal cervical tracheae; d.l.t., dorsal longitudinal tracheae; d.t.c., dorsal tracheal commissure; d - v.c., dorsal - ventral commissure; g.t., ganglionic tracheae; l.l.t., lateral longitudinal tracheae; p.t., proleg tracheae; sbo., suboesophageal tracheae; spo., supraoesophageal tracheae; t/c.c., thoracic/cervical commissure; t.t.c., transverse tracheal commissure; t.t/g.t.c., transverse thoracic/ganglionic tracheal commissure; v.c.c., ventral cervical commissure; v.c.t., ventral cervical tracheae; vs.t., visceral tracheae


head capsule
d.c.t.
coenocytic tissue
d-v.c.
v.c.t.
d.a.
g.t.
t/c.c.
d.t.c.
l.l.t.
d.l.t.
g.t.
t.t.c.
v.c.t.
g.t.
ganglion
g.t.

C. tentans (Fig. 6.10), C. plumosus, C. lugubris, (Fig. 6.11) and C. dorsalis, Glyptotendipes glaucus (Fig. 6.12), Cryptochironomus sp. (Fig. 6.13), Phaenospectra sp., Limnochironomus sp. and Endochironomus sp. (Plate 6.16).

The thoracic tracheae follow the pattern described in other Chironominae larvae - eg. Polypedilum nubeculosus earlier in the text and Whitten's (1960) account of the system in Chironomus dorsalis larvae.

The main difference which has been observed in larvae with the rudimentary thoracic trachael system is that the tracheal fans in some species (eg. Endochironomus sp.) are more extensive than in some other species (eg. Chironomus anthracinus). Generally, the shallow-water species have more ramifying tracheal fans.

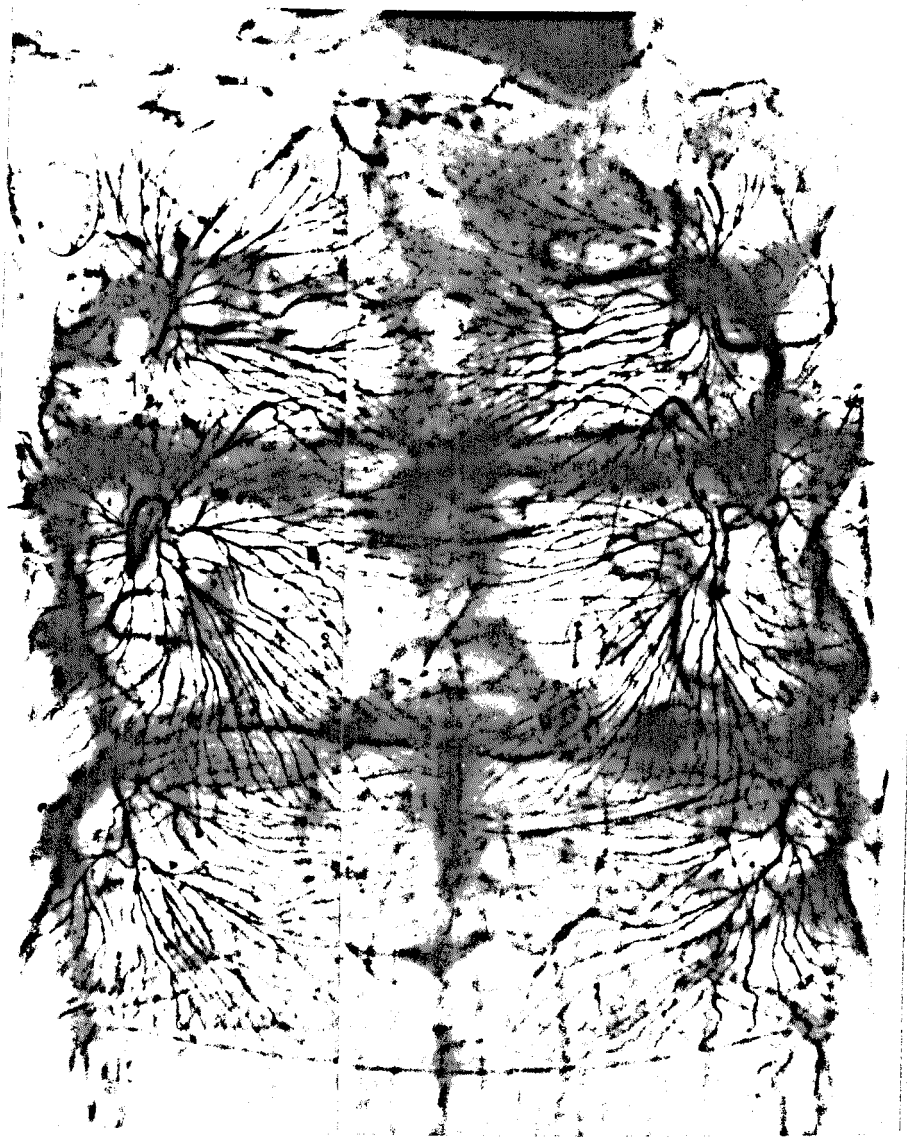
The dorsal longitudinal tracheae (d.l.t.) and the lateral longitudinal tracheae (l.l.t.) are present and run parallel to each other (Fig. 6.9 and Plate 6.15) from the thoracic/cervical commissure (t/c.c.) in segment 1, until they are connected by the transverse commissure in segment 3. The d.l.t. are connected dorsally in segment 2 by the dorsal tracheal commissure.

The l.l.t. give off the 2nd and 3rd ganglionic tracheae. The dorsal cervical (d.c.t.) and ventral cervical tracheae (v.c.t.) branch from the t/c.c. anteriorally and pass into the head capsule. A dorsal-ventral commissure connects the two cervical tracheae immediately before they enter the head capsule.

Across the dorsal surface of the 1st postcephalic segment is an anastomosis of tracheal fans (Plate 6.14) branching from the d.l.t. In Cryptochironomus (Fig. 6.13), the oesophageal tracheae can be clearly seen coming off the d.c.t. and entering the "brain". The v.c.t. give rise to the proleg tracheae and the 1st ganglionic tracheae.

* *

Plate 6.16 Rudimentary thoracic tracheal pattern in Endochironomus albipennis Mg.; segments 1 - 3



Enlargement of Plate 6.16 showing ventral tracheal fans on body wall

It is apparent that the apneustic tracheal system of larval Chironomidae is much reduced from the basic Dipterous plan as described by Keilin (1944) and that each subfamily which has been studied had a distinctive tracheal pattern which may reflect phylogenetic relationships. The variation which does exist between the four tracheal patterns is not, however, extensive, the trend being towards further reduction in specific areas.

A constant feature of the four patterns is the arrangement of the main tracheae in the thoracic segments. The thoracic/cervical commissure forms a pivot from which the ventral and dorsal cervical tracheae and their associated branches travel anteriorally and the dorsal and lateral, posteriorally. In all patterns, at least one (d.t.c.) dorsal tracheal commissure arises from the d.l.t. in segment 2 and the d.l.t. and l.l.t. are joined by a transverse tracheal commissure anteriorally in each segment. This one pattern unit is the extent of the rudimentary thoracic tracheal pattern in Chironomus s.s. groups A and B (Coe, 1951), and is the most reduced which has been found.

Reduction of the basic plan generally occurs beyond the thoracic segments although some thoracic features present in the tricommissural pattern, eg. the ventral cervical commissure and the second d.t.c. are absent from the other three patterns. These are not secondary developments but vestiges from the basic Dipterous plan. Similarly, the dorsal abdominal commissure in some Tanypodinae larvae is unique among the Chironomidae but is typical of amphineustic larvae. The bicommissural pattern seems to be a forerunner to the anterior/posterior pattern.

It seems reasonable to assume that, on the basis of the tracheal system, the Orthocladiinae such as Cricotopus sylvestris, are the most primitive of the subfamilies in the Chironomidae. The criterion for

primitiveness in this context is the number of basic features which have been inherited unchanged and the tricommissural thoracic tracheal pattern incorporates more of the features in the basic larval Dipterous plan than the other 3 patterns.

The four tracheal patterns show sequential reduction of the tracheae and the concurrent development of the respiratory pigment, haemoglobin. This is seen as an evolution towards a semi-sedentary, tubiculous life-style, the less well-developed tracheae of the rudimentary thoracic pattern being due to secondary simplification. It may be argued that tracheae have a hydrostatic function and as the need arose to adapt to a eutrophicating lake system and colonisation of the deeper sediments occurred, so tracheae became inadequate and superfluous. An extensive buoyant air-filled system would indeed be a disadvantage to a photonegative, tubiculous animal inhabiting the profundal.

It would appear that a relationship does exist between the tracheal system of a species and its habitat and distribution. Generally, littoral - dwelling chironomid species have more extensive tracheal systems than those chironomids which inhabit the sediments of deeper, often anoxic waters. This general statement obviously does not apply to those Chironomus s.s. with rudimentary thoracic tracheal patterns which live in the shallow littoral zone, nor to Procladius larvae which roam lake sediments from the littoral to the profundal. The tracheal system, as a morphological feature is therefore stable and does not vary in response to different environmental factors.

* *

SECTION 2 INTRACELLULAR RESPIRATION: STUDIES ON GLYCOGEN

INTRODUCTION

6.2.1 A study was carried out (see: Chapter 2.2.2) to investigate the claim (Augenfeld, 1967) that the ability of some Chironomus larvae to withstand adverse conditons, such as anoxia and starvation, could be correlated with their possession of stores of glycogen.

During the larval cycle in Chironomus anthracinus, the profundal populations are subjected to two periods of deprivation, (Jónasson, 1964; 1965; 1967; 1970; 1972). Firstly, in the 2nd instar, which ceases to feed due to oxygen lack and secondly, during the 4th instar which may be unable to feed if phytoplankton becomes limiting due to low temperatures. Jónasson has frequently stated that C. anthracinus larvae in Lake Esrom cease to feed "during the first few months of the year", when the lake is frozen. However, most of the larvae collected from December - March in Newton Mere had full guts, presumably because the winters of 1971/72 and 1972/73 were quite mild.

It is obvious that the larvae must have some kind of reserve to facilitate even the most minimal energy requirements during periods of deprivation. It was also observed that larvae about to pupate were swollen with white deposits in the fat bodies and were sluggish in their movements. Furthermore, pupae do not feed during metamorphosis and the adults take only occasional liquid meals from drops of water or honeydew.

Therefore it was considered that Chironomus sp. require a substantial energy store: a) for anaerobic respiration in the 2nd instar, b) to counteract starvation in the 4th instar, c) for metamorphic reorganisation in the pupa and d) in the adult, to complete the life-cycle. Jónasson (1970) described a 2-year life-cycle for C. anthracinus larvae in the deep profundal of Lake Esrom. Similarly, a low number of larvae, about $500/m^2$, could always be found at 14 and 16 m in Newton Mere during summer

stagnation. These larvae would therefore have to endure two periods of anoxia during their 18 months to 2-year life cycle.

Glycogen is the most usual storage form of carbohydrate in invertebrates and is found primarily in the fat bodies, oenocytes and sarcoplasm of muscle tissue, (Wigglesworth, 1953). Deposits of glycogen have also been found in neurosecretory cells in the brain of Chironomus riparius, (Credland and Phillips, 1974). Towards the end of the larval period, the storage cells are stuffed with reserves of fat droplets, protein and glycogen granules.

Under normal aerobic conditions of glycogen breakdown, the conversion passes through glucose, pyruvic acid, acetyl coenzyme A and finally CO_2 and H_2O. The anaerobic breakdown of glycogen, however, is only 27% efficient compared with aerobic respiration (Giese, 1968) and therefore some response by the larva to its reduced circumstances might be expected. Augenfeld (1967) found that larvae of Chironomus thummi (= Chironomus riparius; Credland, 1973) increased their use of glycogen tenfold during periods of anoxia, so that nearly as much energy through glycolysis could be supplied as by aerobic respiration. Larvae of Chironomus plumosus responded by reducing their energy requirements so that only a twofold increase in the use of glycogen was required.

6.2.2. The first study, which acted as a preliminary to the second, involved monitoring, from March to July 1973, the glycogen content of freshly collected larvae, particularly of Chironomus anthracinus, but Procladius choreus larvae were also examined. Occasional analysis was made of others including Chironomus plumosus. The monitoring period was rather short as valuable time in the previous months had been lost in following the Folin-Wu method for blood sugar estimation (Myers, 1942).

The results are shown in Table 6.2, together with the prevailing profundal oxygen and temperature conditions.

As conditions in the profundal become more limiting due to rising

temperatures and falling oxygen levels, the amount of stored glycogen increases reaching a maximum during May. This is the month of heaviest emergence and it would appear that these two facts are not unrelated, if the premise is accepted that 4th instar larvae store glycogen to provide a source of energy for the pupae and adults which do not feed. At this time it is not uncommon to find larvae about to pupate, which are fat with white subcutaneous deposits.

TABLE 6.2 Results from monthly monitoring of glycogen levels in freshly collected larvae from Newton Mere, together with the prevailing profundal conditions

	Profundal conditions		Mean glycogen content (% of larval D.W.)		
Month (1973)	Temperature in °C	Percentage O_2 satn.	Chironomus anthracinus	Procladius choreus	Chironomus plumosus
March	5.30°	84%	6.63%	1.11%	8.70%
April	7.50°	75%	11.28%	14.74%	14.04%
May	8.50°	22%	41.88%	52.66%	-
July	10.40°	4%	10.45%	-	-

The values of 41.88% for Chironomus anthracinus and 52.66% for Procladius choreus may seem rather high but are not exceptional. At one stage in the growth of Gasterophilus (the Horse-bot fly), the larva is parasitic in the stomach of the horse and can survive as long as 17 days in the complete absence of oxygen, (Wigglesworth, 1974). Van Kemnitz (1916) measured the glycogen content of Gasterophilus larvae and found it to be 31% of the D.W. Mature honey-bee larvae can contain as much as 33.5% glycogen (Strauss, 1911).

Chironomid larvae collected in July were found to have substantially lower glycogen levels. These larvae are mature 4th instars, which for some reason do not emerge until either October/November or May/June of the following year. Jónasson (1970) suggested that weight was very important as a controlling factor in emergence. If the larvae of Chironomus anthracinus reach the weight of approximately 13 mg in Spring, they emerge and those which are left behind are found to weigh only 10 mg. Why these "left-over" larvae do not put on weight like the others is unclear but intraspecific competition for food and space may be involved.

Augenfeld (1967) described two results from his natural populations which largely support the data for Newton Mere. Firstly, there was a sharp drop in glycogen content of Chironomus larvae during June and July in the anoxic Lake Mendota and during summer stratification, larvae with high glycogen contents were found in the same population as larvae with much lower glycogen levels. The mean value during May for C. anthracinus larvae from Newton Mere was calculated from results which ranged from 18.45% to 60.42%

The main conclusions which can be drawn from the brief monitoring study are as follows. 4th instar Chironomus and Procladius larvae store glycogen which provides the pupa and the adult with an energy source for metamorphosis, emergence, flight, mating and oviposition, etc..

At other stages in the life-cycle, glycogen stores are drawn upon to assist the larvae through adverse conditions such as starvation and anoxia. Unfortunately no tests were made on other instars and conclusions must be made using other sources. 1st instars must feed enough to ecdyse to the 2nd instar before the lake stratifies as they cannot survive low oxygen conditions (Neess and Della Crose, unpublished data quoted by Augenfeld, 1967). The 2nd instars survive the long period of anoxia by the anaerobic production of energy by the process of

glycolysis. Jónasson (1970) stated that in the 3 - 4 weeks following the autumn overturn, the 3rd instar larvae of C. anthracinus increase in weight by 900%. Presumably most of this energy is used for growth but may also provide the 4th instar with the means to survive starvation should low temperatures during winter limit the production of phytoplankton.

6.2.3. Before continuing with the study, the purity of the glycogen which had been isolated was determined by the anthrone reaction (2.2.2iii) and was compared against the purity of B.D.H. (oyster) biochemical glycogen.

The isolated chironomid glycogen was found to be 53.5% pure which compares modestly with B.D.H. biochemical glycogen which was, by the same method, 80% pure.

Calculations

$$\frac{A_{620} \text{ of glycogen}}{A_{620} \text{ of glucose}} \times 100 = \text{purity of glycogen}$$

A_{620} represents the spectrophotometric reading when set at 620 mμ and the blank set to zero.

A_{620} of chironomid glycogen = 26.5

A_{620} of glucose = 49.5

Therefore, the purity of chironomid glycogen = 53.5%.

This result confirmed the impression that the figures for glycogen levels during the monthly monitoring were rather high and reflected some inaccuracy in the technique.

6.2.4 The distribution data show that Chironomus anthracinus, Procladius choreus and Cricotopus sylvestris differ in their ability to

tolerate low oxygen conditions. In the experiment which was set up (2.2.2iv) 4th instar larvae of these three species were subjected to four different oxygen and temperature conditions for a fortnight, and an attempt has been made to relate their survival to their glycogen content.

The results are presented in Table 6.3.

Chironomus anthracinus

In all cases in which an extraction was made, the post-experimental glycogen levels were found to be higher than the pre-experimental and were highest in the 95% O_2/5°C group, all of which survived. No extraction was made from the 95% O_2/20°C group.

It would appear that some sort of relationship exists between survival rate and the ability to store glycogen. As the rate of survival increased, so the level of glycogen was found to increase. The percentage oxygen saturation did not seem to be as important a factor in survival as the temperature, since the 5% O_2 saturation would not unduly affect C. anthracinus (Jónasson, 1965). Tubes were built by all groups except 95% O_2/20°C, which lay just below the surface of the mud. With decreasing oxygen and increasing temperature, the tubes were built further away from the surface: under 5% O_2/20°C conditions, the tubes were all approximately 1 cm high.

Despite its low survival rate the 95% O_2/20°C group was the most "successful" in terms of completion of the life-cycle: 2 adults emerged and 1 pupa was found at the end of the experiment. In none of the other conditions were any pupae or adults found.

Procladius choreus

The glycogen value of 88% for the 5% O_2/20°C group is impossibly high and should be discounted.

TABLE 6.3 Results from experiment into the relationship between survival under varying oxygen and temperature conditions and the glycogen content of 3 species of 4th instar larvae

	Condition	Original no. of larvae	Survival rate	Glycogen content (% of D.W.)	Remarks
Chironomus anthracinus	95% O_2 20°C	20	40%	-	2 adults 1 pupa
	5% O_2 20°C	18	72%	12.40%	all tubes 1 cm high
	5% O_2 5°C	19	89%	15.56%	openings, but not tubes visible
	pre-experimental glycogen value = 10.45%				
Procladius choreus	95% O_2 20°C	9	0%	-	5 found dead
	5% O_2 20°C	17	70%	88%(?)	2 found dead
	95% O_2 5°C	20	85%	21.05%	1 dead pupa
	5% O_2 5°C	14	100%	19.84%	-
	pre-experimental glycogen value = 52.66%				
Cricotopus sylvestris	95% O_2 20°C	8	62%	-	4 adults
	5% O_2 5°C	6	83%	-	nets at base of flask
	5% O_2 20°C	8	87%	-	6 adults 1 dead pupa nets all over flask
	95% O_2 5°C	14	100%	16.6%(?)	3 adults
	pre-experimental glycogen value = 6.88%				

As in Chironomus anthracinus, temperature seems to be a more important factor than oxygen concentration in the survival of Procladius larvae. The two groups with the highest survival rate were both from low temperature conditions.

The post-experimental glycogen value of 21.05% and 19.84% are considerably lower than the pre-test value of 52.66%, and although the two values do not differ markedly, the lower value was found in the group with the highest survival - 5% O_2/5°C. An interesting observation which was made concerned the number of dead larvae recovered at the end of the experiment. In the 95% O_2/20°C group, although all 9 larvae died, only 5 were actually found. Similarly, 5 larvae died in the 5% O_2/20°C condition but only 2 were recovered. A possible explanation for all the results is as follows:

At low oxygen/low temperature levels (5% O_2/5°C), Procladius larvae are quiescent and require no more food than that which they can find in the mud. With increasing oxygen (95% O_2/5°C), the larvae are more active and presumably turn to cannibalism, as two larvae from the latter group were found to be missing.

As the temperature increases (5% O_2/20°C), the metabolism of the larvae increases, and three larvae were found to be missing. With both high oxygen and high temperature (95% O_2/20°C), the larvae are at their most active and four were found to be missing at the end of the experiment.

It is considered that as conditions "improve", and the larvae become more active at the higher temperatures, so they resort to more frequent cannibalism.

Cricotopus sylvestris

The only post-experimental glycogen value of 16.6% (95% O_2/5°C group) must be discounted because there was no food available for the larvae from which they could have synthesised glycogen. The pre-test value was 6.88% of the D.W.

The only conditions from which adults were not obtained was 5% O_2/5°C, although the larvae survived well, having spun nets at the base of the flask. The most "successful" group, as distinct from the best surviving group, was 5% O_2/20°C, from which 6 adults emerged and one dead pupa was found, with one remaining larva.

6.2.5 The uptake of oxygen by 4th instar Chironomus anthracinus larvae was measured at 3 temperatures (see 2.2.3) in order to study the overall increase in oxygen uptake from the "low temperature" to the "high temperature" conditions.

The readings in µl O_2/hr were converted to STP (standard temperature and pressure) and expressed as the QO_2, ie. µl O_2/mg DW/hr.

The Q_{10}, ie. the increase in the rate of a reaction with a 10°C rise in temperature, was calculated using Van't Hoff's equation:

$$\log Q_{10} = \frac{10}{t_2 - t_1} \log \frac{k_2}{k_1}$$

where k_2 is the rate of the reaction at temperature t_2 and k_1 is the rate at t_1.

The Q_{10} was found to be 3.16, which is a very reasonable value for the range in temperature. Giese (1968) gives a Q_{10} of 3.9 for the rate of cleavage in Arbacia eggs over a temperature range of 7 - 17°C.

Fig. 6.14 shows that C. anthracinus larvae in the 21°C ("high temperature") group respired at a rate more than 5 times greater than those larvae in the 6.5°C ("low temperature") group. These results

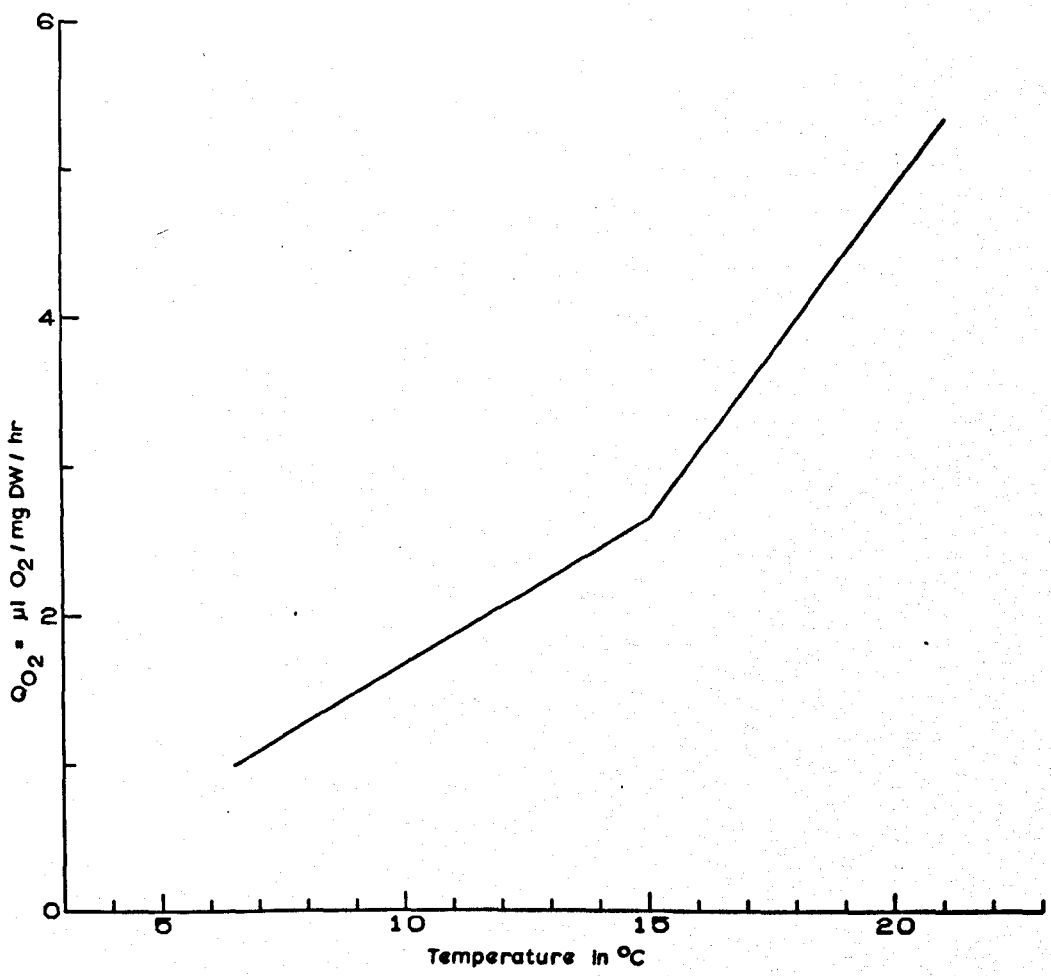


Figure 6.14 Relation between temperature and respiratory rate in 4th instar Chironomus anthracinus larvae.

support the statement made in 6.2.4 that temperature seemed to be a more important factor than oxygen levels in determining survival. There was a lower survival rate of C. anthracinus larvae in both high temperature groups, (Table 6.3). If the larvae were respiring at such a higher rate at 21°, then they would deplete any stores of energy very much faster than at 6.5°.

It would appear from the results of the monthly monitoring that the increase in the amount of glycogen stored by 4th instar Chironomus anthracinus larvae after winter starvation and those larvae's imminent metamorphosis, are not unconnected. Both activities peak in May and it has been suggested that as neither the pupa nor the adult feed, the glycogen is used as an energy store.

The main conclusion which can be drawn from the brief study into survival under stress is that no correlation may be assumed between the survival rate under differing oxygen and temperature conditions of C. anthracinus, Procladius choreus and Cricotopus sylvestris larvae and their glycogen contents. What appears to be a relationship between increasing glycogen and greater survival in C. anthracinus is not significant as the glycogen levels do not differ enough from each other.

C. anthracinus (4th instar) larvae at 21°C respire at a rate five times greater than at 6.5°C. The Q_{10} was found to be 3.16.

* * * *

7.

FINAL DISCUSSION

The initial factor affecting the ecology of chironomid larvae in the Shropshire meres is their history of dispersal. All the species found in these meres are typical of a eutrophic lake system in a temperate latitude and the species lists which have been compiled bear certain similarities to those lists produced by Berg (1938), Brinkhurst and Walsh (1967), Charles, East et al. (1974), Dunn (1961), Hunt and Jones (1972), Jónasson (1972), Maitland, Charles et al. (1972), Mundie (1955, 1957), Slack (1965) and Smith and Young (1973). However, microdispersal, that is the dispersal and distribution of chironomids within one mere, or group of meres, is of more relevance to the present study.

Other factors which have been found or are considered to have an influence in chironomid ecology, have been divided into those which are extrinsic and those which are intrinsic to the species. Extrinsic factors are those concerned with the food supply, enemies, the physico-chemical environment, disease and shelter, ie. those factors which affect the animal from outside itself and over which it has little or no control. Intrinsic factors are those of behaviour, physiology and morphology, ie., those factors inherent in a species.

The two most important factors which have been found to affect the distribution and abundance of chironomids in these meres are extrinsic and are the oxygen content of the water and the time of initiation of thermal stratification. Both are intimately connected with and dependent upon the temperature regime. Species can be divided into those which are found in the hypolimnion (below 4 - 5 m) and those above the thermocline during thermal stratification. In the hypolimnion only those larvae with rudimentary thoracic tracheal systems and haemoglobin are found, ie. Chironomus s.s. group B. Under isothermal conditions Procladius choreus

larvae are found in the deepest profundal but with the onset of stratification, the larvae begin to emerge as adults and also to migrate away from low oxygen levels. This illustrates the disadvantage of the bicommissural thoracic tracheal system and blood with a low concentration of haemoglobin. Despite having been described as ubiquitous, P. choreus larvae cannot withstand low oxygen conditions. Walshe (1948) found that 50% of P. choreus larvae were dead within 12 hours in anaerobic conditions compared to 101 hours for a Chironomus species.

However, if oxygen is the limiting factor in dispersal and distribution during stratification, this raises the problem why other Chironomus s.l. species, ie. those with anterior/posterior or rudimentary thoracic tracheal systems and haemoglobin are found in sediments below 4 m. Genera such as Glyptotendipes, Polypedilum, Limnochironomus, Microtendipes and Tanytarsus are known to live in habitats which may occasionally be low in oxygen, for example, Glyptotendipes glaucus inhabits channels in rotting wood. These genera are certainly found at great depths in other lake systems. Hunt and Jones (1972) found Sergentia coracinus Zett. in Llyn Tegid at 30 and 40 m varying from 1 - 33% of the populations there; Humphries (1936) recorded Endochironomus and Tanytarsus at 60 m and Microtendipes at 9 m in Windermere. Slack (1965) found Sergentia coracinus at a mean depth of 55 m in the Tarbet Basin, Loch Lomond. Therefore these larvae can live at great depths and so pressure is not an important factor.

As it appears that these larvae possess the necessary physiology to colonise habitats which may be anaerobic occasionally, why are they not found beyond the littoral zone in the Shropshire meres during any season? The most reasonable explanation seems to lie in the specific habitats which these larvae have adopted. Glyptotendipes glaucus larvae are found more frequently in rotting pieces of wood than elsewhere; Microtendipes seems to favour empty stems of Carex and the tissue immediately below the

epidermis of Phragmites stems. These larvae are tied to their habitat by their living space as well as food.

Gut contents of these larvae showed that Limnochironomus, Glyptotendipes and Microtendipes all ate substantial amounts of algae, particularly Spirulina, Spyrogyra, Cladophora, Pediastrum (only by Limnochironomus), Staurastrum (only by Glyptotendipes) and diatoms. Included in the gut contents were particles of detritus and what could have been pieces of net which had trapped fragments of animal tissue, particularly oligochaete spicules and parts of Daphnia. Larvae with anterior/posterior patterns and those littoral-dwelling species with rudimentary thoracic patterns are therefore confined by virtue of their food preferences and semi-sedentary habits in fixed, less motile habitats. The block of rotting wood inhabited by Glyptotendipes larvae is unlikely to be moved far across the lake floor except in the strongest currents.

Limnochironomus, Glyptotendipes and Microtendipes have two kinds of feeding styles: one of gathering algae with their anterior prolegs and mouth parts and one of filter-feeding by spinning nets. Both Glyptotendipes and Microtendipes line their adopted homes with silken net; Limnochironomus builds a cigar-shaped tube of detritus and grit which it also lines with silk and Endochironomus joins two leaves together with net, one below and one above. Presumably when oxygen levels fall, even temporarily, the larvae stay in their tubes, irrigate and filter feed while the haemoglobin becomes functional.

All the guts of Microtendipes (which has an anterior/posterior tracheal pattern) which were examined contained a lot of air and also some Angiosperm tissue. It may be that Microtendipes, tunnelling under the epidermis of plants, eats chunks of the spongy tissue and in so doing may obtain some sort of an air supply. This is rather similar to larval Mansonia (a mosquito) and Donacia (a beetle) which have exploited the air

in submerged plants by means of piercing organs (Wigglesworth, 1972).

Procladius choreus larvae do return to the profundal when the autumn overturn has occurred but this is an active swimming larva which searches the sediment for prey and is equipped with both a well developed bicommissural tracheal pattern and an ability to synthesise a limited amount of haemoglobin. This ability is shared by two related Tanypodinids, Anatopynia varia and Pentaneura monilis and has been described for other fauna liable to require the pigment, such as Daphnia and Artemia (Jones, 1972). It is more than probable that P. choreus can adjust its specific gravity like Corethra (= Chaoborus) larvae (Wigglesworth, 1974) by altering the amount of air in the tracheal system.

Surface-dwelling species such as Cricotopus sp. remain at the surface throughout the summer when the life-cycle is 3 - 4 weeks long. These larvae are photopositive and phytophagous and have the most fully developed tracheal system seen in the Shropshire Chironomidae - the tricommissural thoracic pattern - which confers buoyancy upon the larvae. These species are thought to survive winter in the egg stage as several trawls with the fine plankton net during winter and spring failed to catch any larvae from a pond in which, during the summer, the lily pads had been covered quite thickly with the nets of Cricotopus sylvestris and trifasciatus. Larvae were never found in the bottom mud during winter so it is unlikely that they burrowed down to escape the cold. Trawls were made with the plankton nets because it was thought that perhaps the young larvae were pelagic and became part of the plankton.

Of those species which continuously inhabit the profundal the most numerous in the Shropshire meres is Chironomus anthracinus. A small percentage of the population remain behind after the main emergence each year and do not pupate and become adults until the October or even the

spring of the following year. However, the success of the profundal population relies almost entirely on the time of onset of thermal stratification. It was described in Chapter 3.2.2 how a month's "grace" between the beginning of stratification in April/May at Newton Mere, and the lowest oxygen levels (less than 10%) in June had a significant effect upon the profundal chironomid population. C. anthracinus adults emerge during April and May. The eggs therefore have about a month in which to hatch and reach the comparative safety of the 2nd instar before several months of near anoxic conditions ensue. The lifeless zone in the profundal of Blake Mere is caused by the early onset of stratification (a month before Newton Mere) and the almost immediate low oxygen conditions in the profundal. Between March and April 1972, oxygen levels fell from 79% to 3% and remained at these low levels until October/November. As the thermocline develops before the peak of adult anthracinus emergence, any eggs which had fallen into the profundal might not hatch due to the low oxygen conditions and certainly no 1st instar would survive as they do not yet contain haemoglobin. The respiratory pigment does not develop until the 2nd instar. The extraordinary persistence of the thermocline is due to the morphology of the basin. Blake Mere lies in a deep secluded hollow surrounded by trees. Even on the windiest day it was noticed that the surface of the mere would only be ruffled whilst on the more exposed Crose Mere and Newton Mere, the surface would be whipped up into waves.

In addition to the low oxygen levels in Blake Mere, the profundal temperature during summer in 1972 and 1973, never rose above 6.55°C. Although hatching of eggs to 1st instar is not impossible at these temperatures, Sadler (1935) indicates that the lowest mean temperature of water for hatching Chironomus tentans eggs is 8.8° and 7.2° for pupal development.

Two effects of higher temperatures and low oxygen levels under the thermocline are an increase in conductivity and a decline in pH. These two effects are not thought to be of major importance although as shown in Chapter 3.2.3 iii, anthracinus larvae did not survive as well at pH 4 as at pH 7 or 9. The increase in conductivity is due to the liberation of ions under low oxygen conditions (Mortimer, 1941-1942). This was shown in Table 3.2 for the concentration of calcium and magnesium at two depths under stratified and isothermal conditions. Reynoldson (1966) demonstrated conclusively the importance of the concentration of calcium as a factor in planarian distribution but the effect of calcium as a factor in chironomid distribution has not been studied. The determinations served only as an indicator of the level of productivity in each mere (Table 3.4) and in relation to conductivity (Table 3.3).

The most important effect of low oxygen levels and increase in conductivity was the resultant production of hydrogen sulphide in Crose Mere throughout stratification in 1973. H_2S behaves as a weak acid and accounts for the reduction in pH in the profundal. H_2S was detected only once from the profundal in Newton Mere and twice from Blake Mere, but it is considered to be one of the most important factors in determining the low level of abundance of profundal chironomids in Crose Mere. The highest level detected was 6.02 mg/l, twice the level Taylor (1958) found in bore hole water which he described as having "a strong odour". H_2S is a respiratory poison and is believed to account for the paucity of chironomids, particularly C. anthracinus in the profundal of Crose Mere. Table 5.7 shows how the numbers fall with depth as opposed to the situation in Newton Mere, in which numbers of anthracinus increase with depth. This is not thought to be because anthracinus is declining in competition against another more adaptable species. Density data show a decline in abundance with depth for all chironomid species. Further, the

substratum in the profundal of Crose Mere may not be so favourable to tubiculous Chironomus sp. The sediments at 9 m were found to be made up of 51.02% non-combustible material, ie. sand. Edgar and Meadows (1968) verified that Chironomus riparius larvae would not colonise sandy substrata but preferred an algal/mud substratum.

Temperature is important as a triggering factor to development, for instance, the metamorphosis to pupa from larva is initiated by the rise in temperature at the beginning of spring. Concurrent with the rise in temperature is the three month period of minimum opacity of the water in each mere. Light is considered by some workers (Jónasson, 1970) to be a mechanism for the diurnal emergence of chironomid pupae at the surface. It seems no coincidence that the period of emergence of profundal and other chironomids should coincide with the period of maximum transparency of the lake water.

Minor extrinsic factors which have been noted are predation and parasitism. The nematode family Mermithidae is a common parasite of chironomid larvae inducing changes in sex characters (Wülker, 1964). In particular, Limnomermis rosea (Hagm.) emend. Hominick and Welch (1971), lives in the hind gut of C. anthracinus and can destroy the ovaries and suppress testes development. Dr. Richard Tinsley kindly identified some nematodes as Paramermis sp. (= Limnomermis sp.) which had been found in larvae collected from some small marl pit ponds near the University of Keele, but an examination of preserved specimens from the Shropshire meres showed that nematode infestation was non-existant or extremely slight. However, the meres with the largest bird populations eg. Ellesmere were not examined and it may be that the degree of infestation is related to the size and composition of the bird population. Fraser (1974) described the trematode parasites of gulls and recorded Plagiorchis

citellatus Braun from Larus fuscus L., L. argentatus Pont. and L. ridibundus L. from Loch Leven, Kinross. Cercariae of certain species of the genus Plagiorchis are known to encyst in chironomid larvae. Nematode infestation may involve a chironomid host, but Wülker gives no indication of the ecology of Paramermis sp. (= Limnomermis sp.).

Some newly emerged adult C. anthracinus caught in flight over Crose Mere were found to have the parasitic larvae of a water mite, Piona, attached to the thorax and legs. The mites were identified by K.H. Hyatt in the Department of Zoology, British Museum (Natural History). The adult mites are free-living and predatory. Unless the anthracinus adults had harboured the mites from their own larval stage, which seems unlikely, it must be presumed that the mites attack the newly emerged soft-bodied adult as it climbs out of the pupal case.

The head capsules of some chironomid larvae were often festooned with Vorticella sp. but it is unlikely that the ciliate was actually parasitic, although some detrimental effect may have been caused by those Vorticella which had their stalks over the larvae's eyes.

The main predators of chironomid larvae are fish, diving birds (Laughlin, 1974) and leeches, particularly Helobdella stagnalis L. and Herpobdella (Percival and Whitehead, 1929; Badcock, 1949), and insect larvae such as Phryganea. No study has been made of predation, however.

The calorific value of the sediment in the profundal zone of each mere was examined following Mundie's (1957) suggestion that the nutritional nature of the substratum was an important factor in determining the distribution and abundance of chironomids. This aspect of chironomid ecology deserves closer attention as the majority of tubiculous chironomids are detritivores and are dependent upon the sediments for food. It is ironic that the sediments in the lifeless zone

of Blake Mere should have the highest calorific value (4.05 kcal/g) but as this high level is closer to values expected for fresh material, it might be supposed that the Blake Mere sediments would not be suitable for chironomid food as they may not be sufficiently decomposed. Calorific values are positively correlated with the amount of fine organic matter present in the sediment.

This study does show however that such a seemingly important factor as the quality of the food available can be secondary to other factors, such as the levels of oxygen and time of initiation of thermal stratification. Berg (1938) wrote "food decides the issue" and although this may be true in many cases, it does not apply to C. anthracinus in the profundal of the Shropshire meres. This species is considered to be abundant where numbers/m^2 reach 1100 - 1400 and over. This value was estimated from a model of the feeding area required by a full-grown (17 - 19 mm long) 4th instar larva living in its tube and feeding over a circular area. Presumably a substratum of high calorific value would be able to support more larvae than one which was less nutritious. However as larval levels reached over 7000/m^2 in Newton Mere at 16 m, the sediments here are obviously capable of supporting far more than the model suggests.

Competition for space and food in overcrowded areas must be intense. If a square metre of substratum is comfortably full with 1400 larvae, then 7000/m^2 must be perilously close to extreme overcrowding. 7000 larvae/m^2 gives a minimal space of 1.4 cm^2 feeding area per larva which could be sufficient if the sediment were nutritious enough. However there does seem to be evidence that migration does occur from overcrowded areas to those less crowded (Newton Mere data for February/March, 1973). As this migration occurs just before the period of emergence of the adults, it may be supposed that what the larvae lose in their nutrition may not be so damaging to growth as supposed. Larvae about to pupate

consume less food and the pupa none at all. Edgar and Meadows (1968) concluded that substrate selection was less marked in older larvae, so perhaps the older 4th instars were less discriminating about where they would settle. This raises the question of survival and the ability of metamorphosing larvae, the pupa and the adult to continue their existance without feeding and leads on to a discussion of the intrinsic factors which affect the ecology of larvae.

The classic studies on glycogen metabolism in Chironomus thummi Kieff. of Harnisch (1938) were followed by Zebe and McShan (1957) and Augenfeld and Neess (1961) who demonstrated the presence of lactic dehydrogenase and a glycolytic enzyme system in the tissues of Chironomus plumosus. Augenfeld (1967) continued the study by examining the effects of oxygen deprivation on two species of Chironomus, C. staegeri and C. plumosus and a species of Tanytarsus. He found that the amount of glycogen was significantly higher in the Chironomus species tolerant to anoxia than in the intolerant Tanytarsus. This complements earlier work by Walshe (1948) on the oxygen requirements and thermal resistance of some chironomids from still and flowing waters. She found that in a study of the capacity of larvae to withstand anaerobic conditions, 50% of the larvae of C. longistylus and C. paganus were still alive after 68 and 101 hours respectively, compared with Tanytarsus brunnipes (8 hours).

A study was made comparing the effect of different temperature and oxygen conditions upon three chironomid species with different tracheal patterns: Cricotopus sylvestris (tricommissural thoracic), Procladius choreus (bicommissural thoracic) and Chironomus anthracinus (rudimentary thoracic), and if the ability to survive could be related to the glycogen content of the tissues. No conclusions could be drawn from this study as some of the data were suspect, although some interesting observations

were made concerning tube building in anthracinus and cannibalism in Procladius.

However, a monitoring scheme designed to test the level of glycogen in 4th instar C. anthracinus larvae, P. choreus and C. plumosus tentatively showed that after a period of winter starvation due to limiting temperatures, glycogen levels increase up to the beginning of metamorphosis to pupa. Evidently the glycogen is being stored as an energy supply for the radical morphological changes which occur during metamorphosis and for the adult which does not feed, although some species are known to drink drops of water and honeydew (Downes, 1974). Female imagines of Chironomus anthracinus and Endochironomus albipennis have been observed in the laboratory feeding from drops of 20% sucrose solution on filter paper. The labial palps are held aside and the proboscis is extended, probing the drop of sucrose. Peristaltic movements of the proboscis were clearly seen. No similar behaviour was ever observed and it does seem clear that the adults were drinking. Plates 7.1, 7.2 and 7.3 show a sequence as the female, with palps held together under the head located the sucrose, then lowered herself down towards it with the palps moving apart and finally pressed the proboscis onto the sucrose, kneeling on the tibial/femoral joint of each leg. Many aspects of the relationship between feeding and glycogen storage in the late instar and feeding in the adult need closer study and it would be interesting to follow the levels of glycogen at different stages in the life cycle. Male imagines were rarely seen to take sugar drinks and this may be a significant feature.

Unfortunately, C. anthracinus proved to be a most intransigent species to study as the adults never mated in the laboratory even when kept in a large tank with a high cage fitted above. Chironomus tentans however, mated in 3 x 1" glass tubes and the female imagines readily laid eggs in a drop of water. Credland (1973) has described a method for establishing a permanent laboratory culture of C. riparius which has been

Plate 7.1 Female Chironomous anthracinus Zett. adult searching for a drop of sucrose on filter paper. Note palps held together under head.

Plate 7.2 Female Chironomus anthracinus Zett. adult lowering herself onto the sucrose, having located it. Note palps moving apart.

Plate 7.3 Female Chironomus anthracinus Zett. adult feeding from sucrose. Note the palps spread apart over the sucrose and the position of the legs.

seen and which works very well. Caspary and Downe (1971) have described the swarming and mating of laboratory cultures of C. riparius and found that suppression of swarming by lowering the height of the cage above the tank led to reduced mating successes. It would appear that anthracinus requires a large space in which to swarm. Why such closely related species as anthracinus, tentans and riparius should differ in their mating behaviour is unknown and deserves further study.

Some mention has already been made of the relationship between the tracheal patterns of chironomid larvae and their environment. That a relationship does exist has been shown and will be elaborated further.

Those species which live at or near the surface of the meres and amongst emergent vegetation such as Cricotopus sp. have the most fully developed tracheal systems, the tricommissural thoracic pattern, which has been found in the Shropshire mere chironomids. Another orthodladiinid species, Metriocnemus hygropetricus Kieff., was examined after being found at Blake Mere, wandering amongst floating weed and detritus, also in an acid pool at Brown Moss, Whitchurch and amongst the clinker of the sewage beds at the University of Keele. This purple-striped larva is almost terrestrial, living out of water but covered by the water film (fauna hygropetrica) and actually pupates out of the water in a case of mucilage. The dorsal longitudinal tracheae (d.l.t.) of this larva are 6.7 μ in diameter, compared with those for Procladius choreus (which are 2.5 - 4 μ) and run the full length of the body with dense tracheal fans radiating over the whole body wall. This species shows that the trend in tracheal development is towards complexity in surface dwelling and hygropetric forms and that the tracheal system may also function in controlling the equilibrium and support of the larva in or out of the water. In the closely related Corethra (=Chaoborus) larva, the d.l.t. have dilated into two pairs of air sacs, one in the thorax and one in the 7th abdominal segment. The air sacs have been

stated to function solely as hydrostatic organs (Franckenberg, 1915). It seems reasonable to assume that an air-filled tracheal system confers buoyancy upon the owner, the degree of buoyancy depending on the extensiveness of the tracheal system. Therefore, Cricotopus larvae would be more buoyant than, for example, a Chironomus larva and would tend to be found at the surface of ponds rather than living in the sediment.

It was often observed that Cricotopus and Procladius larvae would rise, anal end first, to the surface of a tank or beaker and hang from the surface tension with the anal papillae and anal brush pedestals spread over the water surface. The larvae would stay like this for a minute or more and then contract strongly, breaking the tension and swim away. This behaviour is so similar to that observed by Wigglesworth (1938) for the larvae of Aedes aegypti L. that it may have a similar function. The larvae of A. aegypti rise to the surface of the water and expose their anal spiracles, thus filling the tracheal system with air. Although Cricotopus and Procladius have no spiracles, the cuticle over the anal papillae and around the brush pedestals and anus is so exceedingly thin that, being wet, it would act as a surface for respiration. This behaviour was first noticed in larvae which were being kept in a fish tank which had become rather fouled, so perhaps if not enough oxygen is present in the water, the larvae resort to this method for obtaining oxygen. This may be "escape" behaviour for such species which cannot withstand lowered oxygen levels, for instance at night when submerged plants produce carbon dioxide.

Larvae with adequate haemoglobin have no need for such "escape" behaviour and have never been seen to rise voluntarily to the water surface. Under low oxygen conditions, haemoglobin becomes functional and acts as an oxygen carrier. Haemoglobin only functions when the partial pressure of oxygen in the water falls below 15 mm Hg. So long as the

water passing over the larval body has a pO_2 in excess of 15 mm, the pigment remains fully saturated and non-functional, (Walshe, 1950). Walshe's studies of the role of chironomid haemoglobin have shown that it is an extremely efficient respiratory pigment which remains fully saturated even at extremely low oxygen levels. Why therefore have tracheae been retained in the larval forms which have developed this pigment?

Although the organs of the body may be bathed in the plasma which carries the haemoglobin in solution, the circulatory system is crude and tracheae have the advantage of being able to traverse vital organs such as the brain and retrocerebral complex. Both these structures are found in the thorax which would seem to explain why the tracheae have altered least in that region. Some ultrastructure photomicrographs of the supra- and sub-oesophageal ganglia in Chironomus riparius were kindly shown to me by A.D. Phillips of Bedford College, University of London. These photomicrographs clearly showed cross-sections of tracheoles traversing the innermost part of the nervous tissue.

*

This study has shown that a close relationship exists between the distribution and abundance of larval chironomids in the Shropshire meres, their particular pattern of tracheal system and the physico-chemical environment. Four tracheal system patterns have been described. The most complete and therefore probably the most primitive, is the tricommissural thoracic pattern, typical of surface-dwelling and hygropetric larvae such as the Orthocladiinae. The slightly reduced bicommissural thoracic pattern is found in the predatory, free-living Tanypodinae larvae. Two patterns have been found within the Chironominae:

the anterior/posterior type of the littoral Chironomus s.l. and the much reduced rudimentary thoracic type of the generally profundal-dwelling Chironomus s.s.

Many interesting observations have been made and deserve further study, particularly the storage and use of glycogen throughout the life-cycle; feeding in the adults and its significance; and parasitism by nematodes and mites.

The study of the tracheal systems will be continued and extended to encompass species from widely differing habitats in order to present a more complete hypothesis.

* * * *

SUMMARY

Three North Shropshire meres, namely Blake Mere, Newton Mere and Crose Mere, were surveyed and benthic fauna samples quantitatively collected each month from 1971 to 1973. The factors affecting seasonal distribution and abundance of the chironomid population have been investigated. Sixty-five species have been identified; thirteen are common to all three meres, thirteen common to two, seven unique to Newton Mere, eleven to Blake Mere and twenty-one to Crose Mere. The two predominant species are Chironomus anthracinus Zett. and Procladius choreus Mg. A key to common chironomid larvae from ponds and meres has been compiled and taxonomic difficulties concerning C. anthracinus and P. choreus examined.

The three meres are warm monomictic lakes showing thermal stratification and clinograde oxygen curves in summer but returning to isothermal conditions in winter. Crose Mere is the most productive mere (Ca^{++} 63 mg/l; pH 7.9; conductivity 444 µmho/cm) and Newton Mere is relatively the least eutrophic (Ca^{++} 6.46 mg/l; pH 6.4; conductivity 136 µmho/cm). Blake Mere is slightly more eutrophic than Newton Mere. Variations in the pH, conductivity and the concentration of Ca, Mg and H_2S occur in relation to stratification and deoxygenation.

The calorific value of the profundal sediments is positively correlated with a high percentage of fine organic matter and negatively correlated with the amount of coarse organic matter and the inorganic content. The sediments of Blake Mere show high calorific values for decomposing material (4.05 kcal/g) compared with the lower values of 1.86 and 2.76 kcal/g for Crose Mere and Newton Mere respectively.

Of the total number of chironomid larvae collected, 51% were from Newton Mere, 40% from Crose Mere and 9% from Blake Mere. Over half (52%) were C. anthracinus and 20% P. choreus. C. anthracinus is widely

abundant in Newton Mere only, although it can be locally abundant in Crose Mere temporarily. Average annual densities in Newton Mere reveal a positive correlation between depth and abundance. Reduced population sizes in Crose Mere are related to the unsuitability of the profundal sediments because of the high sand content and the production of H_2S in summer, and in Blake Mere to the early onset of thermal stratification and summer stagnation. Low oxygen levels, combined with low temperatures prohibit the development of a profundal population.

Procladius choreus is carnivorous and its distribution is determined by food, particularly oligochaetes. It is tolerant of a wide variety of conditions except low oxygen levels. Its maximum density is between 3 and 4 m although it is found in the profundal during isothermal conditions. P. choreus is most abundant in Crose Mere.

The ecology of other species found in the meres has been noted and related to the development of their tracheal systems.

The sequential development of apneustic tracheae in chironomid larvae is closely related to the haemoglobin content and the level of activity of the larvae. Four types of tracheal pattern have been found:

1. The tricommissural thoracic tracheal pattern, characteristic of active surface-dwellers such as Cricotopus sylvestris Fab.;
2. The bicommissural thoracic tracheal pattern, as possessed by the predatory P. choreus, which contains some haemoglobin;
3. The anterior/posterior tracheal pattern, typical of littoral Chironominae such as Polypedilum nubeculosus Mg.; and
4. The rudimentary thoracic tracheal pattern found in profundal Chironomus s.s. which possess the most haemoglobin and which are semi-sedentary in habit.

Monthly monitoring of glycogen levels in C. anthracinus, P. choreus and Chironomus plumosus L. showed an increase in glycogen towards

pupation. Neither the pupa nor the adult feed and it is considered that the glycogen is used as an energy store. Experiments into the relationship between survival of adverse temperature and oxygen conditions and glycogen content of C. anthracinus, P. choreus and Cricotopus sylvestris were not conclusive because of experimental error, although some interesting observations were made.

More experiments included: the effect of increasing temperature on the rate of respiration of C. anthracinus larvae; and the effect of 3 pH values on the survival of C. anthracinus and P. choreus larvae.

* * * *

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APPENDIX I

Physical and Chemical Data

Newton Mere 1972

Temperature in ^{o}C

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S	4.65	3.4	4.65	10.1	14.45	15.15	18.38	18.73	13.08	12.08	7.82	5.6
1 m	4.65	3.4	4.65	10.1	14.45	15.15	18.0	18.0	13.08	12.08	7.82	5.6
2	4.65	3.4	4.65	10.1	14.1	14.8	17.3	18.0	13.08	11.72	7.82	5.6
3	4.65	3.4	4.65	10.1	12.74	14.45	16.92	17.3	12.74	11.72	7.82	5.6
4	4.65	3.4	4.3	10.1	11.72	14.5	15.5	16.92	12.74	11.72	7.5	5.6
5	4.65	3.4	4.3	10.1	11.72	14.1	14.45	16.21	12.74	11.72	7.5	5.6
6	4.65	3.4	4.3	10.1	11.4	13.76	14.1	14.45	12.74	11.72	7.5	5.6
7	4.65	3.4	4.3	10.1	11.4	13.08	13.08	13.08	12.74	11.72	7.5	5.6
8	4.65	3.4	4.3	9.76	11.05	12.4	12.4	12.4	12.74	11.72	7.5	5.6
9	4.65	3.4	4.3	9.76	11.05	12.08	12.08	12.08	12.74	11.72	7.5	5.6
10	4.65	3.4	4.3	9.1	11.05	12.08	12.08	12.08	11.72	11.72	7.5	5.6
11	4.65	3.4	4.3	9.1	10.74	12.08	12.08	11.72	11.4	11.72	7.5	5.6
12	4.65	3.4	4.3	9.1	10.1	12.08	11.72	11.72	11.4	11.72	7.5	5.6
13	4.65	3.4	4.3	8.8	10.1	11.72	11.72	11.72	11.4	11.72	7.5	5.6
14	4.65	3.4	4.3	8.8	9.76	11.72	11.72	11.72	11.05	11.4	7.5	5.6
15	4.65	3.4	4.3	8.8	9.76	11.72	11.72	11.4	11.05	11.4	7.5	5.6
16	4.65	3.4	4.3	8.8	9.76	11.72	11.4	11.4	11.05	11.4	7.82	5.6
16.7	4.65	3.4	4.3	8.8	9.76	11.4	11.4	11.4	11.05	11.4	7.82	5.6

Newton Mere 1973

Temperature in ^{o}C

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S		4.3	5.6	7.82	11.4	18.73	21.35	21.35	19.85	14.10	8.80	4.65
1 m		4.3	5.6	7.82	11.4	18.0	20.6	20.6	18.38	14.10	8.80	4.65
2		4.3	5.3	7.82	11.4	15.86	19.48	18.38	18.0	14.10	8.80	4.65
3		4.3	5.3	7.82	11.05	15.15	18.38	17.3	17.65	13.08	8.80	4.65
4		4.3	5.3	7.82	11.05	13.34	15.5	16.92	17.30	12.74	8.80	4.65
5		4.3	5.3	7.82	11.05	11.72	12.74	16.56	16.21	12.4	8.5	4.65
6		4.3	5.3	7.82	11.05	11.05	11.4	14.1	15.15	12.08	8.5	4.65
7		4.3	5.3	7.82	11.05	10.74	11.05	11.4	12.40	12.08	8.5	4.65
8		4.3	5.3	7.82	10.74	10.74	10.74	10.74	11.05	12.08	8.5	4.65
9		4.3	5.3	7.82	8.8	10.74	10.74	10.74	10.74	12.08	8.5	4.65
10		4.3	5.3	7.82	8.5	10.04	10.40	10.40	10.40	12.08	8.5	4.65
11		4.3	5.3	7.5	8.5	10.04	10.40	10.40	10.40	11.72	8.5	4.65
12		4.3	5.3	7.5	8.5	10.04	10.40	10.40	10.40	11.72	8.5	4.65
13		4.3	5.3	7.5	8.5	10.04	10.40	10.40	10.40	10.74	8.5	4.65
14		4.3	5.3	7.5	8.5	10.04	10.40	10.40	10.40	10.40	8.8	4.65
15		4.3	5.3	7.5	8.5	10.04	10.40	10.40	10.40	10.40	8.8	4.65
16		4.3	5.3	7.5	8.5	10.04	10.40	10.1	10.40	10.1	8.8	4.65
16.7		4.3	5.3	7.5	8.5	10.04	10.40	10.1	10.40	10.1	8.8	4.65

Blake Mere 1972 - large basin

Temperature in °C

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S		3.7	4.3	9.1	13.08	17.65	16.92	19.48	13.76	12.4	10.74	5.6
1 m		3.7	4.3	9.1	12.74	16.21	16.56	18.73	13.76	12.4	10.74	5.6
2		3.7	4.3	8.8	12.74	15.15	16.21	18.73	13.76	12.08	10.74	5.6
3		3.7	4.3	8.8	12.40	13.76	16.21	17.30	13.76	11.72	10.74	5.6
4		3.7	4.3	8.5	11.72	13.08	15.15	15.5	13.76	11.72	10.40	5.6
5		3.7	4.3	6.25	10.74	12.40	13.08	12.74	13.34	11.72	10.40	5.6
6		3.7	4.3	5.6	9.45	10.40	10.74	11.05	11.05	11.40	10.40	5.6
7		3.7	4.3	5.3	8.15	8.15	9.45	9.10	9.20	9.76	10.10	5.6
8.		3.7	4.3	5.30	7.18	7.18	8.15	7.5	8.15	8.15	9.10	5.6
9.		3.7	4.3	5.15	6.55	6.87	7.50	7.18	7.18	7.5	8.15	5.6
10		3.7	4.3	5.15	5.6	6.55	6.87	6.55	6.55	6.87	7.18	6.25
11		3.7	4.3	5.3	5.6	6.25	6.55	6.55	6.55	6.55	6.87	6.25
12		3.7	4.3	5.3	5.6	5.93	6.55	6.25	6.25	6.55	6.55	5.93
13		3.7	4.3	5.3	5.6	5.93	6.55	6.25	6.25	6.25	6.55	5.93

Blake Mere 1973 - large basin

Temperature in ^{o}C

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S		5	6.87	10.4	13.08	19.85	19.48	18.38	16.21	13.34	9.76	9.45
1 m		5	6.55	10.4	13.08	19.1	19.48	18.38	16.21	13.34	9.45	9.1
2		4.65	6.25	10.4	13.08	18.38	19.48	18.0	16.21	13.34	9.45	8.8
3		4.65	5.6	10.1	11.72	15.86	18.0	17.3	16.21	13.34	9.45	8.8
4		4.65	5.6	9.45	11.4	13.34	13.76	15.15	16.21	13.08	9.1	8.8
5		4.65	5.6	9.1	11.05	10.74	11.4	12.74	13.76	12.74	9.1	8.8
6		4.65	5.6	8.5	9.76	9.45	9.76	10.74	11.05	12.08	9.1	8.5
7		4.65	5.3	8.5	7.82	8.15	8.5	9.10	9.45	9.76	9.1	8.5
8		4.65	5.3	8.15	7.18	7.5	7.5	7.82	8.15	8.5	9.1	8.5
9		4.65	5.3	7.82	6.87	7.18	7.18	7.18	7.5	7.82	8.8	8.5
10		4.65	5.3	6.87	6.55	6.87	6.87	6.87	7.18	6.87	7.5	8.15
11		4.3	5.3	6.55	6.25	6.55	6.55	6.55	7.18	6.87	7.18	8.15
12		4.3	5.0	6.25	5.93	6.25	6.55	6.55	6.87	6.87	7.18	8.15
13		4.3	5.0	6.25	5.93	6.25	6.25	6.25	6.55	6.55	7.18	8.15

Blake Mere - small basin

Temperature in ^{o}C

1972

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S.		3.4	4.3	9.45	13.08	16.92	18.38	18.73	13.76	12.4	10.74	5.93
1 m		3.4	4.3	8.8	12.74	15.5	18.0	18.73	13.76	12.4	10.74	5.93
2		3.4	4.3	8.7	12.74	15.15	17.65	18.38	13.76	12.08	10.74	5.93
3		3.4	4.3	8.5	12.08	14.10	16.21	17.3	13.76	11.72	10.4	5.93
4		3.4	4.3	7.9	11.72	13.08	14.1	14.8	13.76	11.72	10.4	5.93
5		3.4	4.3	6.87	11.4	11.72	12.08	12.4	13.34	11.72	10.4	5.93
6		3.4	4.3	6.25	9.76	10.74	11.05	11.4	11.72	11.72	10.4	5.93

1973

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S		4.65	6.55	10.4	13.08	19.85	19.48	18.38	16.21	13.34	9.1	10.74
1 m		4.65	6.25	10.4	13.08	19.48	19.48	18.0	16.21	13.34	9.1	10.4
2		4.65	5.93	9.76	13.08	18.0	19.1	17.65	16.21	13.34	9.1	10.1
3		4.65	5.93	9.1	12.74	15.5	17.65	17.3	16.21	13.34	9.1	9.76
4		4.3	5.6	8.8	11.4	13.08	14.1	15.15	16.21	13.08	9.1	9.76
5		4.3	5.6	8.15	10.4	12.08	12.08	13.34	15.5	13.08	8.8	9.45
6		4.3	5.6	7.82	9.45	11.4	11.05	12.08	14.1	12.74	8.8	9.45

Crose Mere 1972

Temperature in ^{o}C

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S			5.3	8.5	10.74	13.76	16.56	17.3	13.34	10.74	6.87	5.6
1 m			5.3	8.5	10.74	13.76	16.56	17.3	13.34	10.74	6.87	5.6
2			5.3	8.5	10.40	13.76	16.56	17.3	13.34	10.74	6.87	5.6
3			5.3	8.5	10.40	13.76	16.56	17.3	13.34	10.74	6.87	5.6
4			5.3	8.5	10.40	13.34	16.21	17.3	13.34	10.74	6.87	5.6
5			5.3	8.5	10.40	13.08	15.15	16.92	13.34	10.74	6.87	5.6
6			5.3	8.5	10.40	12.74	14.1	16.21	13.34	10.74	6.87	5.6
7			5.3	8.5	10.1	12.40	12.74	14.1	13.34	10.74	6.87	5.6
8.			5.3	8.5	10.1	12.08	12.4	13.08	13.34	10.74	6.87	5.6
9			5.3	8.5	10.1	12.08	12.08	12.74	13.34	10.74	5.3	5.6
9.2			5.3	8.5	10.1	11.72	11.72	12.40	13.08	10.74	5.6	5.6

Crose Mere 1973

Temperature in ^{o}C

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S	3.7	4.3	8.5	9.76	17.3	19.1	18.73	22.15	18.73	14.1	8.5	5.3
1 m	3.7	4.3	8.5	9.45	17.3	19.1	18.73	21.75	18.38	14.1	8.5	5.3
2	3.7	4.3	8.5	9.1	17.3	19.1	18.73	19.48	18.0	13.76	8.5	5.3
3	3.7	4.3	8.5	8.8	17.3	19.1	18.73	18.73	18.0	13.76	8.5	5.3
4	3.7	4.3	8.5	8.8	12.74	19.1	18.38	18.0	18.0	13.76	8.5	5.3
5	3.7	4.3	8.5	8.8	12.4	15.5	15.15	18.0	17.3	13.76	8.5	5.3
6	3.7	4.3	8.5	8.8	12.08	14.1	13.34	17.65	16.92	13.34	8.5	5.0
7	3.7	4.3	8.5	8.8	12.08	13.34	12.40	14.80	14.80	13.34	8.5	5.0
8	3.7	4.3	8.5	8.8	11.72	13.08	11.72	12.74	12.74	13.08	8.5	5.0
9	3.7	4.65	8.5	8.8	11.72	12.74	11.40	12.40	11.72	13.08	8.5	5.0
9.2	3.7	4.65	8.5	8.8	11.05	12.74	11.05	12.40	11.40	12.74	8.5	5.93

Newton Mere 1972

% Oxygen Saturation

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S	90	92	97	100	84	91	86	86	76	64	62	81
1 m	90	91	96	100	82	90	87	87	76	63	65	81
2	89	91	95	100	82	89	86	87	73	61	66	81
3	89	90	95	97	75	85	75	75	74	61	66	81
4	89	90	95	97	63	83	51	55	74	61	68	81
5	88	90	94	96	62	78	37	28	75	60	70	81
6	88	90	94	96	61	70	32	15	73	'60	70	81
7	88	90	94	96	59	45	22	9	63	55	71	81
8	87	90	94	91	55	35	18	7	58	54	71	81
9	87	90	93	87	53	27	15	5	34	54	71	81
10	87	90	93	78	52	24	13	5	8	49	72	81
11	87	90	92	76	47	18	11	5	5	38	72	81
12	87	90	92	73	34	15	9	4	4	27	72	81
13	87	90	91	73	25	6	5	4	3	9	72	81
14	87	90	91	72	17	4	5	4	3	4	72	81
15	87	90	91	70	12	3	4	4	3	3	15	81
16	87	90	90	69	10	2	4	4	3	3	9	78

Newton Mere 1973

% Oxygen Saturation

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S		75	80	82	76	90	83	93	98	85	82	89
1 m		75	81	82	76	91	85	91	98	86	81	87
2		75	82	82	77	88	82	96	80	85	80	86
3		75	83	82	78	82	66	70	33	56	79	85
4		76	83	83	79	50	15	52	32	43	75	84
5		76	83	83	79	42	7	40	12	36	75	84
6		76	84	83	79	44	12	7	5	35	74	83
7		77	84	83	77	49	14	4	4	37	74	83
8		77	84	83	74	47	14	4	4	37	74	82
9		77	84	84	65	42	13	4	4	34	74	82
10		77	85	83	62	41	11	4	4	28	73	82
11		78	85	83	58	40	10	3	4	19	72	82
12		79	86	84	52	35	9	3	4	11	70	81
13		79	85	82	50	34	7	3	4	4	68	81
14		79	85	81	44	32	7	3	4	4	20	80
15		79	85	81	28	7	6	3	3	4	18	80
16		75	84	77	24	5	6	3	3	4	16	65

Blake Mere 1972 - large basin

% Oxygen Saturation

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S		77	82	92	81	118	84	95	66	76	52	64
1 m		77	81	91	81	122	81	91	65	77	54	64
2		77	80	91	78	97	75	80	64	68	55	64
3		77	80	88	77	76	69	33	60	60	56	64
4		77	80	86	70	63	42	5	41	59	51	64
5		77	80	65	62	61	25	3	4	57	49	64
6		77	80	50	58	44	20	2	1	44	48	64
7		77	80	43	50	35	12	2	1	4	36	64
8		77	80	36	38	17	7	2	1	2	9	64
9		77	80	7	8	10	6	2	1	2	6	64
10		77	80	5	4	6	6	2	1	2	5	64
11		77	80	4	3	5	6	2	1	1	5	63
12		77	80	4	3	5	6	3	1	1	5	63
13		77	79	3	3	4	6	3	1	1	5	63

Blake Mere 1973 - large basin

% Oxygen Saturation

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S		69	94	96	86	94	90	81	59	63	65	56
1 m		69	94	96	85	94	90	80	60	63	60	54
2		68	91	95	84	93	86	75	61	63	59	53
3		68	89	95	81	52	46	46	60	62	56	53
4		68	86	92	77	28	6	23	60	46	54	52
5		67	85	87	71	29	9	6	7	44	54	52
6		67	82	85	65	37	8	4	4	10	52	52
7		67	80	80	50	31	5	4	4	4	50	50
8		67	78	77	41	8	4	3	3	4	44	50
9		66	75	61	24	5	3	3	3	3	18	50
10		66	72	46	8	4	3	3	3	3	10	50
11		66	69	21	4	3	3	3	3	3	8	49
12		67	60	6	3	3	3	3	3	3	8	49
13		60	51	3	3	3	3	3	3	3	7	49

Blake Mere - small basin

% Oxygen Saturation

1972 Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S		76	81	90	80	111	97	92	58	74	52	62
1 m		78	81	87	79	109	95	91	56	74	53	62
2		77	80	86	77	101	63	72	56	67	54	62
3		77	80	83	75	80	49	28	58	57	52	62
4		77	79	73	70	64	27	4	56	54	47	62
5		77	79	39	50	20	10	2	4	52	46	62
6		77	79	10	8	14	7	2	1	8	34	62

1973 Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S		66	87	91	80	89	88.5	79	59	54	66	47
1 m		65	88	92	80	91	86	79	60	54	64	46
2		65	87	92	81	90	78	70	60	52	63	45
3		64	84	92	81	44	39	41	58	51	62	43
4		62	80	85	76	24	12	24	57	37	60	42
5		61	76	69	40	5	8	7	10	21	57	41
6		53	73	47	10	4	7	5	6	6	56	40

Crose Mere 1972

% Oxygen Saturation

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S			88	93	88	90	90	86	70	56	65	77
1 m			88	93	88	86	87	80	68	50	66	76
2			88	93	90	85	85	78	62	51	66	75
3			88	93	90	85	84	75	59	52	66	75
4			88	93	90	83	81	73	58	52	66	74
5			88	93	90	80	54	71	53	53	66	74
6			87	93	88	74	44	52	53	53	66	74
7			87	93	86	75	36	28	52	53	67	74
8			87	93	84	74	32	18	51	53	67	75
9			87	92	83	65	27	13	47	52	68	76
9.2			85	90	54	25	12	9	9	28	68	76

Crose Mere 1973

% Oxygen Saturation

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S	80	116	88	86	84	92	96	119	76	67	85	103
1 m	79	116	88	87	86	91	96	120	83	67	84	101
2	79	116	87	87	88	92	93	74	70	66	83	100
3	78	116	87	88	88	92	92	36	66	63	83	100
4	78	116	87	87	83	92	88	21	61	63	82	99
5	78	116	86	86	80	28	11	20	7	50	82	99
6	78	116	85	86	65	11	7	11	5	36	81	100
7	77	116	85	86	53	8	6	4	4	27	81	100
8	77	116	85	86	31	7	5	3	4	12	81	100
9	78	116	85	86	5	7	5	3	4	5	80	99
9.2	78	116	84	83	3	6	4	3	4	4	80	99

Newton Mere

pH

1972

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S	7.2	-	7.0	-	7.0	8.8	9.0	8.0	6.3	6.1	6.1	6.1
3.0 m	7.2	-	6.9	-	6.4	-	-	6.7	6.3	6.0	6.2	6.1
4.5 m	7.1	-	7.0	-	7.0	-	-	6.3	6.2	6.1	6.2	6.1
7.5 m	7.2	-	6.9	-	6.2	-	-	6.0	6.1	6.0	6.1	6.0
12.0 m	7.2	-	6.9	-	6.2	-	-	6.1	5.9	6.0	6.0	6.0
16.0 m	7.2	-	6.8	-	6.0	-	-	6.1	6.0	6.0	6.2	6.0

1973

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S	-	6.1	6.7	6.6	6.4	8.8	7.1	7.1	9.3	6.9	6.2	6.8
3.0 m	-	6.1	6.5	6.4	6.3	7.3	6.7	6.7	8.2	6.6	6.8	6.8
4.5 m	-	6.1	6.2	6.4	6.4	8.2	6.6	6.3	6.6	6.4	6.6	6.7
7.5 m	-	6.0	6.4	6.5	6.0	5.9	6.3	6.3	6.4	6.1	6.6	6.7
12.0 m	-	6.2	6.7	6.5	5.9	5.9	6.2	6.4	6.3	6.2	6.5	6.7
16.0 m	-	6.2	6.7	6.4	5.9	5.8	6.2	6.6	6.4	6.2	6.6	6.7

Blake Mere

pH

1972

Depth	AUG	SEP	OCT	NOV	DEC
S	8.5	6.9	6.7	6.5	6.6
2.0 m	8.2	6.7	6.4	6.6	6.6
3.5 m	7.4	6.7	6.4	6.7	6.5
6.0 m	6.4	6.4	6.3	6.2	6.1
9.0 m	6.4	6.2	6.1	6.1	6.0
13.0 m	6.4	6.1	6.0	6.1	6.0

1973

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S	-	6.6	7.3	8.2	7.1	9.3	7.8	7.1	6.3	6.5	6.8	6.9
2.0 m	-	6.5	7.3	8.2	6.9	9.1	7.7	6.9	6.2	6.5	6.8	6.9
3.5 m	-	6.6	7.3	7.9	7.0	8.7	7.0	6.4	5.9	6.2	6.7	6.9
6.0 m	-	6.4	7.2	6.6	6.5	6.9	6.6	6.3	5.9	6.1	6.7	6.8
9.0 m	-	6.7	7.2	6.8	6.4	6.7	6.5	6.1	5.8	6.1	6.6	6.9
13.0 m	-	6.7	7.2	6.4	6.2	6.7	6.5	6.2	5.9	6.1	6.3	6.8

Crose Mere

pH

1972

Depth	AUG	SEP	OCT	NOV	DEC
S	7.8	7.7	7.4	7.5	7.5
2.0 m	7.8	7.6	7.6	7.5	7.6
3.0 m	7.9	7.7	7.6	8.0	7.6
4.5 m	7.6	7.7	7.6	7.5	7.6
6.0 m	7.9	7.9	7.6	7.8	7.6
7.0 m	7.6	7.9	7.6	8.0	7.5
9.0 m	7.2	7.6	7.5	7.8	7.7

1973

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S	7.5	8.6	8.4	8.3	8.6	8.6	8.9	7.7	8.3	7.2	7.8	8.3
2.0 m	-	8.6	8.4	8.2	8.5	8.4	8.6	8.8	8.1	7.1	7.8	8.3
3.0 m	-	8.6	8.4	8.3	8.5	8.4	8.8	7.5	8.0	7.1	7.7	8.3
4.5 m	-	8.5	8.3	8.2	8.3	8.3	8.4	7.5	7.8	7.1	7.6	8.3
6.0 m	-	8.5	8.3	8.3	8.3	7.7	8.0	7.5	7.4	7.2	7.7	8.2
7.0 m	-	8.6	8.5	8.2	8.4	7.6	7.8	7.6	7.2	7.3	7.6	8.3
9.0 m	-	8.6	8.5	8.6	7.8	7.3	7.8	7.3	6.9	7.2	7.8	8.3

Newton Mere

Conductivity in μmho/cm

1972

Depth	AUG	SEP	OCT	NOV	DEC
S	123	124	122	122	126
3.0 m	123	120	122	124	124
4.5 m	121	118	122	121	122
7.5 m	130	120	121	120	122
12.0 m	140	131	124	119	122
16.0 m	149	138	155	121	124

1973

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S	-	125	126	126	127	152	127	128	118	134	142	132
3.0 m	-	125	128	119	125	144	126	125	108	135	137	142
4.5 m	-	124	125	121	125	146	127	126	113	145	133	130
7.5 m	-	129	125	119	125	152	132	136	119	138	132	130
12.0 m	-	124	124	118	127	152	131	146	127	165	137	139
16.0 m	-	126	126	119	126	153	133	151	135	155	134	130

Blake Mere

Conductivity in μmho/cm

1972

Depth	AUG	SEP	OCT	NOV	DEC
S	219	146	139	136	137
2.0 m	220	150	140	135	136
3.5 m	210	145	135	136	136
6.0 m	260	150	136	134	135
9.0 m	240	152	148	146	139
13.0 m	245	155	152	156	144

1973

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S	-	135	135	133	142	114	131	133	134	136	140	144
2.0 m	-	138	136	137	139	119	129	131	133	135	141	144
3.5 m	-	136	132	145	140	112	129	130	130	130	139	142
6.0 m	-	134	130	138	144	122	151	149	148	143	141	147
9.0 m	-	134	133	141	142	118	138	151	149	157	148	144
13.0 m	-	134	133	141	142	124	150	171	195	170	183	146

Crose Mere

Conductivity in μmho/cm

1972

Depth	AUG	SEP	OCT	NOV	DEC
S	460	367	465	520	458
2.0 m	460	400	460	530	455
3.0 m	460	307	460	515	455
4.5 m	460	307	460	545	455
6.0 m	465	309	460	520	458
7.0 m	480	393	460	522	458
9.0 m	530	395	470	522	458

1973

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S	515	445	480	470	454	439	420	390	328	375	429	412
2.0 m	-	440	470	465	450	440	440	360	328	369	429	413
3.0 m	-	440	470	460	460	438	430	410	329	374	430	410
4.5 m	-	445	470	460	470	440	480	420	330	368	425	413
6.0 m	-	445	470	460	470	480	480	430	344	369	432	412
7.0 m	-	450	470	460	478	490	510	440	348	370	429	415
9.0 m	-	450	480	490	500	510	500	560	460	373	430	412

Newton Mere 1972

Light Intensity in lumens/ft^2

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S	9.4	9.6	22	13.6	18	6.4	7.2	26	20	8.8	10.2	6.6
1 m	5.0	6.3	9.6	9.8	8.8	2.2	4.8	9.4	8	3.4	6.0	2.0
2	2.4	3.8	7.4	7.0	4.8	0.68	3.2	6.6	3.6	1.42	4.6	0.90
3	1.2	2.2	7.2	4.4	3.0	0.26	2.0	3.0	1.6	0.52	0.98	0.38
4	0.4	1.18	5.2	2.6	2.2	0.10	0.89	0.89	0.6	0.18	0.38	0.18
5	0.2	0.6	2.0	1.07	1.2	0.02	0.58	0.30	0.22	0.06	0.12	0.06
6	0.09	0.3	0.95	0.48	0.5	0	0.16	0.10	0.06	0.02	0.02	0
7	0.02	0.18	0.42	0.2	0.32	0	0.04	0.04	0	0	0	0
8	0	0.08	0.24	0.08	0.12	0	0	0	0	0	0	0
9	0	0	0.14	0.03	0.06	0	0	0	0	0	0	0
10	0	0	0.08	0	0.02	0	0	0	0	0	0	0
11	0	0	0.02	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0

Newton Mere 1973

Light Intensity in lumens/ft^2

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S		10.2	13.2	12.2	9.2	11.2	10.2	11.0	7.0	7.3	7.6	6.6
1 m		9.4	12.0	8.6	5.2	6.4	7.6	6.6	2.3	0.8	3.0	3.2
2		5.8	9.2	6.8	4.8	3.6	4.8	3.6	0.28	0.06	0.84	1.8
3		3.6	5.6	4.8	3.6	2.0	2.6	1.8	0.04	0	0.33	0.82
4		3.2	4.2	3.2	2.4	0.84	1.04	0.56	0	0	0.12	0.4
5		2.0	2.2	2.0	1.22	0.38	0.58	0.24	0	0	0.04	0.18
6		0.74	1.08	0.98	0.74	0.2	0.28	0.08	0	0	0	0.07
7		0.38	0.64	0.56	0.42	0.07	0.13	0.03	0	0	0	0.02
8		0.2	0.26	0.28	0.22	0.02	0.06	0.01	0	0	0	0
9		0.08	0.12	0.14	0.1	0	0.02	0	0	0	0	0
10		0.04	0.05	0.06	0.05	0	0	0	0	0	0	0
11		0	0.02	0.02	0.02	0	0	0	0	0	0	0
12		0	0	0	0	0	0	0	0	0	0	0
13		0	0	0	0	0	0	0	0	0	0	0

Blake Mere 1972 - large basin

Light Intensity in lumens/ft^2

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S		6	13.6	11.6	20	20	10.2	10.4	10.8	7.4	13.0	8.2
1 m		3.8	9.6	7.6	10.4	6	6.0	4.8	3.3	2.6	6.2	3.8
2		2	6.8	7.0	8.6	3	3.8	1.27	0.92	0.84	2.8	1.6
3		0.8	4.4	5.6	6.8	1.45	2.0	0.90	0.21	0.2	0.76	0.6
4		0.24	2.4	4.2	4.4	0.95	0.82	0.5	0.05	0.04	0.2	0.2
5		0.2	1.06	2.0	3.6	0.6	0.44	0.24	0	0	0.06	0.08
6		0.09	0.48	0.96	0.64	0.34	0.22	0.14	0	0	0	0.02
7		0.01	0.21	0.54	0.36	0.18	0.1	0.08	0	0	0	0
8		0	0.08	0.20	0.10	0.12	0.06	0.04	0	0	0	0
9		0	0	0.08	0.06	0.04	0	0.02	0	0	0	0
10		0	0	0.02	0.02	0	0	0	0	0	0	0
11		0	0	0	0	0	0	0	0	0	0	0
12		0	0	0	0	0	0	0	0	0	0	0
13		0	0	0	0	0	0	0	0	0	0	0

Blake Mere 1973 - large basin

Light Intensity in lumens/ft^2

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S		6.6	17	22	23	14.6	15	10.6	6.4	4.6	4.7	5.4
1 m		2.8	11	8.6	9.4	10.8	9	5.8	3.4	2.4	1.8	2.6
2		0.94	9	4.6	8.2	7.0	2	1.4	0.9	1.06	0.8	1.04
3		0.44	5	3.2	6.8	4.0	1.0	0.82	0.56	0.64	0.58	0.48
4		0.18	1.7	1.34	4.6	2.2	0.4	0.36	0.22	0.32	0.18	0.2
5		0.08	0.5	0.62	2.4	0.96	0.21	0.18	0.08	0.16	0.07	0.08
6		0.02	0.08	0.24	0.56	0.52	0.12	0.09	0.02	0.08	0.02	0.03
7		0	0.02	0.05	0.28	0.28	0.5	0.04	0	0.04	0	0
8		0	0	0.03	0.26	0.14	0.02	0.02	0	0	0	0
9		0	0	0	0.1	0.06	0	0	0	0	0	0
10		0	0	0	0.01	0.03	0	0	0	0	0	0
11		0	0	0	0	0	0	0	0	0	0	0
12		0	0	0	0	0	0	0	0	0	0	0
13		0	0	0	0	0	0	0	0	0	0	0

Blake Mere 1972-1973 - small basin

Light Intensity in lumens/ft^2

1972

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S		18	12.4	12.8	20	18	13.8	9.4	11.0	7.8	8.4	7.2
1 m		10	8.6	10.4	11.4	7.2	6.2	5.6	4.8	1.42	6.2	1.4
2		8	5.6	7.0	8.8	4.0	2.4	1.43	2.2	0.5	3.0	0.6
3		4	3.4	4.4	6.8	3.0	1.5	0.64	0.5	0.18	0.94	0.2
4		2.8	1.7	2.4	4.4	1.6	0.78	0.26	0.12	0.04	0.2	0.08
5		1.4	0.8	1.2	2.6	0.8	0.3	0.06	0.02	0	0.1	0.02
6		0.4	0.34	0.38	0.42	0	0	0	0	0	0	0

1973

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S		6.2	22	20	22	13.8	14	10.6	8.6	6.2	5.2	4.4
1 m		2.2	13	9.8	11.6	9.6	6	5.4	4.8	2.8	2.6	1.6
2		0.98	9	6.2	8.0	6.4	2	1.8	2.2	1.36	0.94	0.58
3		0.48	3.3	2.6	4.8	3.8	1.1	0.9	1.1	0.76	0.46	0.26
4		0.2	2.2	1.06	2.4	2.2	0.5	0.4	0.54	0.38	0.22	0.1
5		0.08	0.8	0.5	1.9	0.92	0.07	0.09	0.14	0.18	0.09	0.04
6		0.02	0	0.24	0.28	0	0	0	0	0.06	0	0

Crose Mere 1972

Light Intensity in lumens/ft^2

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S			10	16.4	20	26	9	8.6	18.4	7.6	11.4	10.2
1 m			6.6	13	10.8	20	4.6	4.6	8.6	3.6	7.4	6.4
2			4.4	9.8	9.2	11.2	4.0	2.4	5.2	2.4	5.4	4.6
3			3.0	8.6	7.4	9.0	3.2	1.2	2.4	1.66	3.0	2.8
4			1.8	5.2	5.6	6.2	2.0	0.4	0.92	1.36	1.58	1.32
5			0.93	3.8	4.0	4.4	1.12	0.16	0.42	0.92	0.92	0.8
6			0.51	1.89	2.6	2.4	0.68	0.05	0.16	0.4	0.52	0.42
7			0.26	0.98	1.4	1.45	0.4	0.02	0.06	0.18	0.30	0.24
8			0.13	0.47	0.92	0.7	0.24	0	0.01	0.1	0.16	0.14
9			0.06	0.18	0.54	0.3	0.1	0	0	0.08	0.08	0.08
9.2			0.01	0.1	0.44	0	0	0	0	0	0.06	0

Crose Mere 1973

Light Intensity in lumens/ft^2

Depth	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
S	6.2	10.4	22	10.4	20	11.4	8.0	12.2	10.8	7.6	8.0	6.2
1 m	3.4	6.4	15	7.0	16	7.4	1.6	6.2	5.6	2.6	5.2	2.5
2	2.5	2.6	8.4	6.2	7.6	4.8	0.16	2.8	2.6	0.76	3.4	1.0
3	1.74	0.9	8.0	4.4	5.2	3.0	0.01	0.78	1.0	0.18	2.4	0.5
4	1.22	0.3	4.4	2.3	3.6	1.32	0	0.38	0.46	0.05	1.2	0.22
5	0.76	0.1	2.4	1.32	3.0	0.68	0	0.24	0.28	0.02	0.78	0.08
6	0.46	0.02	0.66	0.86	2.0	0.28	0	0.1	0.18	0	0.42	0.03
7	0.26	0	0.32	0.46	0.96	0.14	0	0.04	0.09	0	0.22	0
8	0.15	0	0.14	0.36	0.68	0.06	0	0	0.01	0	0.12	0
9	0.08	0	0.06	0.18	0.4	0.02	0	0	0	0	0.06	0
9.2	0.06	0	0	0.13	0.22	0	0	0	0	0	0.04	0

Newton Mere 1973

Hydrogen sulphide in mg/l

Depth	APR	SEP
3.0 m	0.87	0
4.5 m	1.72	0
7.5 m	1.04	0
12.0 m	0	0
16.0 m	0.17	0

Blake Mere 1973

Hydrogen sulphide in mg/l

Depth	APR	SEP
2.0 m	2.92	0
3.5 m	6.02	0
6.0 m	2.92	0
9.0 m	6.02	0
13.0 m	0	0.17

Crose Mere 1973

Hydrogen sulphide in mg/l

Depth	MAR	APR	MAY	JUL	SEP
2.0 m	0.68	2.92	2.75	2.39	0
3.0 m	0	1.20	1.20	1.37	0
4.5 m	0.68	1.71	2.05	3.94	0
6.0 m	0.34	2.05	1.36	2.39	0
7.0 m	0	1.37	1.19	5.66	0
9.0 m	0.34	2.05	1.36	6.02	0

Newton Mere 1973

Water hardness (Ca^{++} and Mg^{++}) in mg/l

Calcium

Depth	JUN	JUL	SEP	OCT	NOV	DEC
S	-	-	3.70	7.40	7.70	6.35
3.0 m	5.50	6.55	3.30	7.55	9.20	5.70
4.5 m	6.00	6.80	3.30	8.35	9.05	5.40
7.5 m	6.25	7.55	3.90	6.70	8.20	6.15
12.0 m	5.80	7.35	3.80	9.05	7.70	5.70
16.0 m	6.00	7.55	4.10	8.30	7.90	5.85

Magnesium

Depth	JUN	JUL	SEP	OCT	NOV	DEC
S	-	-	1.10	-	-	1.42
3.0 m	1.45	1.76	1.20	-	-	1.40
4.5 m	1.50	1.70	1.30	-	-	1.55
7.5 m	1.50	1.75	1.30	-	-	1.55
12.0 m	1.50	1.90	1.50	-	-	1.47
16.0 m	1.50	1.90	1.40	-	-	1.45

Blake Mere 1973

Water hardness (Ca^{++} and Mg^{++}) in mg/l

Calcium

Depth	MAY	JUN	JUL	SEP	OCT	NOV	DEC
S	-	-	10.60	9.00	11.40	10.70	10.10
2.0 m	10.50	-	10.60	9.60	13.90	10.70	11.40
3.5 m	10.35	-	11.00	8.00	11.40	10.70	10.10
6.0 m	10.85	-	15.00	11.20	12.05	11.75	9.40
9.0 m	10.50	-	14.30	10.40	12.40	10.55	9.75
13.0 m	10.45	-	11.90	11.60	13.65	13.15	10.75

Magnesium

Depth	MAY	JUN	JUL	SEP	OCT	NOV	DEC
S	-	-	-	1.58	-	-	1.90
2.0 m	1.40	2.00	1.88	1.70	-	-	1.85
3.5 m	1.43	2.00	1.88	1.38	-	-	2.03
6.0 m	1.67	2.20	2.28	1.85	-	-	1.95
9.0 m	1.43	2.10	2.70	1.90	-	-	1.83
13.0 m	1.43	2.30	2.00	2.10	-	-	1.90

Crose Mere 1973

Water hardness (Ca^{++} and Mg^{++}) in mg/l

Calcium

Depth	MAY	JUL	SEP	OCT	NOV	DEC
S	-	-	50.00	62.25	65.75	55.00
2.0 m	67.00	57.00	44.80	64.00	66.50	55.00
3.0 m	66.00	57.50	42.80	64.00	65.75	55.00
4.5 m	66.00	57.00	44.80	64.00	64.00	55.00
6.0 m	72.00	63.00	50.50	62.25	66.75	55.00
7.0 m	71.00	71.00	44.80	62.25	65.50	55.00
9.0 m	70.00	69.00	64.00	61.50	65.75	55.00

Magnesium

Depth	MAY	JUL	SEP	OCT	NOV	DEC
S	-	-	8.80	-	-	11.40
2.0 m	10.00	10.00	9.40	-	-	11.40
3.0 m	10.00	10.00	10.40	-	-	11.60
4.5 m	9.00	10.00	10.00	-	-	11.40
6.0 m	10.00	10.00	9.90	-	-	11.30
7.0 m	10.00	10.50	10.10	-	-	11.10
9.0 m	10.00	10.50	11.00	-	-	11.30

Statistical evaluation of data from the study on the nutritional nature of the profundal sediments (Chap. 3.2.8) using Student's t ratio.

$$t = \frac{\bar{X}_1 - \bar{X}_2}{SD_{\bar{X}}}$$

When $N_1 = N_2$,

$$SD_{\bar{X}} \quad \frac{\Sigma x_1^2 + \Sigma x_2^2}{N\,(N - 1)}$$

where N = number of pairs

and Σx^2 = sum of squares for each distribution

Mean DW expressed as a % of the FW

Newton Mere	Blake Mere	Crose Mere
$\bar{X} = 7.35\%$	$\bar{X} = 7.14\%$	$\bar{X} = 12.37\%$
$\Sigma x^2 = 18.58$	$\Sigma x^2 = 111.72$	$\Sigma x^2 = 4.22$
$N = 16$	$N = 16$	$N = 16$

Newton Mere v Blake Mere

$t = 0.28$

$SD_{\bar{X}} = 0.74$

degrees of freedom $= N - 1$

$\therefore = 15$

p = not significant

Newton Mere v Crose Mere

$t = 16.73$

$SD_{\bar{X}} = 0.30$

df = 15

$p = 0.001$

Blake Mere v Crose Mere

$t = 7.52$

$SD_{\bar{X}} = 0.69$

df = 15

$p = 0.001$

Mean weight of inorganic material expressed as a % of the DW

Newton Mere	Blake Mere	Crose Mere
$\bar{X}$ = 47.90%	$\bar{X}$ = 30.20%	$\bar{X}$ = 51.02%
Σx^2 = 8915.26	Σx^2 = 1527.43	Σx^2 = 2106.07
N = 16	N = 16	N = 16

Newton Mere v Crose Mere

t = 0.45

$SD_{\bar{X}}$ = 6.77

df = 15

p = not significant

Newton Mere v Blake Mere

t = 2.68

$SD_{\bar{X}}$ = 6.59

df = 15

p = 0.05 - 0.01

Blake Mere v Crose Mere

t = 5.34

$SD_{\bar{X}}$ = 3.89

df = 15

p = 0.001

Calorific values (in kcal/g)

Newton Mere	Blake Mere	Crose Mere
$\bar{X}$ = 2.76	$\bar{X}$ = 4.08	$\bar{X}$ = 1.86
Σx^2 = 36.26	Σx^2 = 1.35	Σx^2 = 15.67
N = 16	N = 16	N = 16

Blake Mere v Newton Mere

t = 3.20

$SD_{\bar{X}}$ = 0.39

df = 15

p = 0.01

Blake Mere v Crose Mere

t = 7.90

$SD_{\bar{X}}$ = 0.27

df = 15

p = 0.001

Newton Mere v Crose Mere

t = 1.95

$SD_{\bar{X}}$ = 0.46

df = 15

p = 0.1

APPENDIX 2

Distribution and Abundance Data

Newton Mere 1972-1973 Species List

Values represent numbers/m^2

15. 3.72	3.0 m	4.5 m	7.5 m	12.0 m	16.0 m
Chironomus anthracinus	0	65	3116	3484	1580
Procladius choreus	800	606	87	216	130
Chironomus riparius	0	173	108	43	690
Phaenospectra flavipes	801	0	0	0	0
Limnochironomus pulsus	368	22	0	0	0
Harnischia viridulus	0	368	0	0	0
Tanytarsini sp.	108	0	0	0	0
Chironomus plumosus	0	0	65	0	0
Microtendipes chloris	0	22	0	0	0
Chironomus lugubris	0	22	0	0	0
19. 4.72					
Chironomus anthracinus	0	0	238	1666	390
Tanytarsini sp.	1018	108	0	0	0
Procladius choreus	368	22	0	108	0
Limnochironomus pulsus	345	0	0	0	0
Harnischia viridulus	65	0	0	0	0
Phaenospectra flavipes	43	0	0	0	0
Microtendipes chloris	22	0	0	0	0
Chironomus plumosus	0	0	22	0	0
Chironomus s.s. pupae	0	0	0	22	0
Chironomus riparius	0	0	0	0	22

23. 5.72	3.0 m	4.5 m	7.5 m	12.0 m	16.0 m
Chironomus anthracinus	0	0	758	606	151
Limnochironomus pulsus	1451	0	0	0	0
Procladius choreus	736	260	0	0	0
Tanytarsini sp.	322	476	65	65	0
Harnischia viridulus	260	0	0	0	0
Psilotanypus rufovittatus	65	0	0	0	0
Pentaneura monilis	43	22	0	0	0
Chironomus riparius	0	0	0	0	23
Chironomus plumosus	0	65	0	0	0
Glyptotendipes glaucus	22	0	0	0	0
Endochironomus albipennis	22	0	0	0	0
27. 6.72					
Chironomus anthracinus	0	0	216	433	931
Procladius choreus	303	130	0	0	0
Harnischia viridulus	43	0	0	0	0
Tanytarsini sp.	0	0	22	0	0
Chironomus plumosus	0	0	108	0	22
23. 8.72					
Chironomus anthracinus	519	87	303	281	563
Procladius choreus	1039	22	0	0	0
Tanytarsini sp.	715	0	0	0	0
Harnischia viridulus	130	0	0	0	0
Chironomus s.s. pupae	130	0	0	0	0
Phaenospectra flavipes	43	0	0	0	0
Chironomus riparius	43	0	0	0	0
C. plumosus	22	0	22	0	0

	3.0 m	4.5 m	7.5 m	12.0 m	16.0 m
29. 9.72					
Chironomus anthracinus	22	130	1774	476	1060
Procladius choreus	346	22	0	0	0
Phaenospectra flavipes	65	0	0	0	0
Glyptotendipes glaucus	22	0	0	0	0
Chironomus riparius	0	0	43	0	0
Chironomus plumosus	0	65	22	0	0
16.10.72					
Chironomus anthracinus	0	1277	1861	974	1233
C. riparius	0	130	66	43	0
Procladius choreus	151	43	43	0	0
Phaenospectra flavipes	217	0	0	0	0
Chironomus plumosus	0	0	43	0	0
Harnischia viridulus	0	43	0	0	0
15.11.72					
Chironomus anthracinus	1082	2683	2056	1515	2142
C. plumosus	325	281	86	0	65
Procladius choreus	260	87	238	43	130
Glyptotendipes glaucus	498	0	0	0	0
Limnochironomus pulsus	325	0	0	0	0
Microtendipes chloris	22	0	0	0	0

1 .12.72	3.0 m	4.5 m	7.5 m	12.0 m	16.0 m
Chironomus anthracinus	108	1190	2077	2294	4177
Procladius choreus	390	173	303	0	108
Chironomus plumosus	0	497	43	22	86
Phaenospectra flavipes	432	0	0	0	0
Chironomus lugubris	0	0	43	43	173
Chironomus sp.	0	0	0	173	0
Glyptotendipes glaucus	65	0	0	0	0
Limnochironomus pulsus	22	0	0	0	0
Harnischia viridulus	0	22	0	0	0
Pentapedilum tritus	0	22	0	0	0
14. 2.73					
Chironomus anthracinus	2207	1904	1450	2424	7281
Procladius choreus	238	216	173	303	498
Chironomus riparius	0	0	0	1190	0
7 . 3.73					
Chironomus anthracinus	0	2294	2272	2856	3289
Chironomus lugubris	0	0	0	996	1213
Procladius choreus	628	87	238	238	368
Glyptotendipes glaucus	22	0	0	0	0

11. 4.73	3.0 m	4.5 m	7.5 m	12.0 m	16.0 m
Chironomus anthracinus	43	1623	887	2448	1407
C. lugubris	0	0	86	433	216
C. plumosus	22	325	86	86	43
Procladius choreus	22	22	65	151	173
Chironomus sp. pupae	0	0	86	151	65
Tanytarsini sp.	65	0	0	0	0
Harnischia viridulus	0	22	0	0	0
9 . 5.73					
Chironomus anthracinus	498	628	2251	1039	3571
C. plumosus	260	303	151	0	0
Tanytarsini sp.	433	0	0	0	0
Chironomus sp. pupae	22	0	86	0	0
C. lugubris	0	0	65	0	0
C. dorsalis	0	0	22	0	0
Procladius choreus	0	0	22	0	0
Polypedilum nubeculosus	0	0	22	0	0
6 . 6.73					
Chironomus anthracinus	119	714	325	2294	1082
C. plumosus	0	325	0	87	0
Chironomus s.s. pupa	0	22	0	0	0
Procladius choreus	0	87	0	0	0

4 . 7.73	3.0 m	4.5 m	7.5 m	12.0 m	16.0 m
Chironomus anthracinus	151	736	628	1191	888
C. plumosus	130	303	22	22	0
Procladius choreus	22	0	87	0	0
Tanytarsini sp.	22	0	0	0	0
Harnischia viridulus	22	0	0	0	0

Newton Mere 1972-1973

Numbers of Chironomus anthracinus/m^2 each month at each sampling depth

Date	Depth					monthly total
	3.0 m	4.5 m	7.5 m	12.0 m	16.0 m	
15. 3.72	0	65	3116	3484	1580	8245
19. 4.72	0	0	238	1666	390	2294
23. 5.72	0	0	736	584	151	1471
27. 6.72	0	0	216	433	931	1580
7.72	-	-	-	-	-	-
23. 8.72	519	65	303	281	563	1731
29. 9.72	22	130	1774	476	1060	3462
16.10.72	0	1277	1861	974	1233	5345
15.11.72	1082	2683	2056	1515	2142	9478
1.12.72	108	1190	2077	2294	4177	9846
1.73	-	-	-	-	-	-
14. 2.73	2207	1904	1450	2424	7281	15266
7. 3.73	0	2294	2272	2856	3289	10711
11. 4.73	43	1623	887	2448	1407	6408
9. 5.73	498	628	2251	1039	3571	7987
6. 6.73	119	714	325	2294	1082	4534
4. 7.73	151	736	628	1191	888	3594

Newton Mere 1972-1973

Numbers of Procladius choreus/m^2 each month at each sampling depth

Date	Depth					monthly total
	3.0 m	4.5 m	7.5 m	12.0 m	16.0 m	
15. 3.72	800	606	87	216	130	1839
19. 4.72	368	22	0	108	0	498
23. 5.72	736	260	0	0	0	996
27. 6.72	303	130	0	0	0	433
7.72	-	-	-	-	-	-
23. 8.72	1039	22	0	0	0	1061
29. 9.72	346	22	0	0	0	368
16.10.72	151	43	43	0	0	237
15.11.72	260	87	238	43	130	758
1.12.72	390	173	303	0	108	974
1.73	-	-	-	-	-	-
14. 2.73	238	216	173	303	498	1428
7. 3.73	628	87	238	238	368	1559
11. 4.73	22	22	65	151	173	433
9. 5.73	0	0	22	0	0	22
6. 6.73	-	87	0	0	0	87
4. 7.73	22	0	87	0	0	109

Blake Mere 1972-1973 Species List

Values represent numbers/m^2

	2.0 m	3.5 m	6.0 m	9.0 m	13.0 m
10. 2.72					
Procladius choreus	43	1861	0	22	0
Chironomus anthracinus	0	43	22	411	0
Glyptotendipes glaucus	173	22	0	0	0
Limnochironomus pulsus	151	0	0	0	0
Microtendipes chloris	108	43	0	0	0
8. 3.72					
Procladius choreus	195	1017	0	22	0
Glyptotendipes glaucus	520	0	0	0	0
Chironomus anthracinus	0	43	0	325	0
Limnochironomus pulsus	238	0	0	0	0
Microtendipes chloris	65	0	0	0	0
Chironomus riparius	0	0	22	43	0
Harnischia defectus	0	0	22	0	0
Chironomus plumosus	0	22	0	0	0
12. 4.72					
Procladius choreus	151	1298	0	22	0
Limnochironomus pulsus	108	67	0	0	0
Endochironomus albipennis	108	0	0	0	0
Glyptotendipes glaucus	108	22	0	0	0
Chironomus riparius	22	0	43	22	0
C. anthracinus	0	0	0	195	0
Pentapedilum tritus	0	43	0	0	0
Harnischia defectus	0	22	0	0	0
Microtendipes chloris	22	0	0	0	0
Tanytarsini sp.	0	22	0	0	0

	2.0 m	3.5 m	6.0 m	9.0 m	13.0 m
17. 5.72					
Procladius choreus	87	606	0	0	0
Hamischia defectus	0	130	0	0	0
Glyptotendipes glaucus	67	0	0	0	0
Endochironomus albipennis	43	0	0	0	0
Chironomus anthracinus	0	22	0	0	0
Chironomus riparius	0	0	43	0	0
14. 6.72					
Chironomus anthracinus	0	303	0	238	22
Chironomus riparius	0	303	0	0	0
Cricotopus trifasciatus	173	0	0	0	0
Glyptotendipes glaucus	216	0	0	0	0
Procladius choreus	173	173	0	0	0
Microtendipes chloris	86	0	0	0	0
Limnochironomus pulsus	43	0	0	0	0
Pentapedilum tritus	22	0	0	0	0
Hydrobaenus sp.	22	0	0	0	0
Parachironomus falcatus	67	0	0	0	0
16. 8.72					
Chironomus anthracinus	0	1428	0	0	0
Glyptotendipes glaucus	43	43	0	0	0
Pentaneura monilis	67	0	0	0	0
20. 9.72					
Chironomus anthracinus	0	584	22	801	0
Procladius choreus	22	238	0	0	0
Limnochironomus pulsus	173	0	0	0	0
Glyptotendipes glaucus	130	22	0	0	0
Chironomus riparius	0	22	0	22	0
Tanytarsini sp.	22	0	0	0	0
Chironomus sp. pupa	0	22	0	0	0

16.10.72	2.0 m	3.5 m	6.0 m	9.0 m	13.0 m
Chironomus anthracinus	0	260	0	22	0
Procladius choreus	130	130	0	0	0
Limnochironomus pulsus	130	0	0	0	0
Microtendipes chloris	43	0	0	0	0
Glyptotendipes glaucus	22	0	0	0	0
8.11.72					
Procladius choreus	86	476	0	0	0
Chironomus anthracinus	0	65	22	281	0
Glyptotendipes glaucus	22	22	0	0	0
Chironomus plumosus	0	22	0	0	0
6.12.72					
Chironomus anthracinus	0	671	22	151	0
Procladius choreus	130	22	0	0	0
C. plumosus	0	43	0	0	0
Glyptotendipes glaucus	22	86	0	0	0
Limnochironomus pulsus	22	0	0	0	0
21. 2.73					
Chironomus anthracinus	0	151	0	692	0
Procladius choreus	0	692	0	43	0
Chironomus dorsalis	0	0	0	433	0
C. plumosus	0	43	0	0	0
Microtendipes chloris	0	43	0	0	0
Glyptotendipes glaucus	22	0	0	0	0

21. 3.73	2.0 m	3.5 m	6.0 m	9.0 m	13.0 m
Procladius choreus	22	995	0	22	0
Chironomus anthracinus	0	130	0	108	0
C. plumosus	0	0	22	0	0
Endochironomus albipennis	22	0	0	0	0
Limnochironomus pulsus	22	0	0	0	0
18. 4.73					
Tanytarsus sp.	0	801	0	0	0
Chironomus anthracinus	0	0	0	195	0
Procladius choreus	22	108	0	43	0
Limnochironomus notatus	86	0	0	0	0
Glyptotendipes glaucus	86	0	0	0	0
Microtendipes diffinis	67	0	0	0	0
Endochironomus albipennis	43	0	0	0	0
Chironomus s.s.	67	0	0	0	0
Cricotopus trifasciatus	0	43	0	0	0

Numbers of Chironomus anthracinus/m^2 each month at each sampling depth

Date	Depth					monthly total
	2.0 m	3.5 m	6.0 m	9.0 m	13.0 m	
10. 2.72	0	43	22	411	0	476
8. 3.72	0	43	0	325	0	368
12. 4.72	0	0	0	151	0	151
17. 5.72	0	22	0	0	0	22
14. 6.72	0	303	0	238	22	541
7.72	-	-	-	-	-	-
16. 8.72	0	1428	0	0	0	1428
20. 9.72	0	584	22	801	0	1407
16.10.72	0	260	0	22	0	282
8.11.72	0	65	22	281	0	368
6.12.72	0	671	22	151	0	844
1.73	-	-	-	-	-	-
21. 2.73	0	151	0	692	0	843
21. 3.73	0	130	0	108	0	238
18. 4.73	0	0	0	195	0	195

Blake Mere 1972-1973

Numbers of Procladius choreus/m^2 each month at each sampling depth

Date	Depth					monthly total
	2.0 m	3.5 m	6.0 m	9.0 m	13.0 m	
2.72	43	1861	0	22	0	1926
3.72	195	1017	0	22	0	1234
4.72	151	1298	0	22	0	1471
5.72	87	606	0	0	0	693
6.72	173	173	0	0	0	346
7.72	-	-	-	-	-	-
8.72	0	0	0	0	0	0
9.72	22	238	0	0	0	260
10.72	130	130	0	0	0	260
11.72	0	476	0	0	0	476
12.72	130	22	0	0	0	152
1.73	-	-	-	-	-	-
2.73	0	692	0	43	0	735
3.73	22	995	0	22	0	1039
4.73	22	108	0	43	0	173

Crose Mere 1972-1973 Species List

Values represent numbers/m^2

	2.0 m	3.0 m	4.5 m	6.0 m	7.0 m	9.0 m
1 . 3.72						
Procladius choreus	454	1125	87	151	130	65
Chironomus anthracinus	108	108	87	151	454	303
Microtendipes chloris	671	43	0	0	0	0
Endochironomus albipennis	455	22	0	43	0	0
Chironomus riparius	0	0	43	238	67	173
Limnochironomus pulsus	151	303	0	0	0	0
Pentapedilum tritus	0	130	0	0	0	0
Chironomus plumosus	0	0	0	0	87	0
Glyptotendipes glaucus	22	43	0	0	0	0
7 . 4.72						
Procladius choreus	303	1147	498	584	108	130
Chironomus anthracinus	0	0	411	563	390	346
Limnochironomus pulsus	173	1126	0	0	0	0
Endochironomus albipennis	151	563	0	22	0	0
Chironomus riparius	0	43	0	433	22	108
Chironomus plumosus	0	0	0	0	87	22
Glyptotendipes glaucus	67	151	0	0	0	0
Tanytarsini sp.	0	0	43	0	0	0
Microtendipes chloris	22	130	0	43	0	0
Pentapedilum tritus	0	196	0	0	0	0
Chironomus s.s.	0	43	0	22	0	22
Chironomus sp. pupae	0	173	0	22	0	0

	2.0 m	3.0 m	4.5 m	6.0 m	7.0 m	9.0 m
3 . 5.72						
Procladius choreus	1147	1428	173	866	346	43
Chironomus anthracinus	65	0	87	952	173	87
Chironomus sp. pupae	22	303	0	22	87	0
Endochironomus albipennis	87	368	0	22	0	0
Limnochironomus pulsus	22	108	0	0	0	0
Chironomus plumosus	0	22	22	67	108	0
Tanytarsini sp.	0	86	0	0	0	0
Chironomus riparius	0	0	0	43	22	0
6 . 6.72						
Chironomus plumosus	67	0	0	0	151	0
Procladius choreus	216	0	43	0	0	0
Cricotopus sylvestris	0	195	0	0	0	0
Hydrobaenus apicalis	0	87	0	0	0	0
Chironomus anthracinus	0	0	0	0	0	43
Trichodadius rufiventris	0	22	0	0	0	0
Chironomus riparius	0	0	22	0	0	0
Psectrocladius sp.	0	0	0	0	0	0
10. 8.72						
Chironomus anthracinus	108	5561	390	303	22	0
Procladius choreus	433	433	108	43	0	0
Tanytarsus sp.	0	108	0	0	0	0
Microtendipes chloris	0	43	0	0	0	0
Chironomus annularius	0	43	43	455	0	0
Chironomus sp. pupae	22	22	0	108	0	0
Pentapedilum tritus	22	0	0	0	0	0
Chironomus dorsalis	0	0	22	22	0	0
Chironomus lugubris	0	0	0	43	0	0

	2.0 m	3.0 m	4.5 m	6.0 m	7.0 m	9.0 m
28. 9.72						
Procladius choreus	563	260	43	887	0	22
Chironomus anthracinus	0	22	22	281	22	0
Chironomus sp. inc. pupae	0	22	0	43	0	0
Endochironomus albipennis	0	0	0	22	0	0
Microtendipes chloris	22	0	0	0	0	0
23.10.72						
Procladius choreus	130	108	325	0	87	22
Chironomus anthracinus	0	43	130	43	43	0
Tanytarsini sp.	0	43	0	0	0	0
Chironomus plumosus	0	22	0	0	0	0
Endochironomus albipennis	22	0	0	0	0	0
22.11.72						
Procladius choreus	65	1948	238	22	87	0
Chironomus anthracinus	0	1104	43	0	22	130
Microtendipes chloris	346	736	0	0	0	0
Chironomus tentans	0	346	0	0	0	0
Limnochironomus pulsus	67	173	0	0	0	0
Chironomus riparius	0	0	67	43	87	22
Chironomus plumosus	0	43	67	0	43	0
Glyptotendipes glaucus	0	130	0	0	0	0
Tanytarsini sp.	0	43	22	0	0	0
Chironomus dorsalis	0	43	0	0	0	0
Polypedilum nubeculosus	0	22	0	0	0	0

	2.0 m	3.0 m	4.5 m	6.0 m	7.0 m	9.0 m
13.12.72						
Procladius choreus	757	2272	216	65	0	22
Tanytarsini sp.	0	2773	22	0	0	0
Microtendipes chloris	1256	130	0	0	0	0
Chironomus anthracinus	0	454	303	43	87	65
Polypedilum nubeculosus	0	108	0	0	0	0
Limnochironomus pulsus	87	0	0	0	0	0
Phaenospectra flavipes	87	0	0	0	0	0
Glyptotendipes glaucus	67	0	0	0	0	0
Endochironomus "cysts"	43	0	0	0	0	0
Chironomus sp.	43	0	0	0	0	0
Chironomus plumosus	0	0	22	0	0	0
Chironomus dorsalis	0	22	0	0	0	0
Pentapedilum tritus	0	22	0	0	0	0
24. 1.73						
Procladius choreus	455	1560	454	65	216	108
Chironomus anthracinus	87	671	390	43	151	216
Microtendipes chloris	541	0	0	0	0	0
Chironomus plumosus	0	108	195	43	0	0
Limnochironomus pulsus	216	0	0	0	0	0
Tanytarsini sp.	67	108	0	0	0	0
Chironomus riparius	0	67	0	0	22	22
Chironomus s.s.	0	87	0	0	0	0
Phaenospectra flavipes	22	43	0	0	0	0
Glyptotendipes glaucus	22	0	0	0	0	0

	2.0 m	3.0 m	4.5 m	6.0 m	7.0 m	9.0 m
28. 2.73						
Procladius choreus	498	541	368	0	87	151
Tanytarsini sp.	195	67	108	0	0	0
Chironomus s.s. -B	599	0	108	0	43	22
Chironomus plumosus	0	87	67	0	0	0
Chironomus anthracinus	0	260	43	130	346	130
Microtendipes chloris	67	0	0	0	0	0
M. diffinis	67	0	0	0	0	0
M. pedellus	67	0	0	0	0	0
Endochironomus albipennis	43	0	0	0	0	0
Glyptotendipes gripekoveni	43	0	0	0	0	0
Chironomus riparius	0	43	0	43	0	0
Chironomus dorsalis	22	0	0	0	0	0
28. 3.73						
Procladius choreus	260	974	173	22	195	43
Chironomus sp. pupae	22	67	108	0	67	86
Chironomus s.s. -B	0	22	0	43	0	0
Endochironomus albipennis	87	130	0	0	0	0
Chironomus anthracinus	0	65	108	151	87	108
Glyptotendipes glaucus	43	108	0	0	0	0
Chironomus plumosus	0	67	108	0	0	0
Chironomus annularius	0	0	22	0	0	0
25. 4.73						
Procladius choreus	22	260	151	87	43	22
Chironomus s.s. -B	0	43	0	0	0	0
Chironomus plumosus	0	0	67	0	0	0
Chironomus anthracinus	0	22	0	22	22	0
Chironomus riparius	0	22	0	0	0	0

	2.0 m	3.0 m	4.5 m	6.0 m	7.0 m	9.0 m
30. 5.73						
Procladius choreus	151	1300	151	0	65	87
Chironomus riparius	0	260	0	0	0	0
Chironomus plumosus	0	67	22	0	0	0
Chironomus lugubris	0	43	0	0	0	0
Chironomus anthracinus	0	22	0	0	0	22
Chironomus sp. pupae	0	22	0	0	0	0
Tanytarsini sp.	0	22	0	0	0	0
Endochironomus albipennis	0	0	22	0	0	0
Limnochironomus pulsus	22	0	0	0	0	0
20. 6.73						
Microtendipes chloris	12005	0	0	0	0	0
Chironomus anthracinus	628	4268	0	22	0	0
Procladius choreus	130	736	0	0	22	0
Limnochironomus pulsus	216	0	0	0	0	0
Glyptotendipes glaucus	195	0	0	0	0	0
Chironomus plumosus	0	195	0	0	0	0
Endochironomus albipennis	130	0	0	0	0	0
Chironomus lugubris	43	0	0	0	0	0
Tanytarsini sp.	0	22	0	0	0	0
Pentapedilum tritus	22	0	0	0	0	0

	2.0 m	3.0 m	4.5 m	6.0 m	7.0 m	9.0 m
18. 7.73						
Microtendipes chloris	4355	0	0	0	0	0
Chironomus anthracinus	0	2708	0	0	0	0
Glyptotendipes glaucus	1906	22	0	0	0	0
Procladius choreus	498	346	0	0	0	0
Tanytarsini sp.	22	823	0	0	0	0
Chironomus riparius	0	715	0	0	0	0
Limnochironomus pulsus	325	0	0	0	0	0
Chironomus plumosus	0	151	0	0	0	0
Endochironomus albipennis	43	0	0	0	0	0

Crose Mere 1972-1973

Numbers of Chironomus anthracinus/m^2 each month at each sampling depth

Date	Depth						monthly total
	2.0 m	3.0 m	4.5 m	6.0 m	7.0 m	9.0 m	
1. 3.72	108	108	87	151	454	303	1211
7. 4.72	0	0	411	563	390	346	1710
3. 5.72	65	0	87	952	173	87	1364
6. 6.72	0	0	0	0	0	43	43
7.72	-	-	-	-	-	-	-
10. 8.72	108	5561	390	303	22	0	6384
28. 9.72	0	22	22	281	22	0	347
23.10.72	0	43	130	43	43	0	259
22.11.72	0	1104	43	0	22	130	1299
13.12.72	0	454	303	43	87	65	952
24. 1.73	87	671	390	43	151	216	1558
28. 2.73	0	260	43	130	346	130	909
28. 3.73	0	65	108	151	87	108	519
25. 4.73	0	22	0	22	22	0	66
30. 5.73	0	22	0	0	0	22	44
20. 6.73	628	4263	0	22	0	0	4913
18. 7.73	0	3419	0	0	0	0	3419

Crose Mere 1972-1973

Numbers of Procladius choreus/m^2 each month at each sampling depth

Date	Depth						monthly total
	2.0 m	3.0 m	4.5 m	6.0 m	7.0 m	9.0 m	
3.72	454	1125	87	151	130	65	2012
4.72	303	1147	498	584	108	130	2770
5.72	1147	1428	173	866	346	43	4003
6.72	216	0	43	0	0	0	259
7.72	-	-	-	-	-	-	-
8.72	433	433	108	43	0	0	1017
9.72	563	260	43	887	0	22	1775
10.72	130	108	325	0	87	22	672
11.72	65	1948	238	22	87	0	2360
12.72	757	2272	216	65	0	22	3332
1.73	455	1558	454	65	216	108	2856
2.73	498	541	368	0	87	151	1645
3.73	260	974	173	22	195	43	1667
4.73	22	260	151	87	43	22	585
5.73	151	1298	151	0	65	87	1752
6.73	130	736	0	0	22	0	888
7.73	498	346	0	0	0	0	844

Hand Sampling

Newton Mere 18.11.71

0 - 1 m	Number
Glyptotendipes sp.	7
Cryptochironomus 'defectus'	11
Limnochironomus pulsus	3
Microtendipes sp.	6
Pseudochironomus prasinatus	4
Endochironomus sp.	1
Phaenospectra flavipes	18
Pentapedilum tritus	1

Blake Mere 18.10.71

0 - 1 m	
Glyptotendipes sp.	36
Tanytarsini sp.	9
Procladius sp.	3

Crose Mere 4.2.72

alder carr

Chironomus lugubris	5
Prodiamesa olivacea	4
Chironomus dorsalis	14

stony shore/Carex fringe

Glyptotendipes sp.	5
Microtendipes sp.	12
Chironomus dorsalis	5

Crose Mere 6.6.72

alder carr

	Number
Cricotopus trifasciatus	5
C. tibialis	1
C. sylvestris	4
Hydrobaenus sp.	4
Trichocladius sp.	1
Cryptochironomus sp.	1
Metriocnemus sp.	1