ECOLOGY OF THE CHIRONOMIDAE (DIPTERA) IN SOME GRAVEL AND SAND PITS

by

Graham Titmus B.Sc.(Bath)

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ABSTRACT

The chironomid faunas of several gravel and sand pits in Staffordshire and Buckinghamshire were investigated. The sites were chosen to reflect a cross-section of the lake-types created by the aggregate extraction industry and were also of varying age.

Emergence traps were operated in 1975/76 on a 39 year old gravel pit and showed a markedly different fauna from that described by workers on other lakes. Subsequent analysis of the benthic communities shows that the pits studied possess a fairly uniform fauna which can be divided into two groups related to water depth and age: this classification does not divide the pits on the basis of their location.

Despite the uniformity of the fauna it is noted that the assemblages contain few species. The distribution pattern and feeding behaviour of the abundant species were investigated at three stations in one lake and it was found that larval distribution is related to feeding habits both at the microhabitat level and in the lake as a whole.

The colonisation of new pit habitats was investigated using a series of purpose-dug ponds. Developing midge populations were monitored by larval and emergence sampling and reveal the speed and replicability of colonisation. It is noted that after two years the pond community structure was similar to that of a much more mature area. The dispersive ability of adult chironomids is dependent upon successful dispersal of fertilized females to new habitats. The distribution and activity of adults shows a clear sex-dependent dichotomy based upon the roles each sex performs. The morphological dichotomy is countermanded in mermithid infested individuals of *Einfeldia dissidens* such that all parasitised individuals are feminised.

The management of wet gravel and sand pits for various recreational uses is considered. In particular the relationship between the chironomid emergence and duckling growth and survival in these lakes is discussed.

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CHAPTER 1

INTRODUCTION

Present limnological research is set against a background of change, both in the physico-chemical and biotic characteristics of many of Britain's natural wetlands (Mason & Bryant, 1975; Morgan, 1972). Also, perhaps more importantly there has been a change in the public attitude to wetlands which have become a focal point in the conflict between recreationalists who want more water space for sporting activities and conservationists who wish to preserve endangered wetland habitat (Haslam, 1973). Although at present water resources do not limit our economy, it does not mean we can neglect the question of how best to use them. Indeed, on a global scale potable water is one of our most highly exploited resources (Wetzel, 1975).

THE NEW WETLANDS

Natural habitats no longer exist in lowland Britain; since the arrival of man they have been steadily and inexorably destroyed and replaced by juvenile agricultural habitats. Until recently man's effect on wetlands was less obvious. Up to the Middle Ages all the larger water bodies were natural, being of glacial origin or formed by subsidence or faulting of underlying rock strata. In the early Middle Ages extensive peat diggings in East Anglia were abandoned and, with a later rise in the sea level, flooded to form a series of interconnected lakes along several river systems (Lambert _et al._, 1960). With this exception man's activities were limited to the creation of smaller ponds for agriculture and fisheries or ornamental purposes.

After the Second World War increased mechanisation of industry radically altered many of the precepts of life. This has affected not only our society but also our environment. For example, in the 30 years from 1939 to 1969 the brick industry changed from a diffuse industry with

1250 active pits to a concentrated one with only 324 pits. Formerly small, local, manufacturers created small derelict areas but, at present, the concentration of production, mainly in North Bedfordshire and near Peterborough, has lead to large areas of land being left derelict (Wallwork, 1974). Dereliction however, is not an obligatory consequence of industrialisation. Indeed, the landscape artists of the 18th and 19th centuries realised that water usually enhanced an area, and created many ornamental lakes. It is therefore not surprising that reservoir construction does not usually raise such violent objections from local residents (apart from those directly involved with the land to be submerged) as the prospect of mineral excavation. Many of the reservoirs built in the last decade are in areas of high rainfall and low population where the need for water space for social purposes is low but the high precipitation makes these sites most economical for water catchment. Reservoirs in lowland Britain are usually for water storage; also, due to the overall lack of water space in the crowded south - east of England they, in part, alleviate the high demand for water space for recreational activities.

The main source of new water space is the aggregate extraction industry which works 1600 ha of land each year for sand and gravel of which c. 1000 ha remain as wet pits (Inst. Geol. Sci., 1972). This is the greatest land consumption for any surface mineral but the size of individual pits is usually relatively small, being limited by the existing infrastructure. Most of Britain's sand and gravel is dug from recent deposits both in river valleys and from the deposits left by the Pleistocene ice sheets. Deposits are usually less than 6m thick and can be as little as 1m. Commercially, the best gravels are those with the clay particles washed out. Such deposits are found along the lengths of river valleys usually above the present river level and are known as river terrace deposits. Due to their proximity to the river, most of the deposits lie below the water table and readily flood when abandoned or even whilst still worked. The Thames valley is the single most important source of gravel in the country, with the Trent second, while the rest of the gravel comes from a range of workings spread across the country. Deposits outside river valleys are generally dry.

Because of the relative thinness of the deposits, gravel and sand pits can be reclaimed at relatively low cost and also rapidly after extraction, hence minimising disturbance and ultimately providing a useful recreational resource (Hartwright, 1974). Reclamation is controlled by local authorities and permission to excavate usually includes conditions of after-treatment geared to local requirements. Transport costsaccount for a high proportion of the market cost of gravel, hence there are more pits where most building occurs. These factors indicate that the wet-pits formed by the sand and gravel industry are the most significant single contribution to our needs for more water space for a wide range of recreational uses.

However, this is a relatively modern view, for as recently as 1942 wet gravel pits were seen as problem areas in need of reclamation. Solid refilling of old workings can cause problems since the pit is intimately connected with groundwater. The filler material used must therefore be non-toxic and low in organic content; domestic refuse is not usable unless it is first incinerated but near large coal-fired power stations pulverised fuel ash waste has been used.

More recently in the 1960s a major change took place in the lifestyle of most of the population. Dower (1965) describes it thus:-

> "Three great waves have broken across the face of Britain since 1800. First, the sudden growth of dark industrial towns. Second, the thrusting movement along far-flung railways. Third, the sprawl of car-based suburbs. Now we see, under the guise of a modest word, the surge of a fourth wave which could be more powerful than all the others. The modest word is leisure."

Within the sand and gravel industry the potential of this wave has been taken up by Ready Mix Concrete Ltd. who formed a subsidiary company to manage the leisure use of their worked-out pits and to develop the sites to satisfy local demand for water-based recreational activities. The Government, through the Sports Council has commissioned studies on the use made of such recreational areas (DART, 1972) in an attempt to formulate some overall strategy for water-sports.

Conservationists have shown little interest in wet gravel pits, although a few local Nature Conservation Trusts do own gravel pit reserves. However such reserves have often been left unmanaged, allowing the natural cycle of succession to occur. The Sevenoaks reserve owned and managed by the Wildfowlers Association of Great Britain and Ireland is an exception (Harrison, 1972). Here extensive planting and landscaping, using the techniques detailed in the Game Conservancy (1969) booklet on wildfowl management, have been used. Wet gravel pits have been extensively used for angling and the fish fauna has been investigated in detail. A group from the City of London Polytechnic is currently working on the growth and feeding of the species of fish commonly found in gravel pits (Barber, 1976; Gee, 1978). One of our rarer species, the spined loach (*Cobitis taenia* L.) is found in abundance in gravel pits along the upper Ouse (Robotham, 1977). The avifauna of gravel pits was studied by Tydeman who found that the breeding bird communities contained a wide variety of species, many of them abundant (Catchpole and Tydeman, 1975). He attributed the high density to the intimate apposition of open water with marsh, field and scrub vegetation; he suggested that with increasing pressure on existing natural wetlands, these new wetlands could become important for the conservation of many marshland and aquatic species. The interaction of recreation and conservation was shown in a later paper (Tydeman, 1977) where close-season fishing caused both a marked decrease in the number of birds using the site for breeding and a change in the composition of the communities.

In 1972 the Amalgamated Roadstone Corporation, (a member of the Consolidated Gold Field Group) one of the countries largest gravel operatives, set up a research project, managed by the Game Conservancy, at a pit near Newport Pagnall in north Buckinghamshire. The main aim of the research was to investigate factors influencing the use by wildfowl of disused wet gravel pits. Early work indicated that whilst the pits provided a suitable winter roosting area both summer populations and breeding success were low. Subsequent provision of nesting cover and the natural xerarch succession lead to a higher summer population but no increase in juvenile survival. An analysis of mallard chicks' guts in 1972 showed that 0-3 day old ducklings were eating 64% animal food and by 12-24 days they were eating only 2% animal food (Lees and Street, 1973). Comparable work in the United States had shown that in traditional wetlands ducklings in these age ranges eat 100% and 60% animal foods respectively. Furthermore the American studies indicated that the predominant food of mallard ducklings was pupal and adult chironomids (Chura, 1961).

It was against this background that I first monitored the emergence of insects from a wet gravel pit in 1975. The majority of the insects caught belonged to the Chironomidae (Diptera) and several Ekman grab samples showed that chironomid larvae were predominant in the benthos. The predominance of this group is not unusual. Indeed their ubiquity and widespread distribution within lake sediments led many workers in the 1920s to attempt a lake classification based upon the chironomid fauna. Within recent years this approach has been abandoned (review in Brinkhurst, 1974).

LIFE CYCLE AND ECOLOGY OF CHIRONOMIDS

Chironomids, like all aquatic Diptera have four distinct morphological forms - adult, egg, larva and pupa. Only the adult stage is non-aquatic in most species, although a number of terrestrial larvae exist (Oliver, 1971). Eggs are laid in large numbers within a gelatinous matrix which expands on contact with water. These egg masses are laid either free on the water surface or, more commonly, attached to plants or debris projecting above it (Davies, 1976). The egg masses float for a short period before absorbing enough water to sink. After several days the larvae break free of the egg membranes and become planktonic. There is evidence that in *Chironomus spp.* the egg hatch is desynchronised within each egg mass by the diffusion of a pheromone from a polar cap, eggs furthest from the cap hatching last (Takeda & Ohishi, 1976). This may serve to reduce intraspecific competition at a time before the larvae have dispersed.

The planktonic first instar larvae arethe main means of dispersal of the aquatic stages. Davies (1976a) observed the distribution of egg masses and subsequent position of the later instars of *Chironomus arthracinus* (Zett.) in Loch Leven. The eggs were blown to one side of the lake whilst later instars were found on the opposite side. The morphology of the first instar larvae shows adaptations to planktonic existence with lipid globules and long body hairs as buoyancy aids; because of these distinct morphological features the first instar has been termed a larvule (Morduchai-Bolovskoy & Shilova, 1955). Dispersion of larvae is facilitated by positive phototaxis and the ability to feed in the plankton (Davies, 1976). Positive phototaxis reverses after a maximum of 3 days and at the end of the larvule stage the larvae settle to the bottom and assume the mode of life of the subsequent larval stages. However, dispersive movements within the plankton are not limited to the larvule stage (Mundie, 1965) and Davies (1973) has shown that whilst the planktonic activity is most pronounced in the first instar it continues until the last larval stage. Cantrell and McLachlan (1977), investigating the competitive interaction of *Chironomus* *plumosus* L. and *Tanytarsus gregarius* (Kieffer) found that the latter species became positively phototactic when displaced from its tube either mechanically or by spatial interaction with *C. plumosus*. Such movements may explain many of the changes in population density within a lake in response to environmental variables such as oxygen and productivity (Nursall, 1952; Mason & Bryant, 1975a).

Larval growth proceeds through a total of four instars, the duration of which is temperature dependent (Konstantinov, 1958). Development to pupation is more rapid at higher temperatures, such that a summer generation which occurs at warmer temperatures, is shorter and produces smaller adults than an overwintering generation (Mackey, 1977).

The free swimming pupal stage is very brief, lasting only hours or days depending upon the species and the ambient temperature (Oliver, 1971). When metamorphosis is completed, the pupa swims to the surface and emergence occurs. The time taken for emergence is usually less than one minute in calm conditions (Mundie, 1956). The subsequent adult life span is rather short, lasting at most one week (Mundie, 1956) but it is at this time that chironomids are at their most noticeable (Mulla et al. 1971). Swarming of adult males is predominantly at dusk, usually in relation to distinct markers (Downes, 1969); females enter the swarm and are inseminated (Syrjamaki, 1966). However, apart from this and ovipositing behaviour, little is known about the adult stage of the life cycle.

Taxonomy of chironomids has, until recently, suffered from an early dichotomy of European and English workers with the European school, following Thienemann, concentrating on larval characters to delineate genera whilst British workers, following Edwards, studied only adult material and the genera constructed were much broader than those of the continental school. In recent years the validity of the European system has been acknowledged (Kloet & Hincks, 1976). The former dichotomy illustrates the problems inherent in the taxonomy of animals which have widely different stages in their life cycle. Since the larval stage is longest lived and most strongly exposed to competition it seems logical to use the morphology of this stage to delineate genera although the reproductive isolation through swarm specificity would seem preferable for species delineation (Lindeberg, 1964).

Adult emergence from a gravel pit near Newport Pagnall in 1975 and 1976 showed that both the biomass and emergence period were reduced compared with traditional wetlands (Street, 1977). There are however few studies of chironomid emergence from lakes in the British Isles. The first major study was by Mundie (1957) who monitored the emergence from one of the London storage reservoirs and related species distribution to depth. In Scotland, Morgan and Waddell (1961) discussed the emergence from a trout loch in relation to day length and as a supply of food for fish. Bracken and Murray (1973) surveyed the chironomid fauna of a series of shallow lakes of differing water quality.

The predominance of chironomids in the emergence from the gravel pit was paralleled by their predominance within the benthos. This is not unduly surprising since larval chironomids have, within the vast range of species, adaptations to all the principle feeding strategies seen in freshwater invertebrates (Cummins, 1973). There are few studies where both the larval and adult stages of the life cycle have been monitored together although there are separate studies of adult emergence and larval populations. Despite the availability of keys in English to larval genera (e.g. Chernovskii (1949) translated from the Russian in 1961) it was not until the early 1970's that such studies became popular although earlier pioneering work had been carried out by Humphries (1936) and Slack (1965). The turning point undoubtedly owes much to the influence of the International Biological Programme (IBP). The early 1970 s saw the introduction of the systems view of ecology and, with its concentration on productivity, resulted in a deeper insight into the energy flows within ecosystems. This led to a more holistic view of ecology. In Britain productivity studies of chironomid larvae were undertaken at Loch Leven (Charles et al., 1974) and on the Norfolk Broads (Mason, 1977). At the same time larval population studies continued along traditional lines relating species distribution to physico-chemical factors (Bowman, 1976; Carter, 1976).

The only substantial concurrent study of both larval populations and adult emergence in Britain is that of Potter and Learner (1974) who investigated the whole macroinvertebrate community in a eutrophic reservoir and included a detailed study of the chironomid populations, estimating production of all predominant species and the loss from the habitat by emergence.

A major omission in ecological research appears to be the combination of productivity studies with the more traditional approach to the analysis of distribution in terms of habitat parameters. Productivity is important since it is the flow of energy through an organism which allows it to maintain its organised state (Calow, 1976), and as such, productivity is a measure of the success of an organism within its habitat. The functioning of an ecosystem cannot be discussed without reference to the energy flow through it but the basic questions of the reasons for faunal diversity and coexistence of competing animals remain unanswered in a solely energetics approach alone. Mere description of changes is not sufficient fully to explain the functioning of an ecosystem. However the partitioning of energy occurs at the species level and a knowledge of why the individuals are distributed as they are is necessary to understand the functioning of the ecosystem. Cantrell (1975) working on a small man-made lake in Northumbria was able to explain the distribution of colonists by substratum conditions and intraspecific competition. Similarly, McLachlan (1976) in a study of an acid bog lake analysed the factors determining species distribution as particle size and food resources. These studies were only concerned with simple habitats and several parameters of the niche hypervolume. Ramcharan and Paterson (1978) similarly managed to separate the niche of all but two chironomid species out of eleven in a acid bog lake using habitat, food, microdistribution and niche breadth as parameters. Perhaps a more widespread application of such an approach to chironomid ecology will help us to understand how and why this insect family is so important in lakes.

CHAPTER 2

THE GRAVEL AND SAND PIT HABITAT

Three sites were selected for field investigations, two near Keele and the third in Buckinghamshire, the majority of the work was carried out at the latter site.

SITE DESCRIPTIONS

The pools at Linford form a complex of disused wet gravel pits along the length of the River Ouse in North Buckinghamshire, just west of Newport Pagnall (Grid Reference SP 8443). The gravel deposit on which they are sited is a lower river terrace up to 3m deep, gravel extraction has taken place from this area over the past 38 years. However, (due to increased demand for aggregate for the construction of Milton Keynes) extraction has been most intense over the past decade. The complex of pits is situated in a shallow river valley surrounded by mixed arable farmland and the area has been in agricultural use since the middle ages, consequently little woodland and few hedges remain.

The term 'lake' will be used for all the water bodies studied. This is not justified in conventional terms since the water bodies do not stratify. However, no suitable and appropriate alternative exists so the term 'lake' will be applied.

The oldest pits (Black Horse and Red House) were dug by a barge-mounted dredge and the aggregate transported by barge to a grading plant for washing and sorting. The lagoon area on the southern boundary of Black Horse Lake was dry dug since the gravel deposit was thin in this area, occurring mainly in pockets of lens-shaped deposits. On flooding, the lagoon area developed into a series of inter-connecting pools. All other pits, which have been more recently excavated, were dry dug, infiltrating ground-water being pumped out of the workings. When excavation of these dry dug pits was completed they were landscaped to ensure that the banks were not dangerously steep, also that the pit did not intrude upon the landscape but became a natural part of it. After reclamation the lakes are used for various recreational pursuits.

The pools are limited in size by the existing infrastructure and the river Ouse and this has resulted in the creation of eleven wet pits in an area of 290 ha (Fig. 1). Over the next decade this complex will be developed into a country park to satisfy part of the demands for water-based leisure activities engendered by Milton Keynes.

Sampling was carried out on two lakes in this complex, Black Horse (and the associated lagoon area) and Dovecote. The lagoon area was fenced off from the surrounding fields in 1973 and designated a conservation area to be used for the study of the ecology of wet gravel pits. Since then the land areas have undergone succession from rough grazing to scrub vegetation, although some initial planting was undertaken to accelerate the process. Littoral macrophytes have also been planted and the lagoon area is almost completely fringed with reeds and rushes. In contrast, the margins of the rest of Black Horse and Dovecote are almost entirely bare; Dovecote lake was dry dug and subsequently flooded in Autumn 1976. No stream inputs or outflows exist in any of the pools in the Linford complex, and water levels are maintained by artesian springs and groundwater seepage augmented by occasional flooding of the river.

Trentham Park pool originated in a disused gravel workings alongside the M6 south of Newcastle-under-Lyme (Grid Reference SJ 855402). It is 20m long, 15m broad and up to 1m deep. It receives run off from a surrounding area of parkland. The lake is bounded on three sides by steep grass-covered banks of gravel-clay soil, on the fourth side a more shallow shelving area of young woodland is present and the main run-off occurs as a transient stream running through this area.

British Industrial Sands operate a sand pit at Congleton (Grid

Reference SJ 848628). Sand is extracted from below the water table by a barge-mounted suction dredge. The sides of the pit are steeply sloping and grass covered, little direct run-off occurs as the catchment area is only slightly larger than the pit. The margins are sandy and no macrophytes are present.

PHYSICAL AND CHEMICAL FEATURES

Introduction

The chemical and physical environment form part of the habitat of any organism. However, chironomid midge larvae have been found in numerous extreme chemical environments, ranging from acidic coal tip run-off to alkaline salt lakes (Currey, 1965). In addition it is well known that organic enrichment of natural freshwaters results in a rapid and large increase in the abundance of chironomids. However, such populations often consist of only a few tolerant species and do not indicate a general ability of all species to withstand a wide range of chemical insults. Whilst the major cations and anions, with the exception of calcium (Reynoldson, 1958), have not generally been implicated as controlling factors limiting the abundance of invertebrates they do provide information on the trophic status of the lake.

The most important chemical in water is oxygen and in eutrophic stratified lakes its controlling effect is clearly seen, with most animals limited to the littoral zone in the period of profundal anoxia (Bowman, 1976). This correlation of species distribution with profundal oxygen concentration earlier led to the development of numerous schemata for lake classification based upon a description of the predominant profundal chironomid populations (Thienemann, 1925). In recent years such classification methods have been abandoned with the realization that all lakes have a high level of individuality which hinders classification. This is due, in part, to the variability in littoral primary production from lake to lake, dependent upon morphology and climate, superimposed upon the trophic status of the open water.

Lake Morphology

Lake morphology will influence both primary production and species composition, depending upon a number of parameters. The most important morphometrics used are surface area (A), maximum depth ($\bar{z}_m$), mean depth ($\bar{z}$) and shoreline development (D_L). Wetzel (1975) produced the formula:-

$$D_L = \frac{L}{2\sqrt{\pi A}}$$

where L is the length of shoreline.

This last measure is important since it is a measure of the potential development of littoral communities as a proportion of the whole lake. In view of Wetzel and Allen's (1970) proposal that the littoral zone can contribute significantly to total lake production and eutrophication, shoreline development is therefore an important parameter in lake morphology.

Man-made lakes owe their shape not to the geomorphology of the basin but to the excavation techniques used. Sand and gravel deposits are usually of uniform depth (except at the edge of a deposit where pockets of aggregate may be found) and hence the final lake will often have a uniform depth throughout, with only the edges shelving. In this case the maximum depth will be almost the same as the mean depth. Furthermore the lakes tend to be regular in outline and hence D_L is close to unity. Therefore gravel and sand pits can be effectively characterised by two parameters, $\bar{z}_m$ and A.

Measurements of these two parameters indicate that all the water bodies were small and shallow (table2.1).

Water Chemistry

The ionic composition of the world's freshwaters is dominated by the alkali and alkaline earth compounds of bicarbonate, carbonate, sulphate and chloride. The four major cations calcium, magnesium, sodium and potassium associated with the above mentioned anions usually account for almost all of the total salinity. Other biologically important compounds such as phosphate only account for a very small fraction of the salinity.

The four major cations (Ca, Mg, Na, K), anions (HCO_3, CO_3, SO_4, Cl), conductivity, pH and oxygen were measured in 1977.

Samples were collected in 500 ml screw top plastic bottles and stored at 5°C until analysis was carried out; in all cases this was within one week of sampling. Samples were collected from the following sites:

British Industrial Sands, Congleton.
Linford: Black Horse
Dovecote
Experimental ponds 1-6
Trentham Park

Calcium and magnesium were measured by atomic absorption spectroscopy (EEL model 240) using an air acetylene flame. Interference from sulphate, phosphate, silica and aluminium was suppressed by the addition of lanthanum chloride solution to give a final concentration of 0.1% to samples and standards (Golterman _et al._, 1978). Standards were run for each determination and a new calibration curve constructed.

Sodium and potassium were measured by flame photometry.

Bicarbonate was determined by titration against 0.1M hydrochloric acid, using methyl orange as indicator; in all cases the phenolphthalein alkalinity was zero. Hence the bicarbonate concentration was equal to the carbonate alkalinity.

Sulphate was measured by a turbidimetric method measuring the absorbance of the suspended barium sulphate precipitate on an EEL spectra at 380 nm (Golterman _et al._, 1978)

Chloride was measured by a potentiometric titration against 0.1M silver nitrate using silver electrodes and a galvanometer to measure the potential between sample and titrant.

Conductivity and pH were measured electronically by laboratory meters.

Oxygen and temperature were measured in the field using a portable meter (Mackareth O_2 meter manufactured by Lakes Instruments Ltd.).

The data showed no distinct seasonal or progressive changes during the year and the data are therefore presented as mean values (table 2.2). The relative order of abundance of cations

$Ca > Mg \approx Na > K$

and anions

$HCO_3 > SO_4 > Cl$

is the same as that found in most surface waters. The standard composition of lake water with a conductivity of 360 µS as given by Rodhe (1949) is also presented in table 2.2 and the agreement is fairly close; exceptions being sulphate and calcium which are considerably higher than that given by Rodhe.

A calcium concentration in excess of 1.2 mEq l^{-1} (24 mg l^{-1}) is sufficient to enable hard water species of molluscs and flatworms to grow (Reynoldson, 1958; Boycott, 1936). The sand and gravel pits investigated show no marked abnormality in composition with respect to major cations and anions.

Oxygen and temperature measurements were recorded monthly at Congleton in 1977 at 1 m depths and depth-time isopleths of dissolved oxygen are given in figure 2.2a. The oxygen value at the mud-water interface was below 80% saturation in two months of the year only. The time-depth isopleths for temperature showed no evidence for thermal stratification (Fig. 2.2b) since no thermal discontinuity was discernible.

Sediment chemistry

Dried samples of sediment obtained by diver's hand cores were oven dried at $60^{o}C$ and stored until analysed. Subsequent analysis was carried out for volatile compounds, carbon and nitrogen.

1) Loss on Ignition. 1 g of dried mud was ignited at $550^{o}C$ for 2 hrs.

2) Organic carbon was estimated by a wet digestion using dichromate mixture (Allen et al., 1974). A 100 mg subsample was used due to the low organic content of the sediment.

3) Nitrogen was estimated by semi-micro Kjeldahl digestion using potassium sulphate-mercurous oxide mixture as a catalyst. The ammonia formed was steam distilled and collected in boric acid which was titrated against standardised hydrochloric acid. Two blanks were run with each batch of samples.

Samples were taken from Congleton and Linford only (table 2.3). The loss on ignition values are low in comparison with those obtained in other lakes. Misra (1938) found a higher value for Ullswater, his most oligotrophic lake in the English Lake district, than those reported here. However, the values are similar to that given by McLachlan (1974) for the sediment of a newly inundated reservoir in Northumbria (7.2%). Mundie (1957) reported a loss on ignition of 37% in the London storage reservoirs and Paterson and Fernando (1971) a value of 32% for settling sediment in a newly created lake in Canada. The low values found in these gravel and sand pits are indicative of the highly mineral nature of the sediment caused by the gravel extraction procedure and the washing of associated clay and silt back into the pits.

In eutrophic lakes the majority of the organic material in the sediments is not available for degradation by micro-organisms since the accumulation of reduced compounds, in the absence of oxygen, limits metabolism to the surface layers (Wetzel, 1975) and it is here that most viable bacteria are situated (Henrici and McCoy, 1938). Tubiculous invertebrates disturb the sediment and displace the oxidised zone downwards. Edwards (1958) suggested that chironomids and other tubiculous animals may markedly stimulate decomposition rates by their aeration of the sediments. The high oxygen concentration at the mud-water interface may have hindered the accumulation of particulate detritus in the sediment by allowing decomposition to proceed without limit other than available food. Carbon-Nitrogen (C:N) ratios were also much lower than those given by other workers where the range was 12-18:1 (McLachlan, 1971; Misra, 1938; Slack, 1965).

Sediment: Physical Analysis

Sediment particle fractionation was carried out to determine the proportion of particles in each of the categories (in mm)

Coarse sand	⩾	0.2	to	<	2.0
Fine sand	⩾	0.02	to	<	0.2
Silt	⩾	0.002	to	<	0.02
Clay	<	0.002			

Silt and clay were determined by dispersing the sediment in water and then measuring the soil density with a Buoyoucos soil hydrometer. Fine and coarse sand were separated by sieving; both coarse and fine fractions were retained and weighed.

The sites in the lagoon area of Linford Black Horse pit (C1-C3, E1-E6) show a range of heterogeneity probably attributable to the variable substratum left following excavation of this area close to the edge of the deposit (table 2.4). Samples varied from predominantly sand through to more silty-clay sediments. The soil classification type is also given. The sample from the main area of Black Horse was not duplicated since diving observations indicated that the whole lake was very uniform. In the lagoon area in contrast distinct substratum types could be easily recognised.

The sample from Congleton was very different in appearance from the others examined due to the high clay content. Here, clay is washed back into the lake from the sand grading plant and has resettled to form a thick layer of soft gelatinous sediment.

DISCUSSION

The physical and chemical study of these gravel and sand pits has shown a number of distinct features which are different from other natural lakes of similar surface area. The morphology of an individual pit is remarkably uniform with an even depth across most of the extent of the lake and also the lakes are more shallow than most natural lakes. Because of these two factors there is no marked thermal discontinuity and consequent summer stagnation of deeper water. Hence, oxygen is readily available at all depths throughout the year. The relative shallowness of the lakes also means that, in the absence of resuspension of sediment by water movement, the bottom of the lake is within the photic zone.

At Linford the substratum in the main lake and the lagoon area has a similar composition with few fine particles. In addition the sediment has a low organic content. These two factors are undoubtedly correlated since it has been shown that organic matter is associated with the smaller particles (McLachlan & Dickinson, 1977). The low C:N ratios in the sediment further suggests that a large fraction of the organic carbon may be contained in viable organisms rather than representing material which has not yet been decomposed since a ratio of 5:1 is obtained from insect tissue and for bacteria (Allen et al., 1974) whilst decaying material rapidly loses nitrogen (Kistritz, 1978; Mason & Bryant, 1975b).

These differences of low availability of detrital food and the presence of high oxygen concentration throughout the year seemingly form a suitable habitat for herbivorous organisms rather than the detritivorous communities found in the benthos of most other lakes.

CHAPTER 3

SAMPLING METHODS AND APPARATUS

Sampling methodology for soft lake sediments has been subject to more development than perhaps for any other freshwater habitat. However, before a particular method is selected it is first necessary to define the type of samples that are required. This is the methodological parallel to defining the area of investigation. The main decisions as to the number, location and timing of sample sets must be decided in relation to the aims of the investigation, not *vice versa*. The following methods were used to determine temporal and spatial variation in standing crop and productivity of larval chironomids in the soft sediments of sand and gravel pits and to provide quantitative adult emergence data from selected sites.

The data required impose the following constraints upon the sampling devices:-

1) The area sampled must be known
2) The sampler must catch all, or a known proportion of the animals from the area
3) Samples should not be biased in favour of catching particular individuals on the basis of size or activity.

Methods meeting these requirements would provide adequate data for this investigation. The actual methods used to estimate larval abundance and adult emergence will be discussed in the light of these requirements and the effect of any departure from them upon the numerical estimates required.

LARVAL SAMPLING

Two types of mechanical grab-type sampler were used, the standard Ekman grab (Edmondson &Winberg, 1971) and the Allen grab (Southwood, 1978). The latter was only used to collect larvae at Trentham Park gravel pit as the water was sufficiently shallow and boat access was not possible.

The Allen grab has been criticized because it has a closed top and thus causes a pressure wave to build up in front of the jaws, thereby disturbing the fine surface sediment (Kajak, 1971). More seriously, a further disadvantage is that the amount of material collected (a measure of the depth of penetration) was observed to be highly variable and care was necessary in selecting samples of similar volume.

The Ekman grab is one of the most widely used samplers for soft sediments. A standard Ekman grab was operated, as described by Welch (1948), using a hand winch attached to a small rowing boat. The sediment was sufficiently firm to prevent the grab from penetrating completely below the surface. Samples of less than 10 cm depth of mud were rejected. Due to the abundance of gravel at certain sites samples were taken until sufficient successful samples were obtained.

The efficiency of the Ekman grab in catching various macroinvertebrates has been investigated by Flannagan (1970). He compared a series of devices in sampling the benthos of two lakes, Ontario and Winnipeg. Not only did the abundance estimates vary with the type of sampler used but the samplers did not perform consistently with different taxa. The standard for 100% efficiency for all taxa was taken to be the diver's hand core. In comparison with this the Ekman grab caught 82% of the chironomid larvae. Furthermore, this sampler was shown to be more efficient than the Kajak-Brinkhurst multiple corer or any other device for chironomid larval sampling. The variation in efficiency with sediment type was pronounced, the Ekman grab producing good population estimates from mud, while in gravel its efficiency decreased.

Animals caught by the sampler were separated from the sediment by sieving using a mesh size of 0.375 mm. The mesh size used was a compromise between a larger mesh which would have made sample processing quicker, and a smaller mesh which would have retained more larvae. Jonasson (1958) observed that the critical dimension in the retention of larvae during sieving is the head capsule width. Larvae with head capsules smaller than the sieve mesh will not be quantitatively retained.

It is apparent that whilst the primary sampling device was capable of fulfilling all the requirements stated at the beginning of this chapter, the subsequent processing of the sediment would bias the population estimates against younger and smaller larvae (with a head capsule width less than 0.375 mm). The importance of this bias on the estimation of standing crop is markedly less than on the estimate of numerical abundance since smaller larvae only contribute a small proportion to the total biomass. Furthermore, the growth increments of smaller larvae contribute less to the production estimates of the species than those of larger larvae, the relative contribution increasing in proportion to the cubed power of length.

ADULT EMERGENCE SAMPLING

Two basic types of emergence trap exist for sampling open water areas, surface box traps and partly- or wholly-submerged funnel traps. Comparisons of the catch between these two types have been made by Kimerle and Anderson (1967), Morgan _et al._ (1963) and Potter and Learner (1974).

Kimerle and Anderson (1967) caught only 5% as many midges in submerged funnel traps as in surface funnel traps indicating that the position in the water column may significantly affect trap efficiency.

Morgan _et al._ (1963) found that a submerged funnel trap caught significantly fewer of each of the abundant species at their study site and also recorded a different pattern of seasonal abundance for certain common species. The main disadvantage of the floating box traps was the increased time taken to empty them in comparison with that needed to service submerged funnel traps.

Potter and Learner (1974) compared surface box traps as used by Morgan and Waddell (1961) with a submerged Mundie funnel trap. Comparison of total numbers caught showed significantly different abundance ($P < 0.05$) on 13 out of 15 weeks; the catch in the surface traps being seven times greater than that in submerged funnel traps. Estimates of percentage composition of the fauna only differed for the less abundant species. The sex ratios of many species in the submerged funnel trap differed from those in the surface traps, the latter being close to unity in most cases.

The traps used in the present study were all surface traps. Three designs were used.

Mundie traps

Five traps were constructed as described by Mundie (1971: 81-82) and used on the surface supported by a flotation collar. The collar was constructed of wood and polystyrene to give an outside length of 1 m with a central well of 0.6 m x 0.6 m in which the trap was supported with its base 0.1 m below the water surface. The flotation collar was retained in position by two ropes and anchors attached, at diagonally opposite corners, such that its movement was limited to an elliptical area between the two anchors. The top of the trap was covered with either a glass jar or an open metal tube covered on the top with nylon mesh of 0.25 mm aperture.

Insects were removed from the trap by replacing the jar (if present) with the mesh covered tube, taking care to retain any insects within the jar, and then inverting the trap underwater so that it was pulled out base first causing all insects caught to be washed through the mesh-covered tube. Exuviae and adults were then removed from the water surface inside the flotation collar and added to the catch. The traps were cleaned each time they were serviced; however, algal growth only occurred on the basal 0.1 m and therefore did not noticeably reduce the transparency of the trap.

Floating box traps

Four traps were constructed to the design of Morgan and Waddell (1961). These traps were supported on a light frame constructed from two lengths of drain pipe sealed at both ends and joined by thin strips of wood. This collar was too fragile for use at exposed sites but caused markedly less shading and disturbance in shallow water (< 1 m deep). Insects were removed by inserting an entomological aspirator (pooter) through a hole in the perspex roof and collecting until no more insects were visible inside the trap. The hole in the roof was covered by a glass jar during use.

Floating sticky traps

Traps were constructed modified from the design of Green (1970). They were made of clear perspex and right-angled strips of aluminium (except for the roof which was made from two sheets of glass), with a square base of area 0.1 m^2 and 0.15 m high (figure 3.1a). The glass plates were cut to fit inside the trap being supported on two J-strips of aluminium; this prevented loss of glass plates in windy conditions: Loss was experienced when the traps were first used with the plates resting on the top of the trap. The whole structure was supported on two polystyrene floats tied to the sides and anchored by a running line from opposite sides which passed through a pulley mounted on a post (further offshore than the trap) and back to a post on shore where the line was tethered (figure 3.1b). The trap could be thus serviced from the shore.

The glass plates which formed the roof of the trap were coated with adhesive by applying a strip of grease band to the plate and then peeling it off, a film of grease was left behind on the surface. The plates were then positioned grease side down on the top of the trap. The trap was emptied by removing the plates, since all emerging insects were stuck to the grease. Insects caught were later removed from the plates by applying a drop of acetone to the insect and gently pulling it free from the grease. Care was necessary to ensure that the legs, wings and genitalia were not left behind on the plate. Condensation was found to occur in the traps with certain types of grease, the most successful type used was Boltac.

Trap efficiency

The efficiency of surface emergence traps has been investigated by Potter and Learner (1974) and McCauley (1976). Potter and Learner calculated trap efficiency (E_t) as

$$E_t = \frac{\text{Number of species } i \text{ in trap}}{\text{Decrease in number of 4th instar larvae of species } i}$$

using the decrease in larval density as a measure of potential emergence. The calculated efficiency of the surface traps was 20-60% for the overwinter generation and 10-60% for the summer generation. This calculation however does not estimate mortality in the pupal stage and hence includes factors other than trap efficiency.

McCauley (1976), in a laboratory investigation of surface trap efficiency, compared the numbers of adults caught in traps with the numbers emerging in a comparable area with no trap. Trap efficiency thus measured did not significantly differ from 100%. However, retention of insects caught declined with an increase in the period between emptying the trap and he concluded that traps should be emptied as frequently as possible, preferably daily. A number of sources of error in emergence trapping have been considered.

Morgan et al. (1963) postulated that insects which fall back on to the water surface will rapidly decompose, sink and be lost. This problem is entirely avoided in the sticky traps, where the animals are held on the roof by the grease, and partly avoided in the Mundie traps where a perspex partition prevents insects falling out of the bottom of the trap.

Predatory insects have been found in traps and it has been postulated that these may have consumed part of the catch (Morgan, 1971).

In traps supported on a flotation collar an epiphytic fauna develops and may contain chironomids and other animals atypical of the lake zone (Jonasson, 1954). This can be avoided by regular cleaning of the floats; cleaning was carried out on the flotation collars and sticky and floating box traps but was not possible on the flotation collars of the Mundie traps due to their size and weight.

One further source of variability in trapping efficiency is the sheltering effect caused by the trap and its associated supporting structures. Kajak (1958) has shown that this can attract certain species of insects to the trap.

Emergence trapping has many unknown important parameters such as efficiency, retention and selectivity. Surface trap sampling is, however, the most reliable method available (Morgan, 1971).

PRESERVATION AND IDENTIFICATION

Larvae

Samples were preserved in Carnoy's fluid immediately they had been sorted from the sediment. This preservative was chosen because it did not cause the larvae to become brittle, as did larvae preserved in formalin, nor did they lose haemoglobin and become flaccid, like larvae preserved in alcohol. In contrast they remained sufficiently pliable for measurement of body length; even in those specimens which had formed a coil on dying.

Imagines

Adult midges were transferred to 70% alcohol with 5% glycerine to avoid complete dessication of uncorked tubes during storage. Adults caught in sticky traps were first washed in acetone to remove as much grease as possible from their bodies (if this was omitted the sample of insects aggregated into a tightly bound mass during storage).

Identification

The larvae were identified using the keys of Bryce and Hobart (1968) and a manuscript key by Mr. P. S. Cranston, British Museum (Natural History); body length was measured to the nearest 0.5 mm. Head capsule width was also measured in a number of samples.

Adults were identified using the keys of Coe (1950) and Pinder (1978) with those of Strenzke (1959) for the Chironominae and Reiss and Fittkau (1971) for the Tanytarsini. Individuals of most of the species identified have been verified by Mr. P. S. Cranston.

CHAPTER 4

ADULT EMERGENCE STUDIES 1975 & 1976

The aim of the initial study was to obtain basic data concerning the aquatic insects emerging from a wet gravel pit as part of a study of duckling survival in this habitat (Street, 1977). The site used was Linford lakes, North Buckinghamshire and the emergence traps were set on Black Horse lake and the associated lagoons area. This relatively undisturbed area had become a major breeding site for waterfowl, a situation parallel to that described by Batten (1977) on Brent reservoir near London. Because of the importance of the lagoons area to the breeding wildfowl population, emergence traps were placed at various sites mainly within this area.

METHODS

Emergent adult chironomids were sampled by means of surface traps. In 1975 the Mundie trap was used because of its durability under the exposed conditions experienced at certain of the selected stations. Each trap had a base area of 0.25 m^2 and was supported on the surface by wooden floats. Traps were emptied daily at all five stations, as far as possible. In 1976 the trap design was changed since the stations chosen were less exposed than previously (table 4.1). A floating box design (Morgan and Waddell, 1961) was chosen, with the dimensions modified to give a base area per trap of 0.5 m^2. Sampling was less frequent in 1976 than in the previous year being restricted to, at most, three collections per week.

The site of each of the five traps used in 1975 was chosen to reflect the visibly distinguishable zones within the lake (figure 4.1). Trap 1 was situated in shallow water, within the lagoon area, and near the mainland. In this shallow water a profuse macrophyte and algal growth was evident. The substratum was the same for all traps within the lagoon area where an organic silt had accumulated. Trap 2 was in deeper water but still within a sheltered area; here, as with the other traps in deeper water no benthic plants were found. Traps 3 and 4 were both in exposed situations, trap 4 being in the main lake where the substratum consisted of gravel overlain by a fine mineral sediment. Trap 5 was sited at the edge of a pool in the lagoon area, actually on a stand of Sea Club-rush (*Scirpus maritimus* L.) in very shallow water, a habitat not usually sampled in insect emergence studies.

In 1976 the traps were paired, the first two were situated in a shallow isolated pool having a silty substratum and extensive plant growth. Traps 3 and 4 were in a nearby shallow, sheltered part of a large pool, again with a silty sediment and plant growth on the bottom.

The faunal assemblages sampled at the various sites were compared using two similarity indices. The first index used (Jaccard, 1912) computed the proportion of shared species between two sites.

This was used in the modified form:

$$I = \frac{100.c}{a + b - c} \qquad (1)$$

where a = number of species in trap A, b = number of species in trap B, c = number of species common to both traps.

When used alone equation (1) ascribes undue importance to sporadically occurring species which only comprise a small proportion of the biomass. Therefore, an additional index based on the degree to which two samples share dominant species was computed, using the formula of Raabe (1952):

$$I = \sum_i \min\,(a_i, b_i) \qquad (2)$$

where a_i = percentage of species i in trap A, b_i = percentage of species i in trap B.

The range for each of the indices is 0 - 100, with identical assemblages giving a total of 100 in both cases. These indices were applied to the monthly totals of males emerging from each trap; females were omitted due to the tentative nature of the determination of species for females.

RESULTS

Emergence periods

Thirty three species of Chironomidae were found and identified in 1975, and 35 species were recorded in 1976. Only 21 species were common to both years. Altogether 47 species were identified (table 4.2). Considering the population as a whole, the patterns of emergence for the two years of this study are similar both in amplitude and duration (figure 4.2). The point estimates of daily emergence were calculated by dividing the total numbers found in the traps by the surface area covered and the number of days the trap had been in position since it was last serviced (due to the short adult life-span of these insects the maximum interval between service was 4 days). Certain differences are, however, apparent between the two years. In 1976 the main emergence period began earlier than in 1975. This may well be due to the higher temperatures in the early part of the second year of this study in contrast to the previous year (figure 4.3) (Meteorological Office, 1975; 1976). Although 1975 was warmer than average, 1976 was even warmer and the higher temperatures in May and June of 1976 will have accelerated the later stages of development.

The duration of the emergence period was restricted in comparison with other studies (Morgan and Waddell, 1961; Bracken and Murray, 1973) where chironomids were still abundant in July. Also of interest is the high variation in daily estimates of abundance, most marked in 1975. Similar variability has also been noted in light trap studies of this family (Albu, 1971). Albu explained these oscillations in terms of climatic factors; for climatic conditions to act in such a short term way, they must influence the pupal stage causing either a decrease in the emergence rate or a change in trap efficiency under adverse conditions. The alternative possibility of operator error, in removal of the sample from the trap, being the cause of the variability can be refuted by the presence of a similar day to day variability in the study of Morgan and Waddell (1961 - figure 6) despite their use of different removal techniques. The more regular pattern seen in 1976 was undoubtedly due to the smoothing out of irregularities by the calculation of a 2- or 3-day mean.

Of the 47 species identified only 18 accounted for more than 5% of the emergence from any trap in any one month. The most important of these will be discussed below, whilst the emergence periods of the less abundant species are summarised in table 4.2.

Orthocladiinae

Of the 7 species found of this subfamily only 2 were numerous, the others occurring sporadically and in low numbers. The emergence patterns of the two most abundant species (figure 4.4) showed no appreciable differences between the two years of this study. *Cricotopus sylvestris* occurred in all traps in May and June in both years. Its predominant position in the fauna is best demonstrated by the rank/percentage abundance graphs for June of both years (figure 4.5). With the exception of trap 4 in 1975 and the two traps (1 and 2) in an isolated pool the following year, *C. sylvestris* was very abundant. The timing of the emergence peak found in this investigation was markedly different from that found by Mundie (1957) in storage reservoirs where maximum numbers were recorded in August with only a few individuals found in May and June. *C. intersectus* was the other abundant orthocladiinid captured and the emergence period of these two species coincided fairly closely, with the maximum in early June. Like the previous species, *C. intersectus* was ubiquitous, being taken in all traps in June 1975, whilst traps 4 and 5 were the only sites where it was not a major contributor to the total monthly emergence (figure 4.5). In June 1976 this species was only abundant in traps 3 and 4, with *Einfeldia dissidens* predominant in the other two traps. The general distribution of these two *Cricotopus* species, both within the lagoon area where they were predominant and to a lesser extent in the main lake, where they were not major contributors to the biomass, is of interest because they are not detritivores but herbivores, utilizing primary production rather than decaying material. Their abundance in the shallow water areas indicates the importance of the productivity of the epipelic and epiphytic microalgae to the chironomid community.

Tanypodinae

The later larval instars of this subfamily are commonly reported to be predatory, feeding on small invertebrates including other chironomids (Bryce and Hobart, 1972). A total of 9 species was taken in this study and of these only 3 were caught in relatively large numbers in either year. The temporal pattern of emergence of two of these species differed between the years whilst the third was not abundant in 1975 (figure 4.6). *Procladius choreus* was most abundant in 1975 and was particularly numerous at trap 4 in June when it accounted for 65% of the total catch. In contrast, the main peak of abundance of *P. choreus* in traps in the more sheltered part of the lagoon area (1, 2 and 5) occurred in May, whilst the emergence at trap 3 was, like trap 4, delayed until June. In 1976 the main emergence of this species occurred in May, c. 15 days before the May peak from the shallow water traps in the previous year.

In 1975 only 3 specimens of *Tanypus vilipennis* were identified.

The following year, however, it was more abundant and was predominant in trap 2, relatively common in trap 1 (8%), whilst absent from traps 3 and 4 in May and did not account for more than 5% of the fauna in subsequent months. The closely related species *T. punctipennis* was most abundant at trap 3 in 1975, although even then it only accounted for 8% of the total June emergence. In 1976 this species was numerous in all four traps, being predominant in trap 1 in May and traps 1 and 3 in June and in all cases it constituted > 5% of the catch for those two months. Trap 3 in 1975 and all four traps in 1976 were situated near the border of the lagoon area adjacent to the main lake. This species therefore appears to have a restricted distribution in the lake.

The main emergence periods of both *P. choreus* and *T. punctipennis* occurred earlier in 1976 than in the previous year but this comparison between years should be treated with caution since the spatial variation in emergence for *P. choreus*, as already described, would clearly influence the interpretation of the data. However, for *T. punctipennis* the inter-year comparison is more valid as the spatial restriction of the population will have introduced less variability attributable to heterogeneity in habitat. It therefore seems reasonable to interpret the earlier emergence in 1976 as a product of accelerated development caused by the earlier arrival of warmer weather in that year.

Whilst *P. choreus* is widely distributed in most lakes in Britain, the two *Tanypus* species are less ubiquitous. The development of a *Tanypus* population was described as a secondary process in lake colonisation by Nursall (1952), being dependent upon the previous development of an extensive chironomid fauna. However, Olah (1976) reported that *T. punctipennis* fed largely on diatoms, thereby showing the direct importance of the annual primary production to the Tanypodinae populations.

Chironominae

While over half of the species identified belonged to this subfamily (29 in a total of 47) only 13 species accounted for more than 5% of the monthly emergence. However, due to the high individual weight of many of this group, they did contribute appreciably to the biomass at the times of their emergence. Of the species caught in this survey only 11 were also found by Mundie (1957) and 10 by Bracken and Murray (1973). The distribution and emergence of the most abundant species is discussed below.

Chironomus cingulatus was, in June 1975, found most frequently in traps near the landward edge of the lagoon area (1, 2 and 5) and was absent from the two more exposed traps during its peak emergence period. The following year it was found in all four traps, being least common in the main lagoon (traps 3 and 4). From figure 4.7 it seems that this species has three generations each year, emerging in early May, mid June and late August with each peak represented strongly in traps 1 and 2. Its distribution revealed a preference for the more shallow, sheltered areas of water and this may account for its rarity in the reservoirs studied by Mundie (1957) where only four specimens were found. The dominant *Chironomus* species found by Mundie were *C. anthracinus* and *C. plumosus*, an association often found in natural, stratified eutrophic lakes (Brinkhurst, 1974). *C. plumosus* was also taken in this survey but (with the exception of trap 4 in May 1975 where it was predominant) was not numerous.

In the first year of this study, apart from one male at trap 3 *Einfeldia dissidens* was caught exclusively in trap 1. The following year it was found in all traps and at the time of peak emergence in June (figure 4.7) it accounted for 16% of the emergence at trap 1 and was the predominant species at trap 2 (figure 4.5). A number of intersex individuals with external male genitalia and female-type antennae were found. This abnormality has been described by Humphries (1938), who identified one intersex specimen and described the nematode parasite which filled its abdominal cavity. The incidence of infection was highest in the early part of the emergence and intersex individuals were absent after early June. The sex ratio in the early June period was initially clearly biased towards males and slowly changed, so that by the end of this period the bias was reversed (table 4.3). Wülker (1964) has described similar morphological changes in male *Chironomus* species where the external, sexual characteristics were modified by infestation with a mermithid nematode parasite.

Parachironomus arcuatus showed two distinct emergence periods in 1975, the first in early May and the second in mid-June (figure 4.8). In 1976 only the latter emergence peak was found although slightly earlier in June. The emergence peak in May 1975 was predominantly due to insects caught at trap 5 over emergent vegetation which was not sampled the following year. The June 1975 peak was caused by an emergence at traps 2 and 3 whilst in 1976 most of those caught were taken in traps 3 and 4; all of these traps were in moderately shallow water (1.0 - 1.5 m).

Endochironomus albipennis was present throughout the survey period in 1975 with the peak emergence in late May being primarily due to the catch at trap 5; those caught later were in traps 2 and 3. The data for 1976 shows a more restricted emergence period, mainly in late June. The limited emergence period in this year may be due to the fact that sampling was from a more restricted area. Mundie (1957) found that this species was bivoltine at all depths from 1.0 to 6.8 m, emergence occurring at the end of May and August, with no variation in emergence timing with depth; similar emergence periods can also be seen in the data of Bracken and Murray (1973).

Microtendipes pedellus (figure 4.8) was most abundant at the marginal trap (5) in 1975 and absent from the main lake. The following year it was found only in traps 1 and 2. As with *E. albipennis*, the main emergence differs from that reported by Mundie who found none before July and cited September as the main emergence period. In one of the lakes studied by Bracken and Murray this species was found in greatest abundance on 30th June 1969, a timing close to that found here.

Polypedilum nubeculosum was found at all stations in both years but was most abundant at trap 1 in 1975. The peak emergence in both years occurred in mid-June with a small number present in May. The extended emergence in 1975 (figure 4.8) was due to a spatial variation in the timing of emergence, with later emergence at traps stationed in deeper water. The peak emergence in mid-June contrasts with the studies of Mundie and of Bracken and Murray who all found this species to be most numerous in May.

Comparison of trap sites

The data show considerable variability of fauna between trap sites. This can be ascribed to two causes:- (1) temporal succession of species and (2) spatial limitations on the distribution of any individual species. The samples were compared on a monthly basis so that both of these causes of variability would be taken into account. The indices used were the Jaccard (1912) index which considers shared species and the Raabe index (1952) which compares the structure of the assemblages between two sites. The results are shown in Table 4.4.

Jaccard index. In May 1975 a gradient of increasing difference can be seen between trap 5 sited on the margin of the lagoon area and those traps (1-4) stationed in progressively deeper water with more exposed conditions (Table 4.4). This correlation is reinforced by considering the trap 1 comparisons in Table 4.4. It can be seen that trap 4 possessed a fauna not closely related to that at any other trap site. In June most of the inter-trap comparisons showed an increase in similarity, probably due to the greater number of both species and individuals present in that month, especially at traps 1-4. As in the previous month, trap 4 was again distinct from the other sites. The correlation between depth and faunal similarity can again be seen if the data from the littoral trap (5) are ignored; the peak emergence at trap 5 occurred earlier than at the other sites and by June the catch was declining. In the following year the traps were paired (1+2, 3+4) and the closest agreement would therefore be expected between trap pairs. Whilst the first pair did show a strong similarity in both May and June the second pair (3+4) were less obviously related in May. It should be noted that in both months trap 3 was more akin to traps 1 and 2 than to trap 4. In July the first pair of traps showed little similarity, with trap 2 being the most individual of the four whilst in August too few imagines were captured to make comparisons valid.

Raabe index. The analysis of the extent to which the dominant species are common to two assemblages is perhaps more important from a productivity viewpoint than the uniformity of the species distribution. The application of the Raabe index to the 1975 data contrasts with the results obtained from the Jaccard index. In May, traps 1-4 were similar with trap 5 being the most unrelated due to the earlier emergence at the littoral site. In June, the conslusions reached from the previous analysis were supported, with the trap in the main lake being the most dissimilar and with trap 5 also differing from the other traps within the lagoon area. As with the Jaccard index a clear correlation of faunal change with depth was found, reinforced by the close agreement between adjacent pairs. In the following year the apparent discrepancy in paired trap correlations for May was refuted by the Raabe index but the close agreement between traps 1 and 3 is supported; this pattern was repeated through July and August (table 4.4).

The inter-trap analysis for identical months in consecutive years revealed the extent to which the emergence in the two years was similar. Trap 4 (1975) showed the greatest difference from any of the stations chosen the following year. In addition it seems clear from the June data that traps 3 and 4 (1976) sampled a fauna similar to trap 3 (1975) whilst the other pair (1+2, 1976) sampled an assemblage most similar to that found at trap 1 the previous year. These conclusions reinforce the idea, outlined earlier in the descriptions of the emergence of the common species, that in 1976, traps 3 and 4 were sampling a fauna characteristic of the lagoon and main lake interface, sampled by trap 3 the previous year.

Comparison of the species assemblages in the traps

Of the 47 species present, 18 accounted for more than 5% of the monthly emergence from any trap site. However, August 1976 added three species to this total although its contribution to the total emergence was low. These three are therefore largely excluded from the subsequent discussion. In 1975, three species predominated in the samples from all traps; these were *Cricotopus sylvestris*, *C. intersectus* and *P. choreus*. The fauna also contained a number of Chironominae found in both May and June. Trap 4 in the main lake was the only trap in which one of the two orthoclads was not predominant in one or both of the months; here, in May, *Chironomus plumosus* was predominant, being replaced by *P. choreus* in June. In May 1975, the fauna at trap 5 was structured like that at trap 1 in June, with a larger number of species more equitably distributed (Lloyd & Ghelardi, 1964) than at any of the other traps in May. In June, trap 5 sampled a more restricted assemblage because the emergence at this unique littoral site above emergent vegetation occurred earlier than at other traps. However, a clear change of the assemblages with depth can be seen with traps 1-4 having decreasing equitability (figure 4.5).

The following year the dominant populations were augmented by two *Tanypus* species and a clear seasonal progression was found with the Chironominae component of the fauna becoming more important later in the year. In May 1976 only 3 Chironominae species represented more than 5% of the emergence per trap; in June, July and August there were 11, 10 and 11 species respectively. Moreover, in June only at trap 2 was a Chironominae species (*Einfeldia dissidens*) predominant, while in July and August members of this subfamily were abundant at all four traps. In May, the traps in the isolated pool were dominated by two *Tanypus* species whilst the other pair had *Cricotopus sylvestris* as their most abundant species.

DISCUSSION

The chironomid fauna sampled in this survey illustrates the effect of a number of controlling factors acting to limit the individual species and total population and although these have been discussed where relevant in previous sections the overall picture deserves further emphasis. The comparison of traps between years revealed a correlation between the fauna sampled at trap 1 in 1975 with traps 1 and 2 in 1976, also trap 3 in 1975 had a similar species composition to traps 3 and 4 in 1976. A number of species showed two emergence peaks and often the timing of these were related to the depth of water at the trap site. For example, *P. choreus* emerged in large numbers in May and again in June 1975. The former peak was principally from shallow sheltered water (traps 1 and 2) and the latter was from traps 3 and 4 in deeper exposed water. This was undoubtedly due to the local effect of higher air temperatures (and associated light intensity) causing the water to warm up more rapidly in the shallow sheltered lagoons, where little gross water movement occurs, compared to the deeper areas of the main lake. In 1976, when the average air temperature increased more rapidly in May and June than previously, the emergence as a whole was seen to be advanced. Temperature therefore affects the development rate and influences the timing of emergence and, in addition to a number of other factors, including substratum and vegetation, it controls the distribution of species. The comparative diversity at each of the trap sites in June 1975 shows, with the exception of trap 5, a general decrease in equitability of the assemblage with depth combined with a decrease in the number of species. In May 1975, trap 5 did show a species assemblage similar to trap 1 in June and the discrepancy with the above series was caused by the earlier emergence at trap 5 compared to the other sites. Other workers on chironomid emergence have not studied the littoral habitat, so no comparison can be made. During May the main growth of benthic plants has not started and therefore a number of species may migrate to the existing littoral plants for shelter and feeding, thus accounting for the greater importance of this site earlier in the year.

The main difference found between this and other studies of chironomid emergence was in the duration of the emergence period. Morgan and Waddell (1961) and Bracken and Murray (1973) caught large numbers until July whereas the emergence from the gravel pit studied here was largely completed in June. It would perhaps be more realistic to compare this pit with other man-made lakes such as reservoirs. Krzyzanek (1970), in a 10-year study of a newly formed reservoir, described three stages of faunal development where first, Chironominae were dominant, feeding on decaying organic matter (Fillion, 1967), then this group became restricted to the profundal and in the last stage oligochaetes became more important and a predatory chironomid fauna developed. The fauna of the Newport Pagnell gravel pit has a high proportion of predatory chironomids dominating the fauna in the deeper water. The absence of a large Chironominae fauna in the main lake may be due to the absence of a suitable substratum, while in the lagoon area a number of species of this subfamily were present. This survey indicates that in a wet-worked gravel pit large midge populations will not develop initially in areas deep enough to limit benthic plant growth.

The species composition of the sites sampled at this gravel pit differ markedly from that found by workers in other wetlands. In particular the predominance of herbivorous species, such as the two orthoclads *Cricotopus sylvestris* and *C. intersectus* and two herbivorous *Tanypus* species (Olah, 1976) has not been reported previously in studies of natural lakes and reservoirs. The habitat is clearly different from other lakes. One further point worth emphasis is that unlike the profundal and, to a certain extent, the littoral zone of large lakes, the chironomid assemblages in a gravel pit have developed following post-excavational changes in substratum. The gradual increase in silt, organic matter and plant growth at the same time enables new species to colonise.

CHAPTER 5

LARVAL POPULATIONS OF SAND AND GRAVEL PITS: DISTRIBUTION AND ABUNDANCE

The adult emergence data presented in the previous chapter revealed a distinct difference between lake zones and also a different species composition from that found by workers in other lakes and reservoirs. Since emergence traps can only be successfully used where public access is restricted it is necessary, in most lakes, to study larval distributions to investigate the spatial and temporal patterns of chironomid abundance. Furthermore, chironomids spend most of their life cycle in the larval stages; thus sampling can be carried out throughout the year, rather than in the summer months alone, to reveal both spatial and temporal patterns of abundance.

The initial study site, Black Horse lake, was further investigated and both larval sampling and emergence trapping undertaken. This provided a check on the relationship between adult emergence and larval abundance. Since most studies of chironomid communities have been based on larval sampling alone, the data gathered from this survey would be more directly comparable with other investigations than that from further emergence trapping alone.

Sites were chosen for this survey of the larval chironomid communities to reflect the range of lake types created by the sand and gravel industry. These were :-

Trentham Park lake
British Industrial Sands, Congleton sand pit
Linford Lakes i.e. Dovecote lake
Black Horse lake

METHODS

Larval samples were collected monthly during 1977 (with one or two exceptions) from all of the sites. At Trentham Park an Allen grab was used whilst for all other stations an Ekman grab was chosen. Two samples were taken at each station on each sampling occasion.

Stations were chosen to form a transect of each lake (table 5.1). However, at Trentham Park only one station was sampled as the lake was very small. Larvae were separated from the mud by sieving, then identified and measured.

Emergence trapping at Black Horse, Linford, was carried out from 18th April until 11th August 1977 using Mundie traps. The traps were emptied once each week; thus the catch will undoubtedly underestimate the actual emergence (McCauley, 1976). The stations used for larval sampling and emergence trapping on this lake were identical.

RESULTS

The data are presented and discussed in relation to both the spatial and temporal pattern within individual lakes and in comparison between lakes.

Spatial and temporal pattern of abundance within lakes

Trentham Park

The total abundance of all species of larvae showed a distinct pattern of maximum abundance during the winter months (Dec, Jan and Feb). Larval abundance decreased from March until July, and August to September but subsequently rose again to just below that found in the previous January (figure 5.1).

In total only six genera of larvae were identified (table 5.2), all genera except *Microcricotopus* accounted for at least 10% of the total population. The most abundant member was *Procladius* which made up 41% of the total population. Both 3rd and 4th instars of *Procladius* larvae were present throughout the year although 3rd instars were most numerous in May and August; this indicates that at least two generations occurred in the year.

The second most abundant genus, *Chironomus*, was also least abundant during the summer. Fourth instar larvae were present in all months except June. Third instar larvae were caught on only three occasions; July, October and November. Since development only occurs slowly during autumn and winter months, due to the low ambient temperatures, the occurrence of third instars in October and November probably represent a single cohort as does the occurrence during July. The two cohorts were more distinct than those of *Procladius* in which continuous recruitment may mask the actual number of generations occurring.

Cryptochironomus larvae were present in both third and final instars throughout the winter and became less abundant during the summer. No distinct summer generation could be discerned from the data and it appeared that recruitment occurred mainly in autumn, with larvae overwintering and emerging the following summer.

Tanypus larvae were not caught until spring. In June a marked increase in abundance was noticed. Instar analysis indicated that a second generation may have occurred during the winter.

British Industrial Sands, Congleton Pit

Four stations were sampled monthly at Congleton and the data analysed separately for each station (figure 5.2). Most larvae were caught at station 1 in shallow water (0.1-0.2 m) on the edge of the lake. Samples from this habitat showed a clear seasonal abundance pattern with larvae most numerous in autumn and early winter with a rapid fall in spring and low numbers present throughout the summer until August (figure 5.2). The fall in December at station 1 may represent a migration of larvae into deeper water or deeper into the sediment. In such shallow water (20 cm) they would be vulnerable to ice formation and may therefore have moved away from this station. During the times of peak larval density the most abundant genus was *Polypedilum*.

In contrast to the marked fluctuations in abundance in shallow water, the stations in deep water were more constantly populated throughout the year. This is especially apparent at stations 2 and 3. Station 4, however, does show a distinct pattern with larvae abundant in April and May and again from July onwards (this was similar to the pattern at station 1 with the February peak missing). However, during these periods the most abundant genus at this site was *Procladius*.

In addition to the greater abundance at station 1 there was also a larger number of species caught (11) in comparison with other stations (4-5). These additional species were mainly of the subfamily Chironominae although *Microcricotopus* was also restricted to this site. Furthermore it is apparent (table 5.3) that both *Procladius* and *Polypedilum* were more abundant near the margin of the lake (stations 1 and 4) whilst *Chironomus* larvae were predominantly located in the deeper water zones away from the edge. These three genera were predominant, accounting for 99% of all larvae at stations 2, 3 and 4 and 90% at station 1.

The seasonal pattern of abundance of these genera (table 5.4) was consistent between stations. *Chironomus* were abundant from February until May but in June numbers decreased, reasonable numbers were found in August and September but there was a marked decrease in October. The length-frequency histograms for the combined data (figure 5.3) for all four stations indicated that the autumnal decline was due either to larval mortality or to sampling error rather than emergence. From this graph it can be seen that larvae overwinter in the fourth instar, at a length of 16-20 mm; at the start of spring they grow slightly more to a maximum length of 24 mm and then emerge. It seems probable that not all larvae emerged at this time since large larvae were present throughout July and August. Smaller larvae, first caught in July, continuedto grow until, by December, they had reached a length of c. 19 mm. Only one generation of *Chironomus* seems to have occurred during the year although the summer emergence period may have been protracted.

Polypedilum larvae were most numerous at three times during the year: winter, spring and autumn. The rapid decrease in abundance during February may have been due to sampling error or mortality as little growth and emergence would be expected during this period. Larvae subsequently pupated and emerged during May, few larvae were then caught until August. The decrease in abundance during September represented the loss of individuals due to emergence since pupae were present in the benthos as station 1 at this time. In contrast, a steady increase in abundance was found at station 4 up to December, this was consistent with the absence of pupae at this site. The rapid development of a generation from July to September was possible at station 1, but not at station 4, due to the higher temperatures in the sheltered, shallow water area at station 1. In addition there was a noticeable growth of macrophytes and algae at station 1 providing better feeding conditions. The life cycle can be completed more rapidly under favourable conditions and the number of generations of a species per year varies within a single lake. Jonasson (1965) found that *Chironomus anthracinus* completed its life-cycle in one year at water depths less than 15 m but below this it took two years,due to the limited food and lower temperatures in the deeper water.

Procladius larvae were present in winter in all length classes (figure 5.4) and two distinct groups were discernable, with modal length of 4-5 mm and 9-10 mm during the period January to April. The first pupae and pharate larvae were found in April. The group of smaller larvae grew during May to c. 8-10 mm and a succession of recruitment occurred throughout the ensuing months until the population structure stabilised in November and December with most larvae 9 mm long. It appears that *Procladius* was bivoltine with a number of overlapping cohorts.

Linford lakes, Dovecote

Four stations forming a transect (table 5.1) were sampled monthly (except in June and August). The total larval abundance at the four stations (figure 5.5) followed the same pattern as seen at Congleton station 1 with larvae most abundant in winter and autumn with low numbers present during spring and summer months. However, at this site, the sampling stations could be paired, on the basis of depth, into two groups 1+4 and 2+3. It is apparent from the marked difference in seasonal abundance (figure 5.5) for these stations that depth was not the only factor determining species distribution. Whilst station 2 showed an increase in larval density during winter, station 3 did not. However, stations 1 and 4 were more alike in seasonal abundance pattern although fewer larvae were caught at station 1.

The species associations found at each station were remarkably uniform with *Polypedilum* and *Procladius* predominant (table 5.5). *Chironomus* larvae were abundant at all except station 1. The only other exception to the uniformity was the presence of a large number of *Pentaneura* larvae at station 3, these larvae were also abundant at station 4 in February but the genus was only present in low numbers at the other two stations.

The low numbers caught during the summer months, together with the infrequency of sampling during this period, made the interpretation of life histories at this site impossible. However, the low summer abundance, repeated at all four stations indicated that the larvae emerging in the spring did not successfully recolonise the habitat; it was not until the autumn that the benthic fauna redeveloped.

Three genera present in the spring were not found the following autumn; these were *Harnischia*, *Pentaneura* and *Clinotanypus*. However, only *Pentaneura* was sufficiently abundant in the spring to state that it had not recolonised. The pattern for the first year following inundation therefore appeared to have been one of a spring emergence with no subsequent substantial emergence until the following year.

Linford Lakes, Black Horse

Three sampling stations were chosen at Black Horse lake corresponding to trap stations 2, 3 and 4 in 1975. This numbering system is retained to facilitate inter-year comparison of emergence data.

The seasonal pattern of larval abundance differed at these three stations (figure 5.6). Station 2 showed a pattern of winter and autumn abundance and low summer populations. At station 3 the population remained fairly constant throughout the year. Both of these stations were at the same depth of water and reinforce the idea that this was not the only factor determining larval distribution and abundance. Station 4 showed a constant decline in larval density during winter and spring with no substantial increase the following autumn.

The genera caught were uniformly distributed between the stations (table 5.6). However, most genera were found at station 3 where the population was numerically most stable; the taxa found only at this site only constituted 1-2% of the population. Several differences in community composition were apparent for the most abundant members of the fauna. Station 4 was dominated by *Chironomus* and *Procladius* larvae which together formed 88% of the total population. These two genera were equally abundant in actual density at all three stations. Their predominance in the fauna here appears therefore to be due to the reduced abundance of other larval genera.

At stations 2 and 3, three additional genera were abundant, *Glyptotendipes*, *Polypedilum* and *Tanypus*. But whilst the species at these stations were similar, the temporal abundance pattern was different. This was mainly caused by seasonal differences in density of *Chironomus* larvae between all three stations (table 5.7). At station 4 larvae became less abundant during the spring until July, subsequently an increase occurred. During the winter larvae were present in all length classes from 9-25 mm although by the end of March they had grown to 16-21 mm. A rapid decrease in density occurred before the next sampling but no young larvae appeared in the samples until September. At station 3 larvae overwintered in most age classes, no small larvae were found until September when a group of 8 mm larvae were caught. This growth pattern was repeated at station 2 although here no small larvae were caught until October.

Glyptotendipes larvae were only abundant in March at station 2 and July at station 3, during these periods numbers rose rapidly to high levels and subsequently fell precipitously before the next sampling period. Only small larvae were caught.

Polypedilum larvae were only abundant in the samples in winter and autumn. The seasonal pattern of abundance was identical at both stations with peak numbers caught in February. Density subsequently declined rapidly until May and then rose again slowly until the end of the year. The major loss occurred in the February/March period. Two cohorts were distinguished in the larval samples at this time, with modal lengths of 4 and 11 mm. By the end of March the smaller larvae had grown to 6 mm and the larger larvae to 12 mm. The rapid increase in abundance in February was due to recruitment of small larvae. The following December only the larger larvae (modal length 10-11 mm) were present. Thus, in contrast to *Chironomus* which overwinter in most length classes, *Polypedilum* larvae develop in distinct cohorts, one which almost reached maximum length by winter and the second which hatched and grew slowly throughout the winter to provide a stock of smaller larvae in late winter.

Procladius larvae were abundant in winter, spring and autumn but only present in low numbers in summer (table 5.7). The spring decrease in abundance occurred earlier at stations 2 and 3 than at station 4. In

January at stations 2 and 4 the larvae were of modal length 9 mm, slow growth occurred until May. During this period at stations 3 and 4 an additional cohort of smaller larvae became evident and grew from a length of 4 mm in February to 8-9 mm in June. In the autumn, at stations 2 and 3, larvae grew to a length of 10 mm by November whilst at station 4 growth was retarded and most larvae had only attained a length of 8 mm by the end of December.

Tanypus larvae were not abundant until late spring. In May at station 3, and June at stations 2 and 4, a rapid increase in abundance occurred. This was followed by a decline in July and then a second peak at stations 2 and 3 (table 5.7). Larvae at station 3 grew to a modal length of 8 mm by May and to 9 mm the following month. Following the decrease in abundance in June smaller larvae (5-8 mm) were caught in September and grew to a modal length of 10 mm by December. Numbers caught at station 2 in spring were too low to distinguish cohorts. However, during the autumn, when more larvae were caught the growth pattern was identical to that at station 3.

Comparison of fauna between sampling stations

The number of species common to both sites was calculated using the Jaccard index (p. 30) and the percentage similarity by the formula of Raabe (p. 30). Cluster analysis by Ward's method (1963) was performed on standardised data using CLUSTAN 1A on the ICL 7600 at Manchester University regional computer centre. Data on which this analysis was based are given in table 5.8.

Jaccard index

The values for comparison within the same site (grouped in boxes, table 5.9) are much higher for Dovecote and Black Horse than for Congleton. At this latter site the similarity was highest between stations 2 and 3 in the deeper water areas and 4. The uniformity of the values at

Dovecote and Black Horse indicates that the genera were uniformly distributed throughout the lake.

Comparisons of stations between sites were generally of lower values than those obtained within a particular lake. However a rough ranking can be obtained with Trentham more similar to Black Horse and Dovecote than to Congleton. Black Horse was also more similar to Trentham than to Dovecote whilst Dovecote was equally similar to Trentham and Black Horse but less similar to Congleton.

Raabe index

The analysis based on common species is largely supported by the percentage occurrence data. The values of the index in between-site comparisons are generally lower than those for intrasite comparisons. However certain exceptions are evident (table 5.9). Station 1 at Congleton was more similar to all four stations in Dovecote and station 3 at Black Horse than to the other stations at the same site. The high similarity to the Dovecote stations indicated that the fauna of this newly flooded site was more characteristic of shallow than of deeper water. This was borne out by the relatively lower values of the comparisons between Dovecote and Black Horse lakes. Another anomalous result (in terms of the high intrasite similarity) was the high values for comparisons between Black Horse station 4, stations 2 and 3 at Congleton and Trentham Park.

These findings suggest that the fauna may be described in terms of three typical associations based on the stations

(1) Congleton 1 + Dovecote

(2) Congleton 2, 3 and 4 + Black Horse 4 + Trentham Park

(3) Black Horse 2 and 3

The following chironomid genera were typical of these three groupings.

(1) *Polypedilum* 30-70%, *Procladius* 18-30%

(2) *Chironomus* 20%, *Procladius* 40%

(3) *Chironomus* 20%, *Procladius* 20%, *Tanypus* 25%

Cluster analysis

The associations of sampling sites delineated agree in general with the categories outlined by the previous analysis (figure 5.7). However, one major exception was seen, station 1 at Congleton. This was found to be highly dissimilar from the Dovecote fauna whilst in the Raabe index method it was seen to be similar. This difference between methods was caused by the high abundance of *Polypedilum* at Congleton station 1 and whilst percentage composition was similar actual abundance was markedly different. Thus, whilst most sites had a total catch of 300-500 larvae the Congleton station 1 total was 1500. This difference in abundance did not affect the percentage similarity since absolute abundance was not considered.

Adult emergence at Black Horse, Linford

The seasonal pattern of emergence in 1977 was markedly different from that found in the previous two years (figure 5.8). Whilst numbers caught increased rapidly in late May, they then dropped precipitously and peak abundance was not achieved until the end of June. The June decrease coincided with a period of cold rainy weather.

Emergence continued throughout July and considerable numbers were still emerging in the first week of August. A total of 22 species were taken; these are listed and emergence periods indicated in table 5.10. The emergence of those species abundant as larvae in the benthos are discussed for each station.

Station 2

The five larval genera abundant in the benthos at this station were *Chironomus*, *Glyptotendipes*, *Polypedilum*, *Procladius* and *Tanypus*. Two species of the genus *Chironomus* were distinguished as adults. The first to emerge was *C. plumosus*, in May. From mid-July onwards the second species, *C. cingulatus*, was taken.

Glyptotendipes was represented by one species *G. glaucus*. Emergence was in late May and early June and again at the end of July.

Polypedilum nubeculosum, the only species of this genus caught, emerged from the end of May throughout June and again at the end of July. Adults were most numerous in early June.

Procladius choreus, the only species of this genus, was present in the emergence traps from mid-May until mid-June and again in early August.

The genus *Tanypus* was represented by only one species, *T. punctipennis*; its imagines were present from the end of May until late June and again in early August. With the exception of *Chironomus spp* all of the above named species had two generations each year a winter generation emerging in May/June and a summer generation emerging in July/August.

Station 3

The emergence patterns for *Chironomus spp* adults and *Glyptotendipes glaucus* were identical to those at station 2. In contrast, the emergence of *Polypedilum nubeculosum* occurred much earlier at this station being complete by mid-May. However, the second emergence occurred at the same time as that at station 2.

The emergence of *Procladius choreus* and *Tanypus punctipennis* extended from late-May until sampling was discontinued in early-August. *Tanypus* adults were most abundant in early and late July; the first emergence peak occurred later at this station than at station 2.

Station 4

Chironomus plumosus emerged later than at the other stations, not being caught until early June. *C. cingulatus* emerged at the end of June as it did at the other stations.

The emergence of *Procladius choreus* continued from late-May until sampling was discontinued. Three peaks were observed, early- and late-

June and mid-July. However, the two June peaks may have been due to the adverse conditions for emergence rather than being caused by discrete generations.

Adult emergence and larval abundance

Since emergence traps were only used for three months of the year it was only possible to compare changes in larval abundance and adult emergence during this restricted period. Furthermore, this was the period when larvae were present in low numbers.

At station 2, the two periods of decrease in abundance of *Chironomus* larvae coincided with the emergence of firstly *C. plumosus* (for the decrease in May/June) and then *C. cingulatus* (for the decline after July). At station 3 few larvae were present until June/July. However all of these had disappeared by September. Similarly at station 4 the main decrease occurred before traps were set and few larvae were present in the May/June period.

Glyptotendipes larvae were only caught during restricted periods and at these times the catch was primarily of small larvae. This species emerged at stations 2 and 3 in late May/early June and late July. The changes in larval abundance of this species were more probably related to changes in habitat than due to emergence. *Glyptotendipes* larvae are filter feeding chironomids building tubes attached to plant or other suitable substrata (Walshe, 1951). Thus the rapid fluctuations in abundance of this taxa can be understood in terms of a period of larval recruitment in February followed by a movement to the aquatic macrophytes when they begin to grow again in April/May. Similar migratory movements of chironomid larvae to feed on the spring periphyton bloom have been reported by Mason and Bryant (1975a). Mundie (1965) has also suggested that the benthic chironomid communities are considerably less static than has conventionally been held; a view supported by the data of Davies (1973) who found final instars of many larvae in the plankton.

Polypedilum nubeculosum larvae showed the same pattern of larval abundance and growth at stations 2 and 3 whilst adult emergence occurred much earlier at station 3. The second emergence peak occurred at the same time at both stations.

Procladius choreus emerged at the end of May at stations 2 and 3 coinciding with the rapid decrease in larval densities during this period. The fall in larval abundance at station 4 did not occur until after June.

Thus, whilst emergence at this station started at the end of May, it was not until early June that significant numbers of adults were caught. The extended emergence period of this species was probably caused by overlapping generations, a view supported by the wide range of larval body lengths observed in the benthos samples of this species.

Tanypus punctipennis had two emergence peaks at stations 2 and 3, early June and late August. This was in contrast to the changes in larval abundance when numbers had declined by June at station 3 but not until July at station 2.

Changes in larval abundance, based on monthly sampling, showed poor agreement with the expected changes based on emergence data. This discrepancy was not found by Potter and Learner (1974) in their study of Eglwys Nunydd reservoir. However, their study was based on weekly sampling. It is apparent that, due to the rapid growth rate of larvae in the summer months, monthly sampling does not provide realistic estimates of larval population dynamics.

DISCUSSION

Larval sampling of this series of sand and gravel pits has shown an overall consistent pattern of species composition, the most abundant genera being *Chironomus, Polypedilum* and *Procladius*. Furthermore the larval associations distinguished divided the sites internally into three distinct types, a littoral community in which *Polypedilum* was predominant (Dovecote and Congleton station 1), a *Chironomus-Procladius* association and a third in which *Tanypus* was also abundant.

Hamilton (1971), in a survey of the zoobenthos of fifteen Canadian lakes, described a *Polypedilum -Procladius* dominated community as characteristic of a shallow, non stratified lake ($z_m = 2.5$ m). This association was found in Dovecote ($z_m = 3$ m) and in the shallow water zones at Congleton ($z < 2$ m). In contrast, Carter (1976) found that *Procladius* was most abundant at 9 m in Lough Neagh with markedly less larvae found at < 3 m and > 12 m. However, this depth preference coincided with a substratum transition from sand to mud at c. 8 m and depth preference may therefore be largely influenced by substratum selection.

McLachlan (1971) found *Polypedilum* larvae in abundance in both the littoral and profundal of the newly flooded lake Kariba. Species distribution in that lake was not correlated with any environmental parameter such as sediment particle size or loss on ignition. *Polypedilum* larvae are also encountered in large numbers on occasion in newly flooded reservoirs (e.g. Krzyzanek, 1970). These findings suggest that in newly created habitats the pioneer colonists can exploit all microhabitats and are later displaced from certain areas by competition (Cantrell and McLachlan, 1977).

Chironomus larvae are found in most lakes and, in many, more than one species is present. For example, Smith and Young (1973) found 3 and 4 species respectively in two small ponds on Merseyside. Carter (1976) has shown differences in depth distribution pattern for three species caught, in abundance, in Lough Neagh. *Chironomus cingulatus* was found at depths < 6 m, *C. anthracinus* at 6-15 m and *C. plumosus* was increasingly common at up to 18 m. The low abundance of *Chironomus* larvae in the newly flooded Dovecote lake was unusual. Cantrell and

McLachlan (1977) found *C. plumosus* larvae to be abundant in a shallow (z_m = 3 m) newly flooded lake (the other abundant species was *Tanytarsus gregarius*) and species of this genus are often amongst the first colonists of newly flooded areas (Sokolova, 1963) and quickly invade newly inundated impoundments and build up to high population densities. However, they subsequently decline and have been reported to be poor competitors (Kajak, 1964). The sediment of Dovecote was essentially the same as that of most reservoirs since the topsoil had been bulldozed back into the lake before flooding. However, the lake was flooded late in 1976 and this may have been after the emergence period of most *Chironomus spp.*.

The absence of larvae during the summer months at Dovecote was probably due to the extensive growth of aquatic macrophytes during this period. Such growth would have changed the habitat by providing additional substrata for larvae to colonise and in addition, restricted level of primary production on the mud surface.

Procladius larvae are abundant in a wide variety of freshwater habitats from eutrophic lakes (Bowman, 1976) to dystrophic ponds (unpublished data, personal obs.) and are commonly regarded as predatory (Bryce and Hobart, 1972), feeding on oligochaetes and small chironomid larvae.

Tanypus larvae were abundant only in Black Horse lake although they werefound at every site. This genus has rarely been found by other workers although two other lakes, Utah lake, Utah (Shiozawa and Barnes, 1977) and Balaton lake (Olah, 1976), are known to have large populations of this genus. Both the above lakes are shallow (z_m < 3.5 m) with little macrophyte growth. It does not feature in publications relating to any other British lake.

The total abundance of larvae at the sites studied was low in comparison with that at other lakes (table 5.11). Abundance estimates are influenced by the mesh size used to sieve the mud samples, these figures are therefore included in the table. The water chemistry of the sand and gravel pits studied was similar to that of most lakes of similar conductivity. The low larval densities may be attributable to the low organic content of the sediments (3-4% C); little organic matter being available for degradation thus limiting available food for detritivores including many chironomid species.

The chironomid fauna of the pits surveyed was uniform across a wide range of pit types and age; the main genera present were *Chironomus*, *Polypedilum* and *Procladius*, larval abundance was low (1000 individuals m^{-2}). The large variations in abundance between sampling periods showed that monthly sampling was not adequate for studies of life history and growth rates during the summer months; emergence trapping was necessary to determine the emergence periods and to distinguish species of the same genus.

The main associations were different from those described for other lakes and reservoirs indicating that the chironomid communities were specific to the habitat. This may be due, in part, to the high oxygen concentrations in all parts of the gravel and sand pits. Thus oxygen is not a limiting factor as it is in many lakes and reservoirs.

CHAPTER 6

FEEDING, DISPERSION AND DISTRIBUTION OF CHIRONOMID LARVAE IN CONGLETON SAND PIT AND BLACK HORSE, LINFORD, IN 1978

INTRODUCTION

The monthly sampling undertaken in 1977 was found to be too infrequent to delineate emergence periods or to follow larval growth patterns. During summer, high temperatures cause growth to occur at a much greater rate than in the winter and the population structure therefore changes more rapidly. In 1978, samples were taken fortnightly throughout the summer months from 4th April until 2nd October. Most of the emergence takes place during this period and the aim of this sampling programme was to investigate the following:-

1) Fluctuations in larval abundance and adult emergence
2) Larval production and calculation of Production:Emergence ratios
3) Dispersal of larval chironomids at the microhabitat level
4) Trophic niche overlap between coexisting larvae.

The estimation of production is the subject of a subsequent chapter and only population abundance changes, dispersal and feeding will be discussed here. Aggregation has been reported to occur in many species, in fact the assumption of random dispersion is usually incorrect (Taylor et al., 1978). The accuracy of the estimation of abundance is also determined by the dispersal patterns of individuals within the habitat. Whilst large scale pattern, such as changes of larval density in relation to water depth in a lake is often studied (Bowman, 1976; Carter, 1977) the small scale pattern is usually ignored. The regular use of one or two Ekman grab samples to estimate larval abundance assumes that the area sampled by these is large in comparison with species dispersion pattern such that the numbers caught will be consistent. If this is not true then contagious distribution will make the method unreliable. Various measures of dispersion are known which may be used to investigate this factor and determine the distribution pattern of individuals within a population.

METHODS

Larval chironomids were taken with an Ekman grab. Five replicates were collected from each station on each sampling interval. These were sieved, preserved and the body length of each larva was measured. Body length changes little following preservation (Mackey, 1977) and is therefore a more reliable measurement than weight which changes unpredictably (Dermott and Paterson, 1974). Instar analysis is of limited value since the majority of growth occurs in the final instar.

Larval growth patterns were followed by plotting length-frequency histograms for each sampling period.

Adult chironomids were caught at Linford Black Horse in Mundie emergence traps.

The stations used for this study were the deeper water area at Congleton (equivalent to stations 2 or 3 in 1977) and Black Horse stations 2, 3 and 4.

To study the larval dispersion patterns the mean and variance was calculated, for each of the predominant larval genera, based on the five replicates from each station. These population parameters were then used to test for aggregation by the following methods.

(i) Taylor's Power Law

When the variance is plotted against the mean for a series of samples it has been found that they tend to increase together. This relationship has been shown by Taylor (1961) to obey a power law. This is true for a continuous series of distributions from regular through random to contagious and is expressed as

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

where s^2 is the sample variance, $\bar{x}$ is the sample mean and a and b are constants; a is largely a sampling factor whilst b is an index of aggregation of the species (Taylor et al., 1978).

The estimates of variance were plotted against the means on a log-log plot.

$$\log s^2 = \log a + b. \log \bar{x}$$

where b is the slope of the regression and a is the value of s^2 when $\bar{x} = 1$.

(ii) Lloyd's index of Mean Crowding

Lloyd (1967) defined an index of mean crowding as

$$\overset{*}{x} = \bar{x} + (s^2/\bar{x} - 1)$$

and an index of patchiness as $\overset{*}{x}/\bar{x}$. Iwao (1968) showed that $\overset{*}{x}$ is related to the mean ($\bar{x}$) over a series of densities:-

$$\overset{*}{x} = \alpha + \beta . \bar{x}$$

The constant α indicates the tendency to crowding or repulsion. The coefficient β expresses the effect of density on the way the animal utilises its habitat.

The extent of trophic overlap was determined by an analysis of gut content data. Freshly killed final instar larvae were dissected to remove the fore- and mid-gut of *Chironomus*, *Polypedilum* and *Cryptochironomus* but only the foregut of *Procladius* and *Tanypus*. This was due to the morphological differences between the guts of the Tanypodinae and Chironominae such that most food was found in the foregut of the former group whilst in the latter subfamily the foreguts were often empty.

The gut portions were opened and the contents washed out, sonicated, to disrupt aggregate, and filtered through a 0.45 µm millipore filter. The filter was then dried and cleared using immersion oil and mounted in DPX neutral mounting medium (Cummins, 1973). The contents were later examined under phase contrast at low power, to find any animal remains, then at x400 to count algal cells and detritus. The categories of foodstuffs recognised are given in table 6.1. Trophic overlap (α_{ij}) was determined by the use of Levins' (1968) equation

$$\alpha_{ij} = \frac{\sum_h P_{ih} \cdot P_{jh}}{\sum_h P_{ih}^2}$$

where P_{ih} is the proportional numerical abundance of resource h in the gut contents of species i, P_{jh} is the same measure of resource h for species j. If two species use the same food resources equally then $\alpha_{ij} = \alpha_{ji} = 1$. If conversely they utilise entirely different resources the $\alpha_{ij} = \alpha_{ji} = 0$.

RESULTS

Congleton Sand Pit

Two genera, *Chironomus* and *Procladius*, were abundant at this site in April at the beginning of the study period. However, the numbers of *Chironomus* larvae caught fell sharply and from mid-June onwards no more members of this genus were found. *Procladius* larvae showed a cyclic pattern of abundance with peak densities in late May, early August and October. The changes in abundance at these times were associated with a recruitment of young larvae (figure 6.1) and marked changes in abundance between sampling could usually be explained by recruitment or death rather than indicating sampling error. However, a clear growth pattern during the summer was not evident and larvae in most length classes were usually found. In addition, pharate larvae were also present in all samples from 25th April until 14th September. This suggests that emergence of this species was nearly continuous throughout the summer with emergence peaks in mid-May, mid-July and mid-August. Other species caught at this site were only taken infrequently. Larval abundance and biomass are given in table 6.2.

Black Horse, Linford: Station 2

Larval abundance was higher here than at any other station within the lake with approximately 2,000 larvae m^{-2}. Four genera were abundant during the sampling period; *Chironomus, Polypedilum, Procladius* and *Tanypus*. *Cryptochironomus* was also fairly common from July onwards (table 6.3).

Chironomus larvae were numerous in early May when most larvae present were pharate. After this the density of larvae longer than 15 mm remained fairly constant until mid-June when this group disappeared (figure 6.2). By early July smaller larvae had joined the population and these became less abundant in late August. Small larvae (5-10 mm) were subsequently caught in October. Thus the overwintering chironomids showed two periods of loss, the first in early May and the second in June. A summer generation subsequently developed and emerged in late August, however this was smaller than the spring generation.

The data from the emergence trap at this station showed an emergence of *C. plumosus* at the beginning of May and again in early June. *C. cingulatus* adults were found throughout June. At the end of August a second emergence of *C. plumosus* was observed.

Polypedilum larvae were present in low numbers in April and by the beginning of May they had decreased . Large numbers were subsequently caught in mid-July but rapidly disappeared (figure 6.3). The emergence trap caught single adults of *P. nubeculosum* infrequently until mid-June. From that time the numbers caught increased steadily, with most adults caught in early and mid-July, after which adult emergence declined. *Polypedilum nubeculosum* had two generations each year, an overwintering generation which emerged in April, earlier than most other species, and a summer generation which grew rapidly and emerged in July; for most of the sampling period the larvae were present at low densities and only appear to exploit the habitat for a restricted period.

Procladius larvae showed a steady decrease in abundance, with growth of smaller larvae continuing from 4th April until the end of June (figure 6.4) by which time very few larvae were present in the benthos. Pharate larvae were present throughout this period of loss. The number of larvae subsequently caught rose slowly with no large obvious recruitment of young larvae until September. However numbers fell again by October. The group which developed from July showed a sudden decrease in abundance in September with many pharate larvae present at that time. *Procladius choreus*, by far the most abundant member of this larval genus, was most numerous in the emergence trap during June although subsidiary maxima were recorded in late July and late August.

Tanypus larvae were present in low numbers during April. These were mainly large larvae (9-12 mm) which disappeared during early May. At the same time a group of smaller larvae were caught and these grew to 8-12 mm by mid-June and then disappeared (figure 6.5). Only low numbers of small larvae then matured until mid-September; a decrease in large larvae subsequently occurred in early August. Emergence data for this larval genus showed two species to be present, *T. punctipennis* and *T. vilipennis*. Both species started to emerge in early June, *T. punctipennis* showed peak emergence in late June when *T. vilipennis* was not caught. Both then emerged in late July and again in late August. In the first emergence maximum *T. punctipennis* was most abundant and continued for longer. However, in the late June and late-August emergence peaks *T. vilipennis* was predominant.

The abundance and biomass of other less abundant species is given for each sampling in table 6.3.

Station 3

Chironomus spp. larvae were found in mid-April and subsequently disappeared until small larvae were first caught in mid-June. This latter cohort grew until, by late-August, most larvae were 20-26 mm long;

the larvae then largely disappeared. Small larvae were later found in mid-September and October (figure 6.2). In the emergence, *C. plumosus* was caught from the beginning of sampling until June. From this time onwards *C. cingulatus* was caught with an emergence peak at the end of June. Secondary emergence peaks for *C. plumosus* occurred in mid-July and mid-August. Emergence sampling was discontinued before the larval loss at the end of August.

The population dynamics of *Polypedilum nubeculosum* at this station was the same as that at station 2 with larvae abundant for a short period. However, larvae at this station were most abundant at the end of June and subsequently rapidly disappeared. *P. nubeculosum* adults were caught in the emergence trap in abundance at the end of April and again at the end of June with a subsidiary peak in mid-July. At other times individual adults were occasionally taken. As at station 2, development occurred rapidly and no obvious growth curve was discernible (figure 6.3).

Procladius larvae showed a persistent pattern of decreasing abundance from early April until the end of May. Low numbers of larvae were present until a major recruitment of small larvae occurred in early September. A decrease in abundance of 8-10 mm larvae occurred in August and September (figure 6.4). Adult emergence peaks occurred in early June and July although minor fluctuations did occur in the whole period throughout which near continuous emergence occurred. For the first peak, larvae had almost completely disappeared from the benthos before the main emergence whilst throughout July few larvae were present. Almost all larvae were probably *P. choreus*.

Tanypus larvae were present equally abundant from the start of sampling until the end of May; these disappeared by the next sampling in mid-June (figure 6.5). Low but increasing numbers of larvae were caught until mid-August when a second decrease occurred. Few larvae were caught up to the time sampling was discontinued on 2nd October. Peak emergence of *T. punctipennis* was in late May and early June with emergence continuing at fairly high levels until the end of June. A second emergence peak occurred in August. *T. vilipennis* was only caught in low numbers in early June.

The numbers and biomass of less abundant species are given in table 6.4.

Station 4

Only three larval taxa were abundant at this station; *Chironomus*, *Procladius* and *Tanypus*. The abundance and biomass of less abundant species are given in table 6.5.

Chironomus larvae were present at low densities until mid-June when an influx of young larvae occurred. These grew until the end of July and then disappeared. The remaining large larvae were augmented by a number of small larvae but no large increase occurred (figure 6.2). The emergence was predominantly of *C. cingulatus* until August when a number of *C. plumosus* were caught. The peak emergence of *C. cingulatus* was in July although it continued from the end of May until August.

Procladius larvae were present in most length classes throughout the sampling period. During the period 4th April until 17th May smaller larvae grew to a length of 7-8 mm; at the following sampling the larger larvae had disappeared (figure 6.4). A group of small larvae were caught on 14th June but the population remained low until a major recruitment of small larvae occurred in September. Adult *Procladius choreus* were caught in very high numbers in early June with a secondary smaller peak in early and late July.

Tanypus larvae were only abundant during August at this station with few larvae present at other sampling times. These larvae had disappeared by early September (figure 6.5). An emergence peak of *T. punctipennis* occurred in mid-June when few larvae were present. Only a few adults were caught in late August. No *T. vilipennis* were caught at this station.

Larval Dispersion Patterns

The sample means and variances from each sampling station were plotted on log-log scales. Since there was no marked differences between stations at Black Horse the data were plotted on one graph (figure 6.6). The values of the coefficients of the fitted regression lines are tabulated (table 6.6).

It is apparent from the graphs (figure 6.6) that at higher densities each species at Black Horse tended to become contagiously distributed with a near random distribution at lower densities. The data for Congleton (figure 6.8) are based on few samples all with a high variance and over a restricted range of mean abundance values; the regression was not significant ($P > 0.1$).

The plots of Lloyd's index of aggregation $\overset{*}{x}$ against mean density show a similar pattern to that of the Taylor plots (figure 6.7 & 6.8). However, only in *Procladius* and *Polypedilum* at Black Horse was there a tendence for $\overset{*}{x}$ to increase proportionally more than mean density. Both *Tanypus* and *Chironomus* showed a near equality between $\overset{*}{x}$ and $\bar{x}$. The data from Congleton clearly show that $\overset{*}{x}/\bar{x}$ tends to decrease at higher larval densities. The values of the intercept also differ between the two pattern types seen at Linford with *Procladius* and *Polypedilum* having values close to zero indicating that there is no natural aggregation at low densities. In contrast *Chironomus* and *Tanypus* had values of 0.99 and 0.61 respectively indicating that these species have a natural tendency to aggregate even at low densities. The regression values are tabulated (table 6.7).

Gut Contents Analysis

The proportion of each food category in the gut contents for each species is given in table 6.8. From these the values of $\sum_h P_{ih}.P_{jh}$ for i and j = 1-5 were calculated. The values on the main diagonal of the matrix of these values (table 6.9) are equal to $\sum_h P^2_{ih}$.

From this matrix the values of α_{ij} and α_{ji} were calculated (table 6.10). These values are plotted to give a graph of the food resource segregation. Only one pair showed a value of α_{ij} close to unity (figure 6.9), this was for the genera *Chironomus* and *Polypedilum*. Since the point falls close to the graph of $\alpha_{ij} = \alpha_{ji}$ both genera also had equal niche breadths. The points for species pairs 3,5 and 1,5 fall below the diagonal indicating that the second member of the pair had a wider niche breadth ($\sum_h P^2_{jh} > \sum_h P^2_{ih}$). However, these pairs had α_{ij} and α_{ji} values less than 0.5 and therefore were considered to show trophic segregation (Ramcharan and Paterson, 1978).

DISCUSSION

Changes in the larval population of *Procladius* during the summer period at Congleton showed a similar pattern to that in 1977 with peak densities of small larvae occurring at three times during the year. However, the population of *Chironomus* larvae showed a steady decrease from an initial period of high abundance such that, from August onwards no *Chironomus* larvae were caught. This contrasts with 1977 when *Chironomus* larvae were abundant in the deeper water stations throughout the year and in increasing numbers from August to September (figure 5.3). The reason for the absence of *Chironomus* from this lake in autumn 1978 remains unexplained.

At Black Horse Linford, the numerical abundance of larvae was much more constant than in 1977 (see tables 6.2, 6.3, 6.4 and figure 5.6). The precipitous drop in larval densities of the previous summer was not observed. The numerical constancy resulted from the presence of summer generations of *Chironomus*, *Polypedilum*, *Procladius* larvae with an increased abundance of *Tanypus* in the spring when other larvae were decreasing in abundance due to emergence. The abundant species present, and their distribution, were the same as in 1977. *Chironomus* larvae showed a summer generation at all three stations, although at station 4 it was slightly earlier than at the other two.

Polypedilum larvae were abundant in July and rapidly completed their life cycle during a period just after final instar *Chironomus* larvae were least abundant following emergence.

Procladius larvae showed a similar pattern of abundance to that in 1977 with low numbers present during the summer period. This is in contrast to the pattern at Congleton where they were present throughout the summer months.

The abundance of *Tanypus* larvae showed a distinctly different pattern from that of the other species, larval numbers in both 1977 and 1978 were found to increase rapidly in spring and then maintained high densities until May/June. Larval growth therefore appears to occur in the spring months since overwintering larvae were not found.

The agreement between changes in larval density and timing of adult emergence was much better in 1978 due mainly to an increasing frequency of sampling. However, certain discrepancies were apparent. For example, *Procladius* larvae had almost entirely disappeared from station 3 before the main emergence at this station commenced. Thus, even with a sampling interval of two weeks, adequate data for the prediction of emergence from larval densities and growth patterns was not obtained in all cases. However, in most instances the agreement was sufficiently accurate to justify the calculation of production:emergence ratios from larval cohorts.

The gross pattern of larval abundance and distribution within a lake are only one aspect of a population ecology study. Indeed, macro-distribution is a descriptive phenomenon and does not indicate the causative effects. Spatial separation and temporal separation are two means of coexistence but are generally caused by underlying factors. Microdistribution pattern is also important as it often indicates the limiting resources by the way in which an animal exploits its habitat. Perhaps the main factor for most populations is the partitioning of available foods. These two aspects, microdistribution and food, were investigated to provide some insight into the causation of observed pattern.

The regression coefficients of the Taylor Power Law equations all show an intercept value (a) not significantly different from zero ($P > 0.05$), this indicates that at low densities the distribution of the animals is random. However, the values of the b coefficient were significantly different from unity ($P < 0.05$) in three of the four genera. Only *Chironomus* had a b coefficient which was not significantly different from unity. This is in agreement with the investigation of Edgar and Meadows (1969) where the spatial distribution of *Chironomus* larvae was investigated by nearest neighbour methods. They also found that this species showed a random distribution. However, the dispersion pattern was only investigated at one density.

Taylor et al. (1978) fitted the Power Law to 156 sets of data and found that most had a b coefficient greater than unity. The mean b value for all samples was 1.45 and the range 0.4-2.8. Of the three genera here with $b > 1$ ($P < 0.05$), *Polypedilum*, *Procladius* and *Tanypus*, the first is tubiculous whilst the latter two are errant. Spatial pattern is thus not apparently determined directly by motility. However, *Chironomus* larvae are much larger than any of these three species and it is well known that observed spatial pattern is a function of the size of the sampling unit (Poole, 1974). Since territory size is a function of body size, the sampling unit is of different effective size for these two groups and the difference in the significance of the b value may therefore be due to the sampling method rather than reflecting actual differences in dispersion pattern.

From these data it is apparent that the stock density of larvae will not be reliably estimated by a single sample due to the high variance caused by aggregation. For an accurate assessment of larval density it would have been preferable to collect a larger number of smaller samples. However, high densities were usually caused by a large number of small larvae and thus the effect of numerical inaccuracies on the biomass estimates will be minimal.

The Iwao plots of mean crowding against mean abundance showed a value significantly different from zero for *Procladius* at Congleton where the value was 6.56. This coefficient is indicative of the number of individuals a single larvae would be expected to be clustered with at very low densities ($\bar{x} \approx 0$). Thus at this site individuals are clustered; all species at Linford were not clustered ($\overset{*}{x} = 0$ at $\bar{x} = 0$, $P > 0.05$) except *Tanypus* for which $\alpha = 0.99$ ($\overset{*}{x} = 0$ at $\bar{x} = 0$, $P < 0.05$). The slope β is a measure of the way the clusters are distributed within the habitat. Thus, since these two coefficients are essentially independent, a species may be aggregated with respect to either or both aspects i.e. clustering at low densities or showing a tendency for clustering to increase with larval density.

The random expectation is for $\beta = 1$. This was found for *Chironomus* and *Tanypus* at Linford and *Procladius* at Congleton. *Chironomus* distribution was not contagious with respect to either α or β measures of crowding and its distribution is therefore random. Both *Tanypus*, and *Procladius* at Congleton, were found to be contagious with respect to the distribution of individuals but not with respect to clusters since mean crowding did not increase with mean density. In contrast *Polypedilum*, and *Procladius* at Linford, were not found to be clustered at low densities but at higher densities the individuals were aggregated ($\beta > 1$, $P > 0.05$).

The F-ratio of the analysis of variance of the regression was much higher in the Iwao plots than in the Taylor plots (table 6.11) and this was undoubtedly due to the strong influence of mean abundance ($\bar{x}$) on mean crowding ($\overset{*}{x}$), and the constraint

$$\overset{*}{x} \geqslant \bar{x} - 1$$

which inevitably leads to a fortuitously strong correlation since the two variables are not independent measurements on the population as are the mean and variance.

Shiozawa and Barnes (1977) have shown that dispersion patterns change during the life cycle of a species of chironomid. This change has also been shown by George (1974) for zooplankton; in addition pattern also changed during the two years of his study.

As mentioned previously the dispersion patterns may be age dependent, the periods of high abundance being caused by young larvae which subsequently became less abundant and concomitantly less aggregated. However, the detection of non-random distributions is not an end in itself, its importance is as an indicator of the factors controlling the distribution of individuals. For sedentary tubiculous species the behavioural reaction to other individuals will be of prime importance in a uniform habitat and the cost of moving and building a new tube must be balanced against the deletrious effects of overcrowding. Errant larvae will respond to small scale, temporary variations in habitat in addition to showing general random dispersal inherent for all mobile animals. Aggregation in such species will be a measure of the microheterogeneity of the habitat with respect to a major resource such as food.

McLachlan (1977) showed in a series of laboratory experiments that at very high larval densities the distribution of individuals became regular. Since territory size is fixed for a particular larval instar this pattern maximised the amount of habitat available. However, he commented upon the fact that in a field situation of larval densities up to 10,000 larvae m^{-2} adequate space would still be present for colonisation by more larvae. Thus one would expect a random distribution for tubiculous larvae at lower densities; this is borne out by the present study.

Since *Chironomus* larvae feed mainly on detritus which is spread uniformly throughout the habitat a random distribution would be expected. However, *Polypedilum* larvae also feed on the same foods in the same proportions as *Chironomus* but were found to become aggregated at high densities. This may be a function of their rapid life cycle such that larvae do not disperse as evenly from initial aggregates or they may be displaced from areas where *Chironomus* larvae live. Cantrell and McLachlan (1977) have shown that larvae of *Tanytarsus gregarius* are displaced by 4th instar *Chironomus plumosus* larvae and were consequently found mainly in newly flooded areas where the latter species was not yet established.

Final instar larvae of both *Procladius* and *Tanypus* are errant. The former was mainly carnivorous feeding on small Crustacea whilst the latter genus was herbivorous feeding mainly on algae with very little detritus present in the diet. The aggregation of *Tanypus* may be caused by patchiness in the algal populations on the sediment surface. However, the pattern of *Procladius* is not so easily understood and it seems probable that aggregation in this species may have been caused by prey patchiness which is in turn caused by the microhabitat heterogeneity in respect of primary production.

Thus dispersion patterns are largely a function of food availability and pattern of the major food of an organism; this is not surprising for freshwater animals living in a medium which protects the individuals from extreme abiotic conditions, in terrestrial organisms the dangers of dessication, freezing, etc. will pose additional constraints upon dispersion patterns.

Of the five genera for which gut contents were examined a distinct difference was found in all except the pair *Chironomus* and *Polypedilum*. Field observations indicate that *Polypedilum* is most numerous just after final instar *Chironomus* larvae were least abundant. These two species may avoid competition by using the same resources at different times. However, densities of these two genera did not reach sufficient levels to use all of the available food resources, so coexistence would be theoretically possible.

The gut contents of the five genera analysed are in agreement with that reported by other workers. Walshe (1951) reported that *Chironomus* (*Tendipes*) larvae fed on the mud in vicinity of their tubes. This produced an area of different texture and this has been used by McLachlan (1977) in his study of spatial dispersion. Kajak and Warda (1968) postulated, from an analysis of algal cell abundance both in the sediment and in *Chironomus* larval foreguts, that they were selective feeders taking algae in preference to detritus. However, algal abundance at the sediment surface was assessed using the top 1 cm of the mud layer; since algal density decreases rapidly with depth this will undoubtedly have provided an underestimate. More recently Baker and Bradnam (1976) have calculated that *Chironomus* larvae could live on the bacteria ingested with the detritus. A more reasonable view, in light of the territorial habit of these larvae is that they are of necessity nonselective feeders. Constant selective grazing of one area would soon reduce the algal population to a low level and thereby force the larvae either to ingest detritus or to move, the former option being chosen in most cases. This same argument applies to *Polypedilum* larvae. Thus feeding strategy is intimately related to the tubiculous habit.

In contrast, *Tanypus* larvae were highly selective feeders consuming single celled and filamentous algae. This is in agreement with the data of Olah (1976) where algae were the major food source of the larvae and stands in contrast to the widely held view that all final instar larvae of the sub-family Tanypodinae are predatory (Wesenberg-Lund, 1943). The herbivorous habit of this genus explains the observed temporal pattern of abundance within Black Horse lake. Larvae are absent in winter but in spring, coincident with the commencement of algal growth, they reappear in high densities.

The two predatory larval genera *Cryptochironomus* and *Procladius* avoided competition by exploiting different resources. Armitage (1968) reported that in freshly killed *Cryptochironomus* larvae, oligochaete chaetae were the only solid food remains found. However, if samples were kept alive before sorting,chironomid remains were also present in the guts. The data here for freshly processed samples support the view of Armitage that in the field this genus feeds predominantly upon oligochaetes.

Kajak and Dusgoe (1970) found that *Procladius* larvae fed on chironomid larvae or crustaceans. No chironomid remains were found in the guts sampled here, however this may have been due to the low number of larvae considered or the time of sampling since small larvae are only present for restricted periods of the year.

In terms of gross pattern within Black Horse lake, the presence of *Chironomus* at all three stations can be understood in terms of the ubiquity of its food resource. In contrast, *Tanypus* larvae are dependent upon the benthic algae and would be unable to exist in the main lake during periods when the sediment had been disturbed by wind causing a high turbidity in the water. They are therefore limited to the more sheltered lagoon area. The absence of *Polypedilum* from station 4 may have been due to the earlier establishment of *Chironomus* larvae there.

Cryptochironomus and *Procladius* larvae were present at all stations since their respective foods (oligochaetes and crustacea) were also widespread.

Spatial and temporal abundance patterns in the chironomids considered here are thus a result of two principle factors,

i) The partitioning of the food resources

ii) The life cycle of the species

and the previous description of the larval populations can be understood in terms of these causative effects.

CHAPTER 7

CHIRONOMID PRODUCTION IN 1978

The analysis of interactions between existing populations as described in the previous chapter answers the question of how the energy resources in the habitat are partitioned. However, actually to quantify the energy flow the production of the predominant species must also be measured. In terms of the ecosystem, production is the means by which energy is assimilated in one trophic level from others and as such is of prime importance in both research work and practical resource management. Since freshwater fish populations rely largely upon macroinvertebrates as food, the production of the latter will be of direct relevance to fisheries management.

Waters (1977), reviewing secondary production in inland waters, pointed out that most interest in such studies has been the direct result of the stimulus of the IBP. The synthesis of effort into studies of whole ecosystems has greatly advanced our knowledge of community and trophic level interactions.

The calculation of production from length-frequency data forms the third section of this chapter. Firstly, however, the sampling efficiency is considered and length-weight relationships discussed.

ASSESSMENT OF SAMPLING METHODS

The calculation of standing stock and production are dependent upon accurate sampling of the population being studied. The retention of larvae during sieving has been shown by Jonasson (1958) to be dependent upon the width of the larval head capsule. Thus by analysing the data for head capsules retained by the sampling procedure it is possible to determine the length range of each species which is quantitatively retained.

Head capsule widths and body lengths were measured from larvae collected in 1977. Specimens had been preserved for c. 1 month in

Carnoy's fluid before analysis. Head capsule widths were plotted against body length for each larval genus.

All larvae with head capsules wider than the sieve mesh aperture will be retained. In addition many larvae with smaller head capsules will also be retained but not quantitatively. Although head capsule width is the critical factor for quantitative retention, the larger individuals of earlier instars are more likely to be retained than smaller individuals, hence the transition point for absolute retention of each length class can be estimated from the scattergrams of head capsule width against body length. Animals shorter than this critical length (minimum lengths) (table 7.1) were not quantitatively retained.

The calculation of sieve efficiency is of crucial importance in studies of production of any macroinvertebrate group. However this process is hindered by the necessity to collect larvae of each instar and size group of each species and then sieving the samples. This process is both time consuming and difficult to carry out, since larvae of earlier instars are usually only present in the benthos for a short period.

The method used here, based on the finding of Jonasson that head capsule width is the critical dimension for quantitative retention, is more readily accommodated within an investigation as it utilises information that is usually gathered routinely. Most estimates of standing crop and production are based on either body length measurement and the subsequent calculation of weight from regression equation parameters or by direct weighing. Biomass estimates are not markedly affected by the absence of smaller larvae. However, if production is calculated by loss-summation methods then erroneous negative values will be introduced if larvae smaller than those quantitatively retained are considered in the calculations. In particular, the Hamilton (1969) modification of the Hynes and Coleman (1968) method, in which negative losses are considered, will be biased towards an underestimate. The minimum length values for quantitative retention were all similar for Linford and Congleton. A small reduction of sieve size would not substantially affect the length range caught since the time spent in earlier instars is comparatively brief (Carter, 1976) and growth in body length is approximately linear. The retention of all 3rd instar larvae and second instars of some species would only reduce the minimum length to c. 4.5 mm, this could have been achieved by using a 0.125 mm sieve. However, a fine mesh sieve would have dramatically increased the time to process samples due to the high proportion of sand in the sediment.

DETERMINATION OF LENGTH-WEIGHT RELATIONSHIPS

The determination of dry weight by killing and drying live larvae is usually impracticable for most freshwater macroinvertebrate population studies. The need to measure body length and head capsule width to determine growth rate and for instar analysis require prior killing of the sample. Furthermore, the large number of consecutive samples taken make it impossible to sort and weigh all the animals in sufficiently short time to prevent mortality and predation within the sample. To overcome this, samples were sorted as rapidly as possible following collection, always within 24 hrs.

Preservatives cause marked changes in dry weight depending both on the actual preservative and the time of storage. Dermott and Paterson (1974) have shown that 70% ethanol causes significant loss of dry weight (up to 50% loss) whilst in formalin, after an initial decrease, the animals increased in dry weight and after 7 weeks weighed more than before preservation. More recently Donald and Paterson (1977) have shown that the blotted wet weight in alcohol-preserved specimens did not change over 150 days in three of four species investigated, the fourth, *Tanytarsus barbitarsus* lost 40% of its wet weight.

Alternative methods used have been based upon the measurement of body length which does not significantly change in preservatives (Mackey,

1977) and the use of a length-volume relationship or an empirically derived length-dry weight regression. The latter option, also chosen by Johnson and Brinkhurst (1971) was employed.

Larvae were collected and separated from sediment. They were then kept overnight in a dish of lake water to allow their guts to empty. Individual larvae were then identified whilst still alive, then killed by immersion in 50% alcohol for 20-30 seconds and measured immediately. After being measured the larvae were transferred to aluminium planchettes and oven dried at 60°C for 12-24 hrs. Dermott and Paterson (1974) have shown that the time taken for drying the larvae, within the range 6-117 hrs., does not significantly alter the dry weight. Dried larvae were stored in a dessicator and weighed on a 5 mg capacity torsion micro-balance.

The length-weight coefficients $\underline{\alpha}$ and $\underline{\beta}$, the number of observations and the range of lengths included in the regression are given in table 7.2. These relate the length in mm to the dry weight in mg. Comparison of the regression coefficient $\underline{\alpha}$ with those obtained by other workers was not possible since the units in which the two regression variables were measured were often not stated. However the value of $\underline{\beta}$ is not affected by the units of measurement since it represents the pattern of growth in weight with respect to length and is dimensionless.

Mackey (1977) found that for larvae which matured at lengths less than 12 mm the value of $\underline{\beta}$ was proportional to length at maturation. However, for many of his smaller animals the samples were only of, at most, 20 individuals which may have caused errors. In addition, the larvae were preserved in formalin for a few days before measuring. This may have resulted in a marked weight loss (Dermott & Paterson, 1974) depending upon the time between preservation and weighing. Values of $\underline{\beta}$ less than 3 indicate that growth was allometric with individuals increasing in length more than in body diameter. However Mackey's

(1977) values of < 2 seem exceptionally low. Johnson and Brinkhurst (1971) obtained highly variable values of $\underline{\beta}$ for larvae of the genus *Chironomus*. This was probably due to chance since their regressions were in all cases based on less than 10 individuals.

The values of regression parameters obtained from a limited length range is seen in the *Chironomus spp.* coefficients ($\underline{\alpha} = 1.38 \times 10^{-5}$, $\underline{\beta} = 6.31$) for samples from Congleton. The coefficients of other species, based on a representative length range all have a $\underline{\beta}$ value > 2, with most being close to three, the value expected if growth is isometric and dry weight is a constant function of volume.

CALCULATION OF PRODUCTION

Until recently the calculation of production of organisms with asynchronous generations was virtually impossible. Most methods (see Waters, 1977) relied upon the identification of a distinct cohort of individuals such that change or loss of biomass between sampling periods could be estimated.

In 1968, Hynes and Coleman described a procedure whereby the losses of individuals between length classes rather than over a time period were used to estimate production. Their original description, however, contained several conceptual errors which were subsequently corrected by Hamilton (1969). This method has been widely used and found to produce estimates comparable with those obtained by other methods (e.g. Waters & Crawford, 1973).

The relationship between production (P) and standing crop (B) has been widely calculated, indeed it has been used to calculate production in some cases, and is known as the turnover ratio. Empirically derived values have indicated that this ratio is sufficiently constant to enable fairly accurate production estimates to be derived from standing crop data. A more recent concept, proposed by Spier and Anderson (1974), is the use of a P:E ratio; where E is the biomass of emergence of the species concerned. They found that this ratio was fairly constant for stream simuliid populations and ranged from 4-5. They also provided some data for chironomid populations where the estimates were more varied. In view of the gross discrepancy between emergence estimates between different trap types this is not entirely surprising. This ratio was calculated from the data gathered in this study and from published data of Potter and Learner (1974).

Methods and Results

Total biomass was calculated from the length frequency data presented previously for each sampling occasion. For those larval genera for which a length-weight relationship was not available the parameters chosen were those of another genus with a similar maximum body length.

Production and biomass of individual larval genera were calculated using Hamilton's (1969) modification of the Hynes and Coleman (1968) method. Only larvae longer than 6 mm were used in the calculations since any less than this length were not quantitatively retained. Emergence biomass was calculated from emergence trap catch using the dry weights of adults given in Potter and Learner (1974: table 6). Weights for *Polypedilum nubeculosum* and *Tanypus spp* were assumed to be the same as that of *Procladius choreus*.

The production, biomass and emergence are presented in table 7.3, the units used are kg, ha and years. In addition the P:B and P:E ratios are also given. Annual biomass pattern is shown in figure 7.1.

The production of *Chironomus spp* is much lower in this study than that of 129 kg $ha^{-1}yr^{-1}$ reported by Jonasson (1972) for Lake Esrom but similar to that found by Potter and Learner (1974) at Eglwys Nunydd reservoir of 35 kg $ha^{-1}yr^{-1}$. Lake Esrom is a highly eutrophic lake in which *Chironomus anthracinus* predominates.

In Loch Leven, Scotland, production of common species was much higher than here, ranging from 100-400 kg ha^{-1} yr^{-1} depending upon species (Maitland & Hudspith, 1974). Production of *Polypedilum*, *Procladius* and *Tanypus* at Linford were much lower than that of *Chironomus*, and similar to the values reported by Laville (1971) for species inhabiting an oligotrophic lake in the Pyrenees.

Total production for the abundant benthic larvae was between 45-70 kg $ha^{-1}yr^{-1}$. Potter and Learner (1974) reported an annual production of 210 kg ha^{-1} dry weight in Eglwys Nunydd and this was similar to values from other eutrophic lakes; Lake Esrom had a production of 160 kg $ha^{-1}yr^{-1}$ dry weight (Jonasson, 1972) and Maitland and Hudspith (1974) reported production estimates of between 150-420 kg $ha^{-1}yr^{-1}$ dry weight in the sandy littoral area of Loch Levan whilst Charles et al. (1974) found production to be 335 kg $ha^{-1}yr^{-1}$ for the muddy area of the same lake.

The P:B ratios calculated fell into two distinct groups; the values for *Polypedilum nubeculosum* and at station 4 for *Tanypus* were c. 2.5, all other values were greater than 4. The first group coincided with cases where the larvae were only present for a short period during the year. P:B ratios of a similar magnitude were reported by Potter and Learner (1974) for univoltine species. Likewise they found a ratio of c. 5 for bivoltine species. The P:E ratio was less constant than that of P:B with values ranging from less than one to 7.0. The values obtained for the P:E ratio by Potter and Learner, (1974), using a correction factor of 7.95 to convert submerged trap catch to surface trap catch (based on the relative catch between traps when the two were used concurrently in that study), also cover a wide range varying from 0.64-13.8; however most values were between 2-6.

DISCUSSION

The low larval production calculated here reflects an overall lower level of productivity in the lakes since chironomids are the most abundant invertebrates present. Whilst larval production was only calculated for larvae longer than 6 mm this would not be expected seriously to bias the estimate. Kimerle and Anderson (1971) calculated that production during the first larval instar of *Glyptotendipes barbipes* (Staeger) was only 5% of the total cohort production. Similarly, Maitland et al. (1972) reported that the loss of *Stictochironomus* larvae through a 0.5 mm sieve only accounted for 3% of the annual production of that group. The production estimates presented here should not be seriously biased due to the sieve mesh used. The sampling period during 1978 was restricted to the period from early April until early October. This coincided with the period of maximum growth of the larvae and also covered the period of emergence. During the months November-March water temperatures were much lower and production therefore markedly less. Furthermore, the agreement of P:B ratios with those from other studies supports the deduction that the shortened sampling period did not bias the estimates of production.

The proposal of Ilies (1971) that emergence was a constant proportion of production, and thus could be used to estimate the latter, is supported by the data presented here. Most values were between 2-3, as were a number of those calculated from the data of Potter and Learner (1974). However the value of 0.6 obtained in this study is indicative of trapping error since clearly adult emergence cannot exceed production over the whole of the lake. Furthermore, the range of P:E ratios for the same species at different stations at Black Horse lake indicates that the ratio is partly a function of trap site: note that, with the exception of *Tanypus* at station 4, the P:E ratio declines from stations 2-4.

Between one third to one half of the annual production is exported from the lake in adult emergence assuming that the emergence traps are 100% efficient. This is in agreement with the findings of Jonasson (1972) who reported that c. 50% of the annual production of *Chironomus* *anthracinus* emerged from Lake Esrom. This high level of export will limit that amount of the production available to fish and other aquatic predators. This also indicates that larval losses before emergence are relatively low. In Black Horse lake the only common fish is the bream (*Abramis brama* L.) which is a benthic feeder (Kennedy & Fitzmaurice, 1968) and does not take insects in the water column. Predation on ascending pupae such as by trout would undoubtedly lower the P:E ratio, trout are however absent from this lake.

Predatory insects were also scarce in the muddy sediments, hence larval losses via predation are probably fairly low.

The production of the sand pit at Congleton was very low. This was due to the low number of larvae present and the absence of *Chironomus spp* during the summer of 1978 since this latter species contributed significantly to the total production at the other site.

Production estimates are important in indicating the major pathways through which energy flow occurs in the chironomid communities. Thus whilst *Chironomus spp* larvae were not as abundant as other species they accounted for most of the production in the habitat. Their *per capita* functional role is thus greater than that of other smaller species. Whilst the production of *Chironomus spp* in this gravel pit is low in comparison with other lakes it is nonetheless the nutrient poor detritus which is the major food resource and is probably the limiting factor in production in the gravel and sand pits.

CHAPTER 8

CHIRONOMID EMERGENCE IN 1975-1978

SHORT TERM CHANGES IN EMERGENCE

The amount of scatter of successive daily estimates of emergence was seen to be fairly large in the 1975 data. Two alternative explanations exist to account for this effect:-

i) trapping error

ii) response of animals to environmental cues.

The former explanation is held to be true by Morgan (1971) who states that "erratic numbers of insects in traps from day to day are an indication that they are not functioning properly...". However, it has previously been noted that the timing of emergence is geared to environmental parameters such that the peak emergence is delayed by adverse weather conditions. Besides these long-term responses to weather conditions perhaps climatic factors may also account for the observed daily fluctuations.

Methods

The 1975 data showed a constant rise in numbers of imagines caught during the period 21st May until 13th June, with daily fluctuations superimposed. The number of insects caught each day for which the trapping period was 24 hrs. was extracted and used as the dependent variable in a multiple regression analysis. The dependent variables used were:-

i) days from start of period

ii) hours of sunlight in trapping period

iii) wind speed during trapping period

iv) maximum temperature during period

v) minimum temperature during period

These meteorological data were abstracted from the daily weather observations taken at Cardington, North Bedfordshire, the nearest meterological station. The data were run under SPSS at Manchester computer centre.

Results and Discussion

The results of the regression are presented in table 8.1, these include the steps at which the named variable was included, the F-value associated with entry, the significance, the multiple R-value and overall F-value.

From these results it can be seen that only the first two variables entered contribute significantly to the proportion of the sum of squares of numbers caught; this is measured by the multiple R statistic. Whilst the overall F-value continues to decline markedly this does not signify a similar pronounced improvement in the significance of the regression due to the associated change in degrees of freedom.

It is therefore apparent that the most important factor influencing emergence is the natural development cycle of the animal which is determined by the number of day-degrees experienced in the larval stage (Mundie, 1957). However, the discovery that the hours of sunlight also influences emergence ($P = 0.17$) is of interest since in these shallow lakes the light intensity changes will be readily detected by benthic animals. In contrast changes in temperature and wind speed will not cause such obvious changes in the physical habitat. This argument does not apply to deep eutrophic lakes where the light is attenuated rapidly in the surface layers. Sunlight is known to be a cue used to synchronise emergence in certain species (Palmen, 1955; 1958) but its use in this context to delay emergence has not been reported previously. Diapause in winter has been shown to be caused by a number of temperature/photoperiod regimes (Danks, 1978) and this has often been interpreted as a means of synchronising population growth (Corbet, 1964). Danks (1978) has shown that photoperiod controls the transformation from larva to pupa. Daily variations in photoperiod thereby enable the imagines to emerge when conditions are most favourable.

LONG TERM CHANGES IN EMERGENCE

The initial survey of insect emergence in 1975/1976 (chapter 4) sampled different stations during these two years. Whilst it indicated the extent and nature of spatial variation in emergence the data could not be used to follow changes from year to year although there was some indication that emergence occurred earlier in 1976 due to the higher temperatures in the earlier months of that year. This initial survey did however provide a basis for the choice of sampling sites for the main study in 1977 and 1978. The aims of this investigation have been outlined in the chapters on larval populations with the choice of stations such that the data would be comparable with those collected in 1975. The sites sampled in 1975 (stations 1 and 5) which were subsequently discarded were above vegetation and the difficulties of sampling larvae from such habitats precluded their inclusion in the detailed study.

The emergence in 1977 and 1978 was investigated in parallel with benthic sampling in order to correlate adult emergence with larval growth patterns; the detailed description of the emergence of the predominant species in the benthos was included in chapters 5 and 6 and is not further discussed here. The periods for operation of the traps are given in the methods sections of chapters 4, 5 and 6.

This chapter is concerned with the temporal changes in emergence between years and the variability between trap sites. In addition, the discrepancy for certain species between larval abundance and emergence trap catch is considered.

Methods

The positions and trap types used have already been described in chapters 4, 5 and 6. In 1977 and 1978 traps were sited at stations 2, 3 and 4 of those used in 1975 (table 4.1). The similarity in emergence between trap stations during the same month and between months for the same station was calculated using the index of Raabe (1952).

Results

Total emergence catch

The emergence data for all species calculated as numbers m^{-2} day^{-1} was plotted (figure 8.1). Due to the different trapping intervals used (varying from daily to weekly visits) between years the actual abundance estimates can only be considered as approximations. However, it is apparent that the numbers caught at the time of peak emergence were approximately constant throughout the four years of the study.

The advancement of the timing of peak emergence in 1976 over 1975 was also seen in 1978 when most adults were caught at the very beginning of June. In 1977 there was an increased emergence at this time but the peak which occurred in early June was not the overall maximum. The decline in emergence in the second and third weeks of June in that year coincided with a period of high rainfall, overcast conditions and low temperatures (figures 4.3 and 8.2). The numbers caught then increased dramatically and peak emergence occurred at the end of June.

The overall pattern of emergence in 1976 was simple; a peak occurred in June and numbers then declined and remained at low level until sampling was discontinued in August. In contrast, that of the following years was more complex. In 1977, three abundance maxima were apparent with the first two separated by a period of hard weather and the third was in late July. However, in 1978 also, in the absence of adverse climatic conditions, the emergence occurred in a series of peaks. The first, and main, emergence was at the beginning of June with minor peaks in mid- and late-June and mid-August. These peaks were attributable to a large emergence of one or two common species. Furthermore, in 1977 and 1978 the emergence continued at much higher levels than in 1976 during July. Whilst this latter observation may be, in part, due to differences between sampling stations the data for the ubiquitous and abundant species, *Procladius choreus* and *Tanypus punctipennis*, also differed between 1976 and 1977/78.

The data for 1977, where peak emergence was delayed, indicated that the timing of pupation and eclosion are open to modification dependent upon environmental cues. Insects emerging at the lake surface during heavy rainfall would suffer a high mortality. Furthermore swarming would be disrupted. However, insects would be able to emerge successfully into a trap, thus the emergence will not be underestimated in such conditions and the delay of peak abundance was a real effect attributable to climatic conditions.

Emergence of abundant species

a) *Cricotopus intersectus*

The emergence pattern of this species changed markedly between years (figure 8.3) although the patterns in 1975 and 1976 resembled each other. In 1977 peak emergence did not occur until the end of July with only a minor peak present at the time of the main emergence peak of the previous year in early June immediately preceeding the period of bad weather. In 1978 the early emergence peak at the beginning of June was followed by a second at the end of the month. Numbers caught throughout July and August were again much higher than in 1976.

b) *Cricotopus sylvestris*

The only notable change in emergence pattern of this species during the study period was the delayed emergence in 1977 when adults did not attain maximum numbers until the beginning of July (figure 8.4). In 1978 emergence occurred slightly later than in the first two years but timing and duration were fairly similar.

c) *Procladius choreus*

The emergence pattern of this species varied widely over the four years (figure 8.5). In 1975 peak emergence was in mid-June whilst the following year it was in mid-May. In 1977 two peaks occurred, the first at the beginning of June and the second in mid-July. In 1978 the early June peak was the only period of high abundance. This species was also abundant in the benthos where it accounted for between 16-34% of the larvae present. It therefore appears that abundant species may undergo large fluctuations in numbers between years with an abundant summer generation present in some years but not in others.

d) *Tanypus punctipennis*

The emergence maxima of this species occurred in late-May/early-June in 1975 and 1976 (figure 8.6). This pattern was also found in 1978. In 1977 peak abundance was not achieved until late-June. This delay was probably due to adverse weather in that year. However, during 1977 and 1978 one further change was seen in comparison with 1976; that of a second emergence peak in July/August. In the last two years of this study *T. punctipennis* completed two generations each year with a rapid summer generation between June and July/August.

e) *Chironomus cingulatus*

The emergence maxima seen in 1975 and 1976 were not apparent in the following years (figure 8.7) when emergence occurred at a low level from mid-June in 1977 and late-May in 1978 until early August. This near continuous emergence was caused by difference in the timing of peak adult abundance at different trap stations (chapters 5 and 6).

f) *Chironomus plumosus*

This species emerged earlier than *C. cingulatus* with most imagines present during May (figure 8.8). However a number of adults were also caught later in the year in 1976 and 1978 during July and August. This latter peak was not seen in 1977.

g) *Einfeldia dissidens*

With the exception of 1977, when emergence was delayed until July (figure 8.9), peak abundance occurred in mid-June. Only one maximum was seen each year indicating that this species was univoltine. The dramatic increase in abundance in 1976 was undoubtedly attributable to the position of the traps in that year.

h) *Endochironomus albipennis*

The emergence peak of this species showed a persistent change during the course of this study. In 1975 maximum abundance occurred in May, the following year in late June and then subsequently in July, with another peak in August (figure 8.10).

i) *Glyptotendipes glaucus*

Two emergence peaks occurred each year, the first in late-May/ early-June and the second in July/August (figure 8.11). In 1976 the emergence occurred earlier than in other years. The second emergence peak was larger than the first.

j) *Parachironomus arcuatus*

Peak emergence occurred in early June except in 1977 when it was delayed until mid-June. A second emergence took place in July/August but fewer adults were taken at this time (figure 8.12).

k) *Polypedilum nubeculosum*

The peak emergence in June during the first two years of this study were delayed until late June in 1977 and July in 1978 (figure 8.13).

Comparison of emergence between years

i) Spatial variability

The percentage similarity calculated by the Raabe index was based upon the total catch of male chironomids of each species during the month. The data are presented as three tables, one for each of the three months May, June and July (August was not included in the analysis due to the low numbers of imagines emerging in that month).

From the data for May it is apparent that there was a high degree of variability between the same station in different years (table 8.2) since only 3 of the 9 values were greater than 50% whilst, with the exception of station 4 in 1977 there was a much higher similarity between different stations in the same year. The highest values occurred in the station 2 column indicating that the fauna at this station was most typical of the lake as a whole. However, by June, the time of peak emergence, this relationship had changed (table 8.2). At station 2 there appeared to have been a change from 1977 to 1978 with the lowest value for the 1975/1978 comparison; this stands in contrast to the other stations where 1977 was clearly seen to be anomalous. The emergence from station 4 had also become more similar to that at both stations 2 and 3 during the four years whilst stations 2 and 3 remained at c. 67% similarity in 1975 and 1978 with a lower value in 1977 due to the delayed emergence in that year.

The data for July, based on three years only show that there was a low similarity between the same station in different years and also that the relative distinctiveness of the stations was maintained during this period but was greater than that in June.

In general terms similarity between traps was greatest at the time of peak emergence.

ii) Temporal variation

The changes between years during individual months have already been outlined. In this section both changes between months and years at individual stations are presented.

The data for station 2 (table 8.3) show that, in general, the values obtained for comparisons between months are lower than those between the same month in different years (circled values). This pattern is partly disrupted by the data for 1977 when the June emergence peak was delayed causing the highest similarities to occur between July 1977 and June in the other years (boxed numbers). Similar principles hold for the data from stations 3 and 4.

Discussion

The pattern of insect emergence from Black Horse lake has shown an overall change during the period of this investigation. The effect of climate upon emergence was also seen to be marked. The data here have indicated two types of effect of weather on chironomid emergence

(i) Short term - causing the high daily variation in emergence in 1975

(ii) Long term - emergence being delayed by some persistent adversity such as rain.

Morgan's (1971) comment that short term variability is caused by errors in trap operation seems unlikely since all traps were operated by a single operator each year. Furthermore, the presence of the long term effect of delayed emergence indicates that chironomid larvae or pupae can respond to environmental cues. It is therefore not unreasonable to expect similar responses to occur on a much shorter time scale.

Changes in the overall pattern of emergence occurred with an increase in the abundance of imagines during July and August in 1977 and 1978. This was due, in 1978, to the successful growth of a summer generation of a number of species. This may have been prevented in 1976 by the very high summer temperatures prevalent that year which in the shallow water stations sampled may have been supraoptimal for larval development.

The common species found in the emergence traps did not in all cases coincide with species which were abundant in the benthos. Several factors may account for this

(i) The growth of an epifauna on the flotation collars

(ii) Movement of pupae in the water from their original site to where they were caught.

The first cause possibly provided a significant contribution to the emergence of tubiculous midge larvae since, when the flotation collars were removed from the water at the end of each year, the undersides were seen to be covered with tubes. However, I have also observed pupae swimming close to the surface for considerable periods of time before eclosion. Thus the larval habitat may not be directly underneath the trap in which the adults are caught due to lateral migration of the pupae. This problem would probably be less apparent if submerged funnel traps had been used. These two factors may also account for part of the higher catch of surface traps in comparison with submerged funnel traps.

Cricotopus larvae are known to inhabit tubes built on the underside of leaves and other aquatic debris and are found in both static and flowing waters (Mundie, 1957), these larvae may have formed a part of the epifauna of the flotation collars. Other genera known to be abenthic tubiculous filter feeders are *Endochironomus* and *Glyptotendipes* (Walshe, 1951). Walshe also reported that *Einfeldia* larvae are tubiculous and live in the bottom sediments. This latter genus was only trapped in abundance in 1976 in the emergence from shallow water.

It therefore appears that many of the apparent anomalies in species composition between the benthic samples and the emergence were due to the characteristic epifauna of the flotation collar. Whilst this does not distort the characterisation of the lake fauna as a whole, since the epiphytic species would also have been present on other suitable substrata, it does complicate the interpretation of changes in fauna between areas. The effect of the second cause of trapping error was probably less marked but may account for the presence of a few individuals of species found in other areas. The use of flotation collars which cannot be regularly cleaned (i.e. weekly) should therefore be avoided where possible if the aim of the investigation is the characterisation of benthic chironomid communities from emergence data; under such circumstances submerged funnel traps may be superior despite their high loss rate.

The variability in emergence between years for individual species indicates that the major controlling factors acting upon the populations are extrinsic. Abiotic factors such as temperature, light, etc. will have a greater effect in shallow water bodies than in the profundal zone of larger lakes and the populations were seen to readily respond to adverse climatic conditions by delayed emergence. However, to substantiate this, a detailed knowledge of the environmental cues which initiate or retard emergence and the responsive pre-imaginal stadia are needed.

The spatial and temporal comparisons of emergence showed that the seasonal fluctuations in emergence accounted for most of the variation in the data with annual change over the four years of the study being less important. Whilst spatial variation was apparent in the larval data this was partially masked by the emergence of the flotation collar's epifauna which caused a basal similarity independent of sampling station.

Thus the use of emergence data alone, in the absence of a knowledge of the larval populations, may lead to an erroneous description of the fauna of a particular zone and comparisons of chironomid communities based on different sampling methods are not directly comparable.

CHAPTER 9

THE COLONISATION OF NEW GRAVEL PIT HABITATS

INTRODUCTION

Wet gravel pits are becoming an increasingly common feature of the British countryside with c. 1000 ha of new water space created annually, exceeding all other sources of new wetlands. Therefore the speed and efficiency with which chironomids colonise this new habitat is an important aspect of the ecology of sand and gravel pits. Despite the extent of aggregate excavation,most research relating to colonisation of wetlands has been on reservoirs,where the process of invasion and succession has been studied in some detail.

Non-biting midges usually predominate amongst the first colonists of reservoirs (Fillion, 1967; Krzyzanek, 1970; Nursall, 1952; Paterson & Fernando, 1970) and the macrobenthic fauna of sand and gravel pits is also dominated by chironomid larvae. This study of larval populations and emergence of chironomids has shown that the communities differ considerably from those of natural lakes and reservoirs.

The ability of the chironomids to colonise new habitats efficiently is facilitated by the widespread dispersal of fertilized females; although their flight is not strong, large numbers have been found in the middle of the English Channel (Cheng & Birch, 1977). Their high fecundity also means that only a few females need arrive at a new water body to effect colonisation, dispersion within the water body being effected by the planktonic first larval instar (Davies, 1976).

Until recently, the colonisation of new wetland had not been studied in relation to the constancy of the association of species within a particular habitat, however, Clement et al. (1977) have shown that in flooded rice paddies the fauna at replicate sites was very constant.

This study investigated both the constancy of the colonist association and the extent to which the predominant species in the nearby more mature area were able to colonise new experimental ponds.

METHODS

This study was undertaken at Black Horse, Linford. Six square, vertical sided ponds, each 36 m^2 surface area and 1 m deep were excavated in November 1976. The ponds were in line, one metre apart and they were partly filled with water from an adjacent pit until flood-water from the nearby river Ouse filled them completely in January 1977. The bed of the ponds consisted of sandy-gravelly clay. In order to simulate some of the conditions of newly filled reservoirs, namely high levels of allochthonous material and a mineral rich sediment, barley straw was added to pond 1 on 24.5.1977 at a rate of 1 kg m^{-2} and a 50 mm layer of topsoil to pond 3 on 24.6.1977.

Adult chironomids were caught using small surface emergence traps of 0.1 m^2 surface area (described under sticky traps in Chapter 3) in the centre of each pond. These were chosen in preference to the Mundie traps because they were easier to empty and any epiphytic fauna could be removed from the trap or floats at each service.

Benthic samples were collected in 1977 using methods similar to those of previous colonisation studies by other workers to compare with the results from emergence trapping. These samples were taken with an Ekman grab and then sieved through a box sieve with a 0.375 mm mesh.

Water analysis of these ponds was carried out in 1977 using the methods outlined in Chapter 2.

Diversity indices (H') were calculated from the Shannon-Weaver information theory formula (Pielou, 1977)

$$H' = - \sum_i p_i \ln p_i$$

where p_i is the proportion of species i in the community.

The evenness (J) of the community was calculated using the formula of Pielou (1977) assuming maximum evenness (H_{max}) when all species are equally abundant

$$J = \frac{H'}{H_{max}}$$

The emergence from the ponds was also compared using the similarity index of Raabe (1952). Log rank percentage frequency curves were drawn to illustrate the structure of the pioneer pond community in comparison with that of the nearby mature area in 1977 and with the pond community in 1978. The curves were compared with those predicted by MacArthur's third model (MacArthur, 1957) where the proportional abundance (p_i) of the i^{th} rarest species is given by the equation:

$$p_i = \frac{1}{S} \sum_{i} \frac{1}{S + 1 - i}$$

Where S is the total number of species found in the community.

RESULTS

Larvae

The results of larval sampling are expressed as total larvae found at each sampling, the species composition of the larval population was similar each time.

The diversity and evenness of the larval communities were lowest in May and June, when *Chironomus spp.* were predominant but increased in July and August when fewer larvae were present (Table 9.1). Two types of *Chironomus spp.* larvae were found, corresponding to two adult species of this genus. The first type, *Chironomus sp. A* was present from the first sampling in April, when the population consisted predominantly of small larvae up to 15 mm long, whilst at the same time the *Chironomus spp.* larvae in the adjacent mature area were all larger than 20 mm. *Chironomus sp. A* may have developed from eggs laid in early April, and the first emergence was of *C. riparius* Mg. suggesting that this was in fact species *A*. Larvae of *Chironomus sp. B* were not found until mid June, and this species was probably *C. cingulatus*. It seems likely that these larvae developed from eggs laid by the adults which emerged from the nearby lake in late May.

Adults

The total number of chironomids emerging from the experimental ponds showed two peaks, one in late May/early June and one in July (Figure 9.1). The peak emergence from these ponds of 440 m^{-2} day^{-1} was significantly higher than the peak from the more mature area (180 m^{-2} day^{-1}). The similarity of the total catch from each pond and the mature area for the period 20.4.1977 - 5.8.1977 was compared using the Raabe index (Table 9.2). In 1977 pond 1 was the only site for which all comparisons did not show more than 70% similarity in total emergence and all six ponds were very dissimilar from the mature area. In all cases the fauna was similar enough in composition and phenology to justify discussion of the emergence of individual species using pooled emergence data from all six ponds.

In total, 22 species of adult chironomid were identified in the 1977 catch (Table 9.3). Eight species were found which each accounted for $\geqslant$ 1% of the emergence, with 86% of the catch accounted for by only 3 of those species; *Tanytarsus gracilentus, Procladius choreus* and *Cricotopus sylvestris*.

T. gracilentus was the single most abundant species in all ponds, it had two generations within the sampling period with the first emergence peak at the end of May and a second smaller peak in July (Figure 9.2) with a generation time of c. 45 days. This species was largely responsible for the peaks in total emergence at these times, since it alone accounted for c. 60% of the total emergence. The following year only 4 males of this species were caught.

Procladius choreus had an extended emergence period from mid June onwards, with a peak in mid July (Figure 9.2). It accounted for c. 17% of the total emergence.

Cricotopus sylvestris was abundant in early June (Figure 9.2) with only one generation in the ponds, where it accounted for c. 10% of the total emergence. The communities from each pond, as shown by emergence, had both a low diversity and low evenness compared to values calculated from the catch of a similar trap in a nearby mature gravel pit (Table 9.4). Pond 1 had a much higher diversity than the other ponds due to the presence of a greater number of sub-dominant species and lower numbers of *T. gracilentus*. The structure of the community in the ponds in comparison with that of the nearby mature area is best shown in the rank % frequency curves (Figure 9.3). The slope of the line is a measure of the equitability of the community (Lloyd & Ghelardi, 1964), and the dotted line shows the slope predicted by MacArthur's broken stick model.

In 1978, the second year of the study, 28 species were caught. The communities in the individual ponds were less similar than in 1977 (Table 2) and in addition, both total and peak emergence was much reduced, with a peak emergence of only 80 m^{-2} day^{-1}.

The community structure in the ponds (Figure 9.3) was much more even in 1978 than it was in the previous year and more like that of the mature area.

Chemical analysis of the water showed that the pH and concentrations of the common cations and anions were very similar in each pond, and these in turn were similar to the nearby more mature area (Table 9.5).

DISCUSSION

In newly inundated reservoirs the initial fauna is normally derived from the tributaries, with an initial dominance of rheophilic forms (Krzyzanek, 1970). Later, reservoirs are invaded by a number of chironomid species (Paterson & Fernando, 1970) especially members of the genus *Chironomus* which are adapted to the anoxic conditions created by the decomposition of the flooded organic matter (Sokolova, 1963). Subsequent development leads to an increase in the proportion of oligochaetes and the restriction of *Chironomus spp.* to the profundal (Nursall, 1952). Little is known however, about the colonisation of new wetlands, such as gravel pits, that do not have an organically rich sediment, apart from the study of Cantrell and McLachlan (1977) on a lake formed in opencast coal workings, where two species, *Chironomus plumosus* and *Tanytarsus gregarius*, were found to be abundant in the benthos. *Chironomus plumosus* is commonly encountered in pioneer situations, especially in lakes with an anoxic sediment where, despite the low partial pressure in the water, it is able to obtain sufficient oxygen by a combination of respiratory movements and haemoglobin-facilitated diffusion. In low carbon sediments such anoxic conditions are not present and the sediment can be colonised by species which cannot tolerate low oxygen concentrations, such as members of the Tanytarsini (Cantrell & McLachlan, 1977).

Chironomus spp. larvae were found to be predominant in the benthic samples in this study. This is in marked contrast to the low numbers of *Chironomus spp.* adults in the emergence traps, where they accounted for only 5% of the total. Their predominance in the benthic samples here, as in other studies, is thought to be due to the mesh size of the sieve used, which favoured the retention of large larvae such as *Chironomus spp.* Head capsule width is the critical dimension which determines retention in a sieve (Jonasson, 1958). The head capsule widths of final instars of *Chironomus plumosus* and *Tanytarsus gracilentus* are 0.8 mm and 0.52 mm respectively (Paasivirta, 1972), whilst the mesh sizes of the sieves used vary from 0.25 mm (Cantrell & McLachlan, 1977) to 0.5 mm (Sokolova, 1963; Krzyzanek, 1970). In sieves of smaller mesh most second instar larvae of *Chironomus* species will probably be retained, whilst some third instar larvae of the *Tanytarsus* species will pass through (assuming head capsule width doubles at each moult (Hall, 1951)).

The mesh size of the sieve used in this study, 0.38 mm, would only retain final instar *Tanytarsus gracilentus*, whilst also retaining both third and final instars of *Chironomus spp.* larvae. Hence the abundance of the smaller Tanytarsini larvae must have been underestimated. It appears therefore that the importance of the larger species as pioneers may have been overestimated in previous colonisation studies based on larval sampling.

Tanytarsus gracilentus has a circum-polar holarctic distribution and Paasivirta (1972), in a study of the ecology of a population at Valassaaret in the Baltic Sea, found larvae only in the muddy areas. In contrast all the experimental ponds have a gravelly base, showing a possible difference in habitat between permanent and colonist populations. This species had not been collected in the surveys of the adjacent gravel pit (Chapters 4, 5 & 6) and must therefore have invaded from some other habitat. Its virtual absence from the ponds in 1978 although very common in the emergence traps there the previous year indicates that *T. gracilentus* can be an important pioneer colonist of new wetlands which is rapidly displaced by other species. The obvious ability of *T. gracilentus* to colonise new waters is not explained by the reasons normally proposed to account for the success of other chironomids, such as *Chironomus plumosus*, which have been recorded as pioneers, namely an extended emergence period and the ability to tolerate low oxygen conditions.

Colonisation of a new water body confers several advantages on a successful species, for example reduced competition and predation. This is illustrated by the greater numbers of chironomids which emerged from the newly dug ponds than from the nearby mature area in 1977. In the first year the structure of the pond communities showed low evenness, with the assemblage dominated by one species, typical of pioneer situations. The following year the community structure became more even, similar to that predicted by MacArthur's broken stick model (MacArthur, 1957).

In 1977 the emergence from pond 1 was less similar to that from all of the other ponds (Table 9.2) and this was probably due to the presence of an uneven layer of barley straw on the bed of this pond, increasing the range of micro-habitats available. The dissimilarity in species composition of the ponds in 1978 is in contrast to the constancy of the colonising fauna of the previous year. The constancy of the communities in 1977 may be attributed to the relative simplicity of the habitat in its first year when the benthos was the only habitat available (except in pond 1). In the second year however, an extensive growth of macrophytes in all ponds provided further habitats for colonisation (Stimac & Leong, 1977). The greater variability of the habitat structure resulting from the development of the flora (mainly *Myriophyllum spicatum* L., *Callitriche spp and Elodea canadensis* Michx. , with some *Potamogeton natans* L., *P. pectinatus* L. and *Zannichellia palustris* L.) probably accounted for the heterogeneity of the emergence in the second year.

Both the addition of barley straw and the development of the flora disrupted the previously uniform substratum, splitting it up into patches and providing additional patches of a different nature. The small size of the experimental ponds meant that all available habitats could have been colonised by any planktonic first instar chironomid larvae present, but the development of patchiness within the habitat probably increased the diversity and evenness of the community by limiting different species to particular microhabitats (Southwood, 1977). Species succession and changes in diversity of the chironomid community within this developing ecosystem were dependent upon habitat succession and within two years the structure of the community came to resemble that of a much more mature habitat.

New wetland habitat created by the sand and gravel industry is therefore rapidly colonised by chironomid midges. The colonist fauna described differed markedly from that in reservoirs and this was seen to be due to sampling errors inherent in sieving in coarse mesh sieves. The colonising fauna also differed markedly from that of the older gravel pit and this was probably due to differences in depth and substratum in the first year, and macrophyte growth in the second. However, the fauna was also very different from that found in Dovecote in 1977, its first year after flooding (Table 5.8). In the experimental ponds the predominant larvae were *Chironomus spp*. with few *Procladius* or *Polypedilum* (except in July when 23% of the larvae were *Polypedilum sp*, see Table9.1). This was in contrast to the predominance of these latter two larval genera in Dovecote. In the emergence from the ponds *Procladius* was proportionally as abundant as in the benthos of Dovecote. In Black Horse *Polypedilum* larvae were only found in the benthos for a restricted period during the summer months and larval densities at this time were roughly comparable to those in the ponds. Thus the real difference between the benthos of these ponds and the larger lakes was the high densities of *Chironomus spp.* larvae, a situation similar to that described in man-made reservoirs.

The two main facts which emerge from this study are that colonisation is remarkably uniform and secondly that the faunal composition rapidly changed to that typical in structure of a more mature habitat. These facts illustrate the effectiveness of the adult stage of the chironomid life cycle in dispersion.

CHAPTER 10

DISTRIBUTION AND BEHAVIOUR OF ADULT CHIRONOMIDS

Male imagines of chironomids are most noticeable at dusk in summer when they form dense clouds of mating swarms. Whilst many anecdotal tales are known about the extent and duration of such swarms, there is a dearth of accurately recorded instances of the location, extent and time of swarming for most species. Gibson (1945), in an extensive study of the swarms of midges associated with sewage treatment, investigated the abiotic factors limiting the timing and duration of swarming and found both light intensity and wind-speed to be critical factors. Downes (1969), reviewing swarming in the Nematocera, emphasised the importance of swarm markers in delinating the location of the mating aggregation. Investigators of the timing of swarming have shown a peak of flight activity at dusk although swarming can occur at any time of day.

However, little is known of the activity and distribution of either males or females during the periods when the adults are not swarming.

Observations of swarming, and sampling of the vegetation were carried out in early June, the time of peak emergence, at Black Horse lake. Swarms of adults were observed, and tested for responsiveness to a white swarm marker approximately 0.6 m diameter, and then a number of the individuals were caught and identified. During the day chironomids were observed whilst resting on vegetation and their activity was recorded. To determine the distribution of non-swarming adults transects of the vegetation away from the waters edge were sampled with a sweepnet and a D-vac. The influence of different species of plants on the distribution was investigated by suction sampling of an area with a number of vegetation types and foliage of different heights. Temporal patterns of abundance in the vegetation were monitored by 24 hr sampling of a uniform area of grass 3 m from the water's edge.

SWARMING

The sites, timing and response to a white swarm marker for the species identified is given in table 10.1. The two most abundant species were *Cricotopus sylvestris* and *Tanypus punctipennis*. The latter species was attracted by any light object and rapidly formed a swarm above it; in contrast, *C. sylvestris* was unaffected by a white swarm marker. The two most abundant species of the genus *Cricotopus* found at the pits appear to be separated spatially in their swarming sites. *C. intersectus* being responsive to a white swarm marker whilst *C. sylvestris* is not. This contrast in swarming behaviour in congeneric species suggests that behavioural changes in adult swarming may be the initiating factor in speciation amongst chironomids, and supports the view of Lindeberg (1964) that the swarm of males is the ultimate unit for species recognition. Heimbach (1978) identified a difference in the diel periodicity in emergence between two *Clunio spp.* which caused genetic isolation in the absence of morphological differences, suggesting that descriptions of new species should, when possible, also give data on swarming behaviour.

NON-SWARMING ACTIVITY

During day-light periods when adults are not swarming they are nonetheless very active, individuals resting on vegetation are frequently disturbed by other insects and move rapidly. The non-swarming period is not a period of inactivity but the flights are short and directed towards vegetation rather than being oriented above swarm markers. During the non-swarming period transects from the water's edge showed no decrease in abundance of chironomids with distance from the water on a uniform area of grass approximately 0.3 m high. In addition there was no noticeable change in the species caught. In shorter transects starting amongst the willow trees at the water's edge and extending into a grassed area there was a marked change in the species composition between the water's edge and further inland (Table 10.2). At the water's edge, amongst the willows, *Cricotopus sylvestris* was predominant whilst further inland this species was less common, and other species, such as *Einfeldia dissidens* and *Tanypus punctipennis*, were predominant. The fauna at the water's edge was also far more diverse than that further inland. Another noticeable fact is that the sex ratio for the total chironomid catch is nearer unity amongst the water's edge vegetation than in the vegetation further inland with females generally less abundant than males suggesting that the males stay in the locality of their swarming sites during the non-swarming period whilst females move to the lake-edge.

The quadrat sampling, of an isolated area of mixed vegetation on an island, using a D-vac revealed a uniform abundance over most of the sites. One quadrat, which contained a stand of reeds, had much higher numbers of *Polypedilum nubeculosum* and *Tanypus punctipennis*. Several other sites also contained higher numbers than average and these anomalies were probably caused by swarm markers within the quadrat. Comparison of samples from adjacent plots, of long and short grass, revealed a greater number of chironomids in the long grass. This is probably due to the preference of non-swarming chironomids for higher humidities (Syrjamaki, 1963).

The temporal pattern of abundance showed marked changes during a 24 hr period (Figure 10.1). Samples from a site 3 m from the water's edge showed a minimum abundance at midnight with a decrease during the evening and night and again during the morning after 6.00 a.m. Females were present in approximately the same numbers throughout the period.

The only other study of the non-swarming distribution of chironomids is that of Wilson (1969) who investigated the distribution of a population of *Chironomus plumosus* during a period of peak emergence when the adults had reached nuisance levels. In his study, during the day, the midges were resting on the foliage near the lake, however, during the early evening they settled on the shoreline over which they had previously been swarming. At dawn they moved back into the adjacent foliage. A similar pattern of movement can be seen in the data here for the 24 hr sampling where the midges were most abundant at the water's edge sampling site at midnight. However, the movements seen by Wilson were undoubtedly accentuated by the presence of a sandy beach with little natural shelter and consequently, to avoid dessication, the adults were forced to move to the nearby vegetation. At the site of this study movement from the swarming site was less vital, because suitable high-humidity areas were present throughout the site, although the water's edge willow stand undoubtedly attracted many adults, and especially females.

The choice of daytime resting site is therefore determined both by the need to conserve water and also to avoid dispersion away from the swarm markers. The latter is obviously of greater importance for less abundant species, but it seems to be true also for the common species; these were usually taken in abundance only in occasional samples, indicating a contagious distribution. The imbalance in the sex ratio away from the water's edge indicates that the females rapidly move away from the swarms to the lake edge or disperse to other wetlands after emergence and insemination. Such behaviour is essential in these short lived insects which nonetheless possess extraordinary dispersive powers.

The dearth of available information on the ecology of adult chironomids is due to the difficulty of sampling the population and also to the limited importance of this stage of the life cycle in terms of energetics. Since adult chironomids have been observed feeding on sugary solids, such as the honeydew of aphids (Downes, 1977), their life cycle may therefore be more complicated than was once thought, with adult feeding possibly enabling survival for prolonged periods under favourable conditions. The high densities of adults near the waterside and the aggregative swarming behaviour may also provide an abundant source of food for waterside birds. The high level of activity of the adults throughout the day will however make them difficult prey items for many bird species. However, they may be caught fairly easily when swarming.

The importance of adults in speciation has already been outlined and the possible role of behaviour to swarming markers mentioned. The larvae live for much longer than the adults, so changes in larval habitat preferences will ultimately determine the distribution of any species. However, the similarity of specific larval morphology within each genus in comparison with the diversity of genitalia types in the adults attests to the crucial role of the imagines in the maintenance of species identity. Thus, whilst this stage of the life cycle is short lived it is perhaps subject to more rapid evolutionary change than are the larval stadia.

CHAPTER 11

PARASITISM OF EINFELDIA DISSIDENS BY A MERMITHID NEMATODE

INTRODUCTION

The occurrence of individuals with intersexual characteristics in the chironomids has been recorded by many taxonomists and ecologists; early records are summarised in Humphries (1938) with more recent data in Wülker (1961: p. 129). The most striking sexual changes were described by Rempel (1940) for the midge *Chironomus rempeli* (Thien.). Intersexual midges had male genitalia but the front tarsi were not bearded and the antennae were short with six segments only and a few short bristles like those of the female. The position of the cross vein between the radius and the medial vein was also like that of the female. In addition to these external changes in the parasitised individuals, the genital ducts and glands were poorly developed.

Wülker (1961) has shown that morphological change is not limited to parasitised males but also extends to the females where the 8th and 9th sternites were found to be modified.

Gotz (1964) first introduced the use of quantitative characters to the study of parasitic infection when he investigated the change in length of the anal point in normal and parasitised males and females. He further used measurements of the 8th and 9th sternites and antennae to investigate the factors causing strong intersexuality in parasitised midges. However, the factors investigated lead to different conclusions dependent upon the intersexual character chosen and the primary sex of the infested midge (summarised in Wülker (1964: p. 571)).

The term 'sex character' can be used in widely differing senses, from being narrowly restricted to the organs directly concerned with sexual reproduction to more broadly including all characters which show sexual dimorphism. Previous investigations have been restricted to those which show obvious sexual dimorphism such as antennae, tarsal beard, and the genitalia. Discussion of changes in body morphology have been largely ignored.

Infection with the mermithid nematode occurs in the larval stage with entry occurring through the larval integument (Wülker, 1965). The humoral defence mechanism of encapsulation is effective against some larvae but in established infestations the effectiveness of encapsulation is impaired (Vey & Gotz, 1975) due to lowered phenoloxidase activity in the haemolymph (Maier, 1973). This will lead to a greater susceptibility to fungal infection and higher mortality of infested chironomid larvae. Since host infection occurs during the larval stage the parasite must either leave the host before the latter emerges or use the dispersive activities of the adult to facilitate its colonisation of suitable habitats. The first strategy, as seen in mermithid infestations of simuliids (Condon & Gordan, 1977), would enable the parasite to exploit all the food in its host but dispersion would be limited. The second strategy, the one practiced, involves a balance between parasite and host growth such that the dispersive ability of the adult is not severely impaired.

This study investigates the extent of a morphological alteration in imagines of *Einfeldia dissidens* under the influence of a nematode infection.

METHODS

Adults caught in emergence traps in 1976 were stored in 70% alcohol for two years before this analysis. Individual imagines were then dissected to remove wings, head, foreleg and genitalia and measurements of various body lengths were taken (Table 11.1). Ten adults from each of the four groups of parasitised or unparasitised males and females were measured. To check on the assignment of individuals to a particular group, on the basis of infestation, the abdomen was opened to see if any nematodes were present.

The data were then subjected to canonical variates analysis with the groups defined by sex and infestation. Canonical variates analysis has been used extensively in taxonomic research (Blackith & Reyment, 1971) and is an extension of discriminant function analysis to more than two predetermined groups. This multivariate technique calculates a set of axes which maximise the distinction between groups. These are obtained from the matrix of pooled within group sum of squares and products of deviations from the group means (W) and the matrix of between groups sum of squares and products of the deviations of the group means from the overall means (B).

The canonical variates are the latent vectors associated with the latent roots (λ) such that:

$$|B - \lambda W| = 0$$

The number of non-zero latent roots generated is the lesser of the number of groups minus one or the number of variables. In the data used here three latent roots and vectors were obtained. The latent vectors were calculated and standardised to give the canonical axis. The value of the latent root is a measure of the contribution of the axis to the sum of squares of the data.

The analysis was performed using interactive statistical software at Keele.

RESULTS

The three latent roots and latent vectors generated by the canonical variates analysis are given in table 11.1. The first latent root accounted for 90.6% of the total variability within the data whilst the second latent root contributed a further 8.4%. This suggests that the first two variates alone are sufficient to account for the variability in the original data. The weights given to the 12 variables are given by the latent vector associated with each latent root (Table 11.1).

The first canonical variate gives greatest positive weight to head measurements and tarsal beard length in contrast to a negative weighting for the length of the first tarsal segment and several wing measurements (r - m to M_1 tip and r - m to R_{4+5} tip). The second vector is a contrast between head width, first tarsal segment length, wing length and the other measurements.

The positions of individuals and group centres is plotted against the first two variates, C1 and C2 (Figure11.1). The major source of variability, accounted for by the first variate, is an expression of sexual dimorphism. Thus a larger head and inter-eye distance and longer tarsal beard was found in normal males (group 1) than in the other groups. This variate gave an equal value for normal females and both groups of parasitised individuals. The second variate showed some distinction between parasitised adults (groups 2 and 4) and non-parasitised females. Although the cluster centres were distinct considerable overlap of individuals occurred. Furthermore, these two variates did not distinguish between the two separate groups of parasitised individuals. Parasitised individuals were the same size as normal females.

DISCUSSION

The alteration of morphology by the nematode parasite is such that a female-like body is produced (with the exception of the male genitalia) irrespective of the chromosomal sex of the host. Earlier descriptions of the changes in morphology have concentrated upon the alteration of the genitalia and antennae (Wülker, 1964) whilst less obvious sexual characters have been overlooked. The form of the genitalia is determined during an early stage of larval development when the imaginal discs are formed (Agrell & Lundquist, 1973); these show a clear sexual dimorphism in the larval instars of *Chironomus spp* (Atchley, 1971). The extent of morphological plasticity in determined imaginal discs would be expected to be less than that in undifferentiated discs and this may account for the lack of reversal in genitalia morphology.

The development of the other secondary characters are more amenable to alteration under hormonal control during metamorphosis. During the pupal stage all the larval tissues with the exception of the imaginal discs, nervous, circulatory and tracheal systems are broken down. The available nutrients are then used by the differentiating and dividing imaginal discs which grow to form the adult. In chironomids at this time, the process of oogenesis and vitellogenesis are also taking place (Wülker & Winter, 1970).

The nematode parasite is therefore present in a highly nutritious environment and can grow rapidly. However, if the host is to remain viable the amount of nutrients that can be taken by the parasite is limited. The actual limit,and the way in which the nutrients are partitioned in the host-parasite system,is clearly seen from the data. The nematode causes the pupae to develop into a female form, a process known as parasitic castration. This is well known for parasites living in the haemocoel of insects (Wilde & Loof, 1973) and is usually effected via an endocrine pathway.

By this process the parasite is able to exploit the resources that would otherwise have been used for ovary development and egg formation without limiting the resources needed by other vital organs. Wülker has shown that egg maturation is prevented by the presence of a mermithid nematode in the abdomen of *Chironomus spp.* Normal development was prevented by the inability of the follicle epithelium to invaginate and form ovarioles, the eggs were therefore unable to migrate into these structures and mature. Mechanical damage was not the cause of the degeneration of the ovaries. Since the energetic cost of reproduction is much greater in females than in males the advantage of causing males to become feminine in their physiology is apparent.

The energy is partitioned, in the pupa, into two pools, that for somatic growth, and that for reproduction. In the female, the amount of energy needed for egg production is much higher than that, in the male, for sperm development. The female body has therefore less energy for development. The nematode can take all the energy from the reproduction pool without impairing somatic growth. Therefore, in the female, the available energy is potentially greater, given the constraint that the host remains viable although castrated.

The observation of abnormal behaviour in parasitised male chironomids (Wülker, 1961) can be understood in terms of the morphological changes in the parasitised males. The behaviour during swarming and recognition of females is dependent upon sight and sound (Downes, 1969). Thus the change in head size and antennal form will limit the ability of males to swarm and mate successfully. The effect of the nematode on dispersive behaviour of parasitised adults is not known. However, the observation of the complex interaction between the nematode and adult males, causing feminisation and thus ensuring adult viability, would indicate that the parasite is able successfully to complete its life cycle in male *Einfeldia dissidens*. If this were not so the most obvious strategy for the parasite to adopt would be to kill the host at the pupal stage as in the case for other chironomid genera such as *Tanytarsus* (Poinar, 1968).

In conclusion, this host - parasite system provides an ideal subject for the investigation of the role of hormones in metamorphosis and behavioural change. The coexistence of parasite and host in a closed system such that each remains viable indicates a high degree of interaction, with feminisation necessary for both the formation of a host/vector, and nematode growth.

CHAPTER 12

FINAL DISCUSSION

The study of ecology is based upon our need to understand how animals and plants interact with each other and the physical environment. Since man has changed the world so markedly it has become necessary for him to manage a large proportion of it. Sound management can only be founded upon a basis of knowledge of how communities interact and function. However, if ecology is restricted to drawing specific conclusions about specific areas then it would be expected to contribute little to the practical management of the global environment. Only by generalising from a number of specific cases can the mass of empirical data be ordered in such a way that it is possible to reach an understanding of how ecosystems function.

The system studied here, that of the chironomid populations of gravel and sand pit benthos, can be considered both in terms of the specific, individual study and in relation to the data of other studies and general ecological principles. The first two parts have been considered in the individual chapters and will not be extensively considered here. However, the main results of this research will be briefly outlined and then discussed in relation to general ecological principles.

The gravel and sand pits studied were found to differ from natural lakes in a number of abiotic characteristics. In particular, they are shallow and have no inflow or outflow streams and the water level is maintained by groundwater seepage. In the wet-dug pits studied there was a constant resuspension of sediment leading to a high turbidity in exposed areas of water. Thus, whilst the lakes were shallow enough for plants to grow over their whole extent this did not occur due to the instability of the sediment. The water was fairly similar in major ion composition to that of lakes of similar conductivity (Rodhe, 1949). However, the level of orphophosphate was too low to detect (see also Powell & South, 1978). The sediment had a low organic content (c 3%

organic carbon) and this was probably due to several causes, the relative "newness" of the pit and the absence of profundal anoxia in these shallow water bodies.

The initial study of emergence showed that the chironomid communities present were different from those described from other lakes principally due to the absence of a large Chironominae fauna. In particular, it was noted that most of the species were herbivores or predators rather than detritivores. Subsequently, a study of the benthos of a number of pits showed that the fauna found, a *Polypedilum-Procladius-Chironomus-Tanypus* association, was characteristic of gravel and sand pits with some differences between shallow and deeper water areas although this was less marked than in eutrophic lakes due to the absence of stratification.

An intensive study of Black Horse lake showed that the benthic larvae of the predominant species of chironomid larvae fed on different food resources. Only two genera, *Chironomus* and *Polypedilum*, showed little separation in food niche and these were both tubiculous detritivores. The larvae of the other three species were errant and all highly selective feeders. *Tanypus* larvae fed on algae, *Procladius* on Crustacea and *Cryptochironomus* on oligochaetes. The lack of separation between the two detritivores was undoubtedly a function of their life style; they are limited in their feeding range by the tube in which they live and can therefore only consume resources which are abundant. However, it is important to note both that these two genera appeared to avoid excessive competition by being numerous at different times and also that they consumed the most abundant food resource.

The pattern of larval distribution both at the microhabitat level and over the lake as a whole was seen to be related to the feeding habits of the larvae. If the food resources are ubiquitous or randomly distributed then the animals should also show a random distribution. However, only one of the four genera examined, *Chironomus*, was randomly distributed. The other detritivore, *Polypedilum*, was not randomly distributed, this may have been due to a behavioural mechanism and an avoidance of established *Chironomus* larvae. The two errant Tanypodinae both showed strongly contagious distributions at higher densities and these were undoubtedly a reflection of their feeding behaviour. The distribution of algae on the mud surface is non-random (Round, 1965) and this will have directly caused the observed dispersion pattern in *Tanypus* larvae and, via an intermediate consumer, in *Procladius*. The ubiquitous distribution of *Chironomus* within the gravel pit can be understood in terms of the abundance of its main food resource. In contrast *Tanypus* larvae were limited to areas where benthic algal growth occurred and were unable to invade the exposed areas of the lake until late summer due to the instability of the sediment during the spring. The two predatory genera *Cryptochironomus* and *Procladius* were widespread since their foods were also ubiquitous.

Production estimates for the most abundant species confirmed that the pit had a low annual production. Of the total production of chironomids > 70% was due to *Chironomus* larvae at each station, indicating that the nutrient-poor detritus was still the major food resource within the lake. The loss of energy due to emergence of imagines accounted for between one third and one half of the annual production.

New gravel pit habitats were rapidly colonised by chironomids. The high emergence from newly dug ponds in the first year of their existence supports the idea that colonisation of a new water body confers advantages upon successful species. The structure of the communities changed during the two years of the study from one with a low equitability to that similar to the structure predicted by MacArthur's broken stick model and also to that of the adjacent mature area. Furthermore, the initial colonist fauna was highly uniform in a number of separate adjacent ponds indicating that colonisation proceeds with a high degree of replicability.

Over the four year period of this study the emergence pattern changed. This was probably an expression of long-term successional changes, since the area around the lake has matured and now provides a higher allochthanous input leading to a change in both the sediment structure and in food resources. In addition the emergence was variable on a more immediate basis showing changes in response to adverse weather and especially to daylight.

The above summary indicates, to some extent, the major pathways of energy flow and what physico-chemical processes control them. As such, this information forms the basis of management of the habitat and will be further discussed later.

Ecologists have attempted to organise their knowledge into a hierarchical structure ranging from the requirements of individuals (the niche) through to the properties of the ecosystem.

Obviously there is a certain amount of overlap between levels and the organisational principles may act at one or more points. The concept of the "ecosystem" was first defined by Tansley (1935) and has since gained a prominent position in ecological thinking. An ecosystem is delineated by certain characteristic features - often the species present - and has had certain abilities attributed to it (see Odum, 1971). Some ecosystems, such as lakes, have been regarded as closed, the geochemical cycles being driven by a flow of solar energy. In other words, the production within the lake was balanced by decomposition and deposition within the sediments. Recently the results of a number of studies have indicated that a large proportion of the energy input can be of terrestrial origin (e.g. Jordan & Likens, 1975; Sorokin& Paveljeva, 1972). This has gone some way to destroy the closed system idea. The results here and also in several other studies (e.g. Jonasson, 1972; Kimerle & Anderson, 1971) have shown high levels of export of production via insect emergence. This shows that lakes are indeed very open systems, not just in relation to inflow and outflow streams but also to other adjacent ecosystems to which they are linked by reciprocal exports of energy.

Whilst the energy input to the lake is much greater than the export, the importance of this export should not be under-estimated since its effect is principally at a higher trophic level than the import. It is apparent that chironomids are an important food of many freshwater fish (secondary consumers) and as such the level and fate of chironomid production is of importance to the ecosystem structure. The fact that a proportion of between ⅓ to ½ of the production by chironomids is lost from the ecosystem thus has considerable consequences within the lake.

The input of allochthanous material enters straight into the decomposition cycle. In most ecosystems this pathway is the one through which most energy is processed (Odum, 1971). The predominant position of this pathway is theoretically a stabilising influence on the ecosystem since it processes energy at a fairly constant rate (Howard-Williams & Davies, 1979; Mason & Bryant, 1975b)and provides a constant supply of nutrients for further primary production. In lakes the availability of nutrients is determined mainly by two factors:

(i) the redox potential of the sediments
(ii) the presence of littoral macrophytes

Whilst the second of these is partly dependent upon lake morphology, the first is intimately linked to the decomposition pathway. This lowers the sediment redox potential, due to the activity of bacteria and fungi, thereby releasing nutrients into the water.

The shallow nature of gravel pits affects the sediment redox potential by constant reoxidation. Thus, decomposition does not result in a release of nutrients and this accounts for the low level of orthophosphate in the water. The low nutrient levels lead via low phytoplankton production to a low level of decomposition within the lake. It is therefore apparent that these shallow lakes are of low productivity in part as a consequence of the morphology but also frequently due to the low level of allochthanous material input from the environs of newly formed gravel pits, due to the absence of inflow streams and of trees.

The feeding habits of the common species and their biomass reflects the overall paucity of food and also the relative abundance of different types of food. Whilst the level of organic material in the sediment is low, detritus is nevertheless the major food resource within the lake. In addition, the levels of chironomid production dependent upon other consumers or plants are typical of that of oligotrophic lakes. Thus the abundance and diversity of species are controlled by the physical and chemical characteristics of the habitat, in particular the nature of the sediment which controls the geochemical cycles. In more mature (eutrophic) lakes it is found that biologically driven processes control the same geochemical cycles.

Considering the next organisational level one can ask what factors control the species composition of the community. The answers to this question for any particular animal species in new habitats is dependent upon whether it has arrived yet and if it can exist in the habitat. It is therefore important to study both colonisation and the factors influencing abundance when considering recently created lakes. The colonisation study showed how rapidly a new habitat is colonised; furthermore, the presence of a number of species not previously found in the nearby pits indicated that chironomids possess powerful dispersive capabilities. The high degree of similarity of the fauna of all six ponds in the first year indicates that colonisation is carried out with a high level of determinacy. During the second year of the colonisation study the replicability between the ponds decreased markedly. This decrease was attributed to an increase in heterogeneity of the habitat by the growth of macrophytes. There was also a change in community structure over this period of time such that the equitability approached that predicted by MacArthur's broken stick model. This variation in time in community structure related to habitat heterogeneity was also seen in spatial terms in the study of insect emergence in 1975. Here it was noted that the communities associated with areas of macrophyte growth had a higher equitability than those from deeper water areas with only a mud substratum thereby reinforcing the conclusion that the main factor controlling diversity was habitat heterogeneity.

It is apparent therefore that, at the level of the individual species, the effects of lake morphology act upon the level of production and habitat heterogeneity since plants are limited to restricted areas due to the instability of the substratum in much of the lake. The diversity of the insect fauna is thus a result of habitat heterogeneity (i.e. by macrophyte growth) rather than of colonisation, as would perhaps be suggested by the experiments using replicate ponds.

In this study MacArthur's broken stick model was used solely to provide a means of comparing the structures of two communities rather than to indicate the underlying organisational principles. The main proposition of the model, that one major resource is partitioned randomly between species, cannot be interpreted in terms of any of the factors studied. Thus whilst I have shown how the individual species coexist, an explanation of community structure is not possible.

At the species or population level, the ecosystem is divided into a sequence of niches which prescribe the physical and biotic factors which an organism exploits. In some animals, such as aquatic insects, the niche changes markedly during the life cycle. It is therefore necessary for two or more separate niches to be juxtaposed to ensure the completion of the life cycle.

In chironomids the adult stage of the life cycle is fairly short lived. The animals do not feed extensively although they have been reported to take sugary substances, e.g. dried aphid exudate, nectar from extrafloral nectaries, etc. (Schlee, 1977). The main function of this stage of the life cycle is dispersal and colonisation. The main requirements of imagines are primarily certain physical factors, i.e. suitable conditions to enable swarming, which is disrupted by wind, rain, cold, etc. (Gibson, 1945) and for dispersal, i.e. a light wind since chironomids disperse passively using gross air movements in a manner similar to aphids. The necessity of ensuring fertilisation (some are however parthenogenic (Lindeberg, 1971)) means that adult males and females must meet. This is achieved by swarming which is performed often over a district marker; females fly into the swarms of males, are inseminated and then disperse (Downes, 1969). This stage of the life cycle ensures species integrity.

In contrast, in the larval stage, when all species are growing, they must partition a number of biotic resources, mainly food. In this stage the physical environment is more stable (or predictable) and therefore the main factors influencing an organism will be biotic. The competitive exclusion theory is demonstrated by the coexisting chironomid genera which showed either a segregation of food niche or a temporal segregation. In view of the powerful dispersive abilities of chironomids the number of species in the benthos is only a small proportion of the possible colonists. The stage of exclusion is therefore probably early on in the larval stage, perhaps in the first or second instar when the larvae attempt to settle on the sediment. Site selection by adult females is unlikely due to their mode of dispersion. Evidence for this is provided here for *Polypedilum* - *Chironomus* abundance, where *Polypedilum* were only abundant when *Chironomus* larvae were scarce, and by Jonasson (1972) and Cantrell and McLachlan (1977).

The specific adaptations of certain species enable them to feed on characteristic foods most efficiently. Since the animals are then segregated by food availability, the overall community structure should bear a direct relationship to this. The regularity of structure suggests that the food niche is to some extent variable and community structure is perhaps to be explained in terms of the subdivisions of the food resources.

In addition to providing further understanding of the functioning of ecosystems in general terms the data resulting from this study form the basis of a consideration of practical management techniques for disused gravel and sand pits. In the previous part of the discussion the controlling mechanisms were related to the maturity of the system, with those controlled principally by abiotic factors regarded as juvenile. In such a situation the effect of altering a particular factor is inherently more predictable and more controllable. For example, if the level of phytoplankton production is controlled by the level of phosphate concentration then we may, by altering the level of phosphate cause a set change in phytoplankton. If one is able to control the phosphate level then one could return the phytoplankton level to its original value. However, if the rise in phosphate causes a change in aquatic macrophytes and associated fauna then the level of prediction of the outcome of altering the phosphate level is much lower. Therefore for sensible management one needs to know not just the controlling factors but also any interaction.

Thus reliable, predictable management can only be carried out in simple systems where interactive effects are less numerous. However, it must be borne in mind that under certain management regimes the systems may become more complex with a consequential loss of control by the manager.

Gravel pits are at present used primarily to provide water space for leisure activities, mainly fishing, other water sports and informal recreation. Since the demands of these three groups are often in conflict, spatial zoning of lakes or pit complexes is practised. With competition for this water space from the various user groups, the most obvious question to ask is "are gravel pits more suited to one particular use than another?" This is, in essence a question of economics. Which is the most expedient management plan? - Are any impracticable?

The simplicity of the animal communities and the controlling factors within the pit showed that the controlling factors, were mainly physical in nature. Therefore, they could be easily altered towards a desired end use. Considering first production, this should preferably be fairly high if the lake is to be developed as a fishery but low if informal recreation or water sports are planned. The level of production would respond rapidly to the introduction of fertilizer. However, due to the aerobic sediment the application would need to be maintained for a prolonged period of time since the added nutrient would be absorbed by the clay particles. Whilst this is expensive, it is also highly controllable.

The daytime distribution of midges make them a serious nuisance for informal recreationists, since they are found at sites close to the lake where many people would wish to picnic or sit. Low midge populations can be achieved by avoiding fertilization of the lakes.

Because the production within the lake is controlled mainly by abiotic factors it is obvious that the processes of excavation and reclamation will play an important part in the final structure and functioning of the gravel pit ecosystem. For example, in dry dug pits where the topsoil has been returned to the lake sediment (e.g. Linford lakes, Dovecote) there is a more pronounced growth of macrophytes than in wet dug pits. This is probably due to the presence of fine silt in wet-dug pits which inhibits plant growth by causing high turbidity in the water. Management for after use must therefore be considered before reclamation takes place,to ensure greatest efficiency.

As was mentioned at the beginning of this thesis, the work undertaken originated from a study to investigate the factors influencing duckling mortality in wet gravel pits. Whilst this is out of the mainstream of reclamation work, ducks are an important feature especially in informal recreational situations. In conclusion, the implications of this study for the management of ducks in wet gravel pits are summarised.

The most important items that a water body must supply to enable ducks to breed successfully are nesting sites and an adequate supply of invertebrate food. The provision of the former is easily undertaken by the restriction of public access and planting of certain vegetation types. However, the critical phase follows hatching,when the young ducklings must be able to gather adequate food of a high protein content (Street, 1978) if they are to survive and grow. This cannot be supplied by vegetation since the protein content is too low. The two common duck species in Britain, tufted duck and mallard, have both colonised gravel and sand pits. However, the former has fared very well with a vast increase in its population whilst the mallard has not been at all successful. This has been related to the ability of young tufted ducks to dive and feed on benthic invertebrates whilst the mallard is restricted in feeding to the scanty insect emergence,since it is unable to dive and feed on benthic larvae (Lees & Street, 1973). Improved breeding success is therefore dependent upon increasing insect emergence such that ample food is available to the duckling chicks. The levels of the chironomid populations were found to be limited by food availability and any increase in this would lead to an increase in emergence. The decomposition cycle and sediment organic matter were very low; increasing this, either by the addition of allochthanous material or by stimulating phytoplankton growth with inorganic fertilizers would undoubtedly increase the chironomid populations. The finding of a constant relation between chironomid emergence and production enables the former to be predicted from data obtained of larval abundance, thus facilitating the monitoring of potential food supply. The survival of mallard chicks in adverse weather conditions is known to be low, this is attributed to an abstenance from feeding and to heat loss following soaking (Kear, 1965; Nye, 1964). However, under these conditions insect emergence is much reduced so the exact cause of mortality may be due to lack of food rather than the inactivity of the duckling. Gravel pits are therefore inhospitable habitats for mallard ducklings, active management to provide shallow feeding areas and high levels of aquatic insects are needed, this can best be achieved by fertilization. The main aim should be to stimulate the flow of energy through the detritus pathway which, in lakes, is connected, via the extensive invertebrate detritivore communities, to higher trophic levels both within and outside the ecosystem. Stimulation of direct primary production is not of immediate importance since the herbivore food chain represents a minor energy flux. However, phytoplankton later enters the detritus food chain and is available to chironomid larvae. The management of this ecosystem therefore rests in changing the patterns of energy flux in the detritus pathways. Lakes represent an ideal system for studying the functioning of the decomposition system since both the organisms involved and the inputs are readily sampled and quantified, it is therefore to limnology that we should look for a fuller understanding of the interaction between nutrient cycling and energy flow.

Gravel and sand pits present both an opportunity and a challenge to ecologists. We have available a new resource which, if managed intelligently, can be used to meet part of this nation's need for water space in the future. The realisation of this will rely upon the cooperation between the gravel industry, local government and ecologists and we should look towards a interdisciplinary approach to habitat management for the optimum solution of how to use these resources.

SUMMARY

1. The gravel and sand pits sampled were shallow lakes ($z_m < 6$m) with surface water chemistry similar to other lakes of similar conductivity except for the low availability of phosphate ($<<10 \mu g\ l^{-1}$).
2. The sediment was very low in organic content (*c.* 3 % organic carbon) and was always aerobic.
3. The chironomid comunities, studied by emergence trapping in 1975/76, were found to differ from other lakes described in the literature. A subsequent study of the benthos in a number of gravel and sand pits showed that the fauna was predominatly a *Polypedilum* - *Procladius* - *Chironomus* - *Tanypus* association. Both gravel and sand pits had a similar fauna.
4. The predominant benthic larvae in Black Horse lake fed on different food resourses with the exception of *Chironomus* and *Polypedilum* which both fed on detritus. *Tanypus* fed on algae, *Procladius* on Crustacea and *Cryptochironomus* on oligochaetes. *Polypedilum* and *Chironomus* may have avoided competition by being abundant as final instars at different times of the year.
5. The pattern of larval dispersion (as judged by b of Taylor's power law and the Iwao index) at the microhabitat level, and over the lake as a whole, was related to feeding behaviour. Only *Chironomus* was randomly distributed: $b \neq 1$ ($p < 0.05$). Aggregation in *Polypedilum* may have been due to a behavioural mechanism and an avoidance of *Chironomus*. *Tanypus* was not found in the main lake until summer, due to sediment instability in the spring which prevented benthic algal growth.
6. Production estimates varied from 45 to 70 kg ha^{-1} yr^{-1}. Of this over 70% was due to *Chironomus* at each station. Between one third to one half of the annual production was exported from the lake as adult emergence.
7. New gravel pit habitats were rapidly colonised by chironomids. One species predominated - *Tanytarsus gracilentus*. The initial colonist fauna rapidly changed both in composition and structure with an increase in equitability ($\bar{J}$ (1977) = *c.* 0.5 ; (1978) = *c.* 0.8)
8. Emergence was seen to change over the study period in relation to climatic factors such as temperature, and on a daily basis in response to daylight, being delayed in colder years.

9. Adult male chironomids were found to rest in the vicinity of their swarm markers during the day. In contrast females were found mainly near the water's edge.
10. Parasitism of *Einfeldia dissidens* by a mermithid nematode was seen to cause changes in adult morphology, particularly in head shape, with the adult body being female-like irrespective of the primary sex of the infested individual.
11. Wet gravel and sand pits can be readily managed to suit a variety of recreational uses. Their inherent low productivity could be increased by chemical or organic fertilization if desired.
12. Fertilization of the shallow water areas increase insect emergence and have a beneficial effect on the survival of mallard ducklings. It is known that these suffer a high mortality in wet gravel quarries and this is probably due to the restricted and scanty emergence, since ducklings feed mainly on emerging chironomids and are unable to feed on the benthos.

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