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**Charles, W.N., East, K., Brown, D., Gray, M.C. & Murray, T.D., 1974 The production of larval Chironomidae in the mud at Loch Leven, Kinross. In: *Proceedings of The Royal Society of Edinburgh Section B (Biology)* vol.74 241-258.**

*PROC. R.S.E. (B), 74, 15, 1972/73*

# 15.—The Production of Larval Chironomidae in the Mud at Loch Leven, Kinross. By W. Nigel Charles,† Kenneth East,† David Brown,* Muriel C. Gray and Thomas D. Murray,† The Nature Conservancy, Edinburgh and London.* (With 5 text-figures and 6 tables)

## SYNOPSIS

The production of four dominant species of larval Chironomidae (*Chironomus anthracinus*, *Glyptotendipes paripes*, *Polypedilum nubeculosum* and *Limnochironomus pulsus*) was measured and compared between different sections of the mud zone covering a total area of 662 ha (50 per cent of the loch bed) from March 1971 to March 1972. The results showed that the performance of *Chironomus* was very similar throughout the area in respect to numbers, growth and production but it was more variable in other species. The mean annual dry weight production of *Chironomus* over the whole area was 26 g/m$^2$ and the four species together raised this to 29 g/m$^2$ (equivalent to 579 k J/m$^2$). The numbers of *Chironomus* increased and *Glyptotendipes* decreased through the sampling period. Estimates of biomass are given for other larval Chironomidae present in the mud. The accuracy of the results is discussed, as well as the variations in the seasonal growth of larvae and the changing composition of the community; some tentative estimates are given of assimilation by larval Chironomidae. The methods used for analysing these data are described in an appendix.

## INTRODUCTION

As part of the IBP project at Loch Leven we measured the production of larval Chironomidae of the deeper water within 662 ha of the mud zone between March 1971 and March 1972. In this paper we compare the major characteristics of these populations and give estimates of mean production by four important species. Analyses of the relationships between larval populations and environmental factors at different points within the mud zone will be published later.

The four large, univoltine chironomids (*Chironomus anthracinus* Zett., *Glyptotendipes paripes* Edw., *Polypedilum nubeculosus* Mg. and *Limnochironomus pulsus* Walk.) were studied in detail, and together accounted for most of the production by zoobenthos in the mud. There were also a number of less common univoltine species and some smaller species which were multivoltine. For these we measured biomass and only give tentative estimates of production by the whole larval community. Among these latter groups the Tanypodinae were abundant, and were represented by five multivoltine species; the results for these will be published later when the field material has been fully analysed.

This study concentrated on the Chironomidae because they were the dominant member of the zoobenthos in the mud (Maitland 1974) and because they were part of the food chain leading to fish and diving duck. With the exception of *Cryptochironomus* and the Tanypodinae, which were at least partly carnivorous (Morgan 1972), larvae mainly fed on phytoplankton. Analyses of the contents of trout (*Salmo trutta* L.) and perch (*Perca fluviatilis* L.) stomachs from fish caught in deep water between May and September 1968 showed that larval Chironomidae formed 66 per cent and 92 per cent respectively of the volume of their diet. However, Thorpe (1974) suggests that between July and September 1971 they were less important, contributing

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only 14 per cent and 12 per cent to the diet of these fish. Some of this discrepancy may be due to differences in methods of collection.

Preparatory studies in the mud zone lasted for several years. Morgan (unpublished data) carried out preliminary surveys in 1966–68. In 1968 changes in the standing crop of larvae were measured at points in the mud zone (Maitland *et al.* 1972) and in October 1968 there was a wide survey of all the zoobenthos in this area (Maitland 1974). Methods of estimating production were studied during 1969–70 and tested in an 80 ha section of the mud zone during the following year (Charles in press). These investigations also provide some comparisons of the status of larval populations in the mud through a 7-year period.

## STUDY AREA

Loch Leven, sited on the plain of Kinross in central Scotland, has a surface area of 1331 ha. Mud covers 756 ha or about 57 per cent of the loch bed, but areas >10 m deep were excluded from this study, this reduced the sampling area to 661·5 ha (text-fig. 1). About 65 per cent of the boundary abutted on to sand, 30 per cent on the deeps and 5 per cent on the stony shores. To facilitate comparisons between populations occupying different sections of the loch, the area was divided geographically into seven strata, each of 94·5 ha. Each stratum was divided into 378 0·25-ha squares from which random sampling stations were chosen.

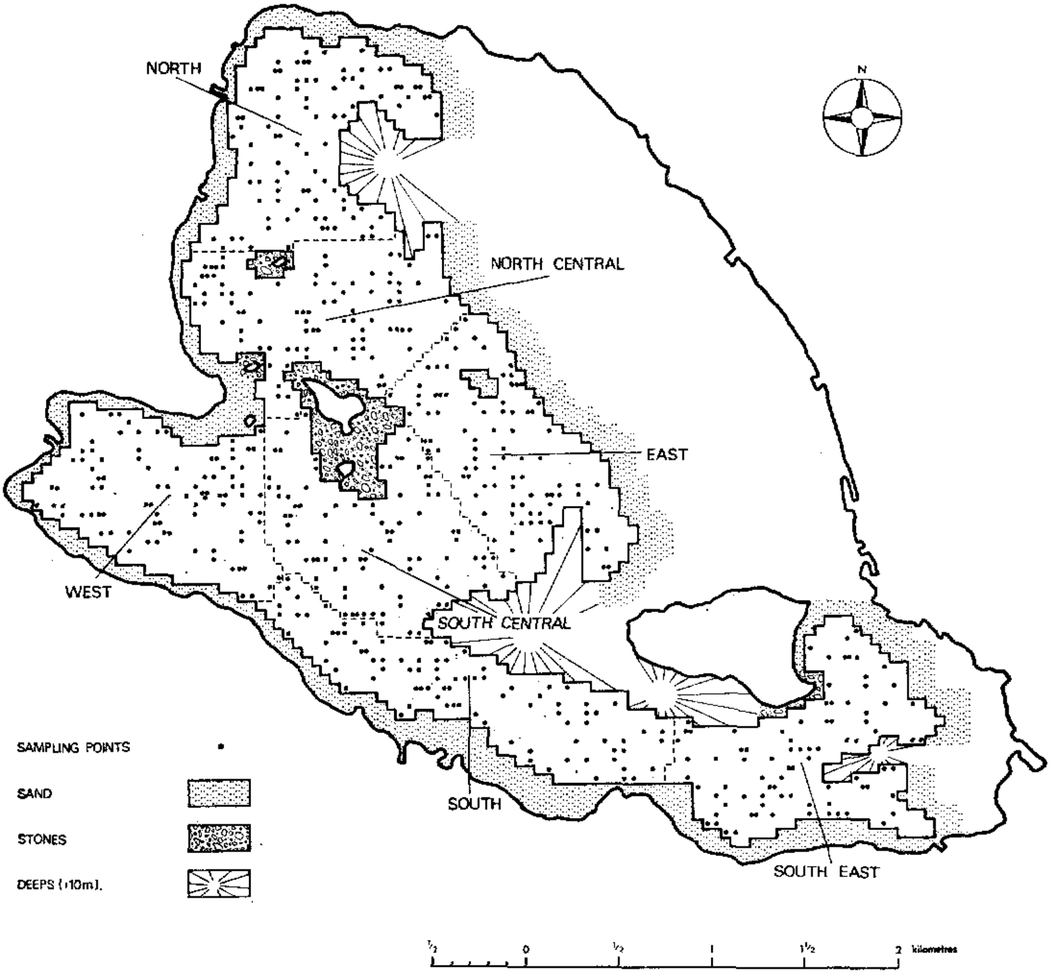
TABLE 1

*Some features of the strata in the mud zone at Loch Leven* (see text-fig. 1)

| Stratum | Mean depth (m) | % Stratum with median grain size $<16\ \mu m$ | % Stratum with organic carbon $>5\%$ | % Solids in fresh wet mud samples |
|---|---|---|---|---|
| North | 4·1 | 19 | 26 | 6·8 |
| North Central | 3·8 | 31 | 45 | 7·1 |
| West | 3·0 | 45 | 13 | 8·5 |
| South Central | 4·7 | 91 | 82 | 5·8 |
| East | 5·5 | 54 | 37 | 5·3 |
| South | 4·1 | 67 | 39 | 7·5 |
| South East | 4·6 | 32 | 29 | 6·1 |

Water temperature exceeded 20°C for short periods in summer and dropped to 0·8°C in winter at the bed. There was little stratification within the study area during the summer of 1971 and the loch was virtually ice-free during the following winter. It is subject to current and wave action which occasionally disturbed the mud in the shallower points of the study area (Smith 1974).

The loch bed sloped gently towards the north and south deeps, giving a mean depth of 4·5 m within the study area. It usually had a flat unbroken surface, but occasionally, perhaps as a result of storms, a series of small humps and depressions were noted by divers. No macrophytes were found within the area. The broad physical characteristics of the loch bed varied between strata (table 1). The mud became increasingly flocculent in the deeper parts of the loch, with solids forming about 15 per cent of the volume at 3 m and falling to 4 per cent at a depth of 10 m. These figures only applied to the surface layer and below 7·5 cm the mud became noticeably thicker. Core profiles from shallow water usually had a brown oxidised layer of 1–2 cm, often with a green film of algae, overlying a thin layer of black reduced mud. Below 5 cm the cores were composed of brown or dark brown mud. The black reduced layer of mud became progressively thicker with depth until in samples taken at 10 m it often reached the bottom of the core.



TEXT-FIG. 1.—Loch Leven showing the division of the study area into seven strata, together with sampling points and the characteristics of adjoining areas.

## METHODS

### *The Sampling Scheme*

Some preparatory investigations into methods have already been described (Maitland *et al.* 1972) and will only be mentioned briefly here. The Jenkin mud corer (Mortimer 1941), collecting a 6·9 cm core, was chosen because it was shown to give significantly higher counts of larvae than the F.B.A. automatic mud sampler and the

Ekman mud grab suggesting that it was more efficient in mud at Loch Leven. The numbers of larvae in Jenkin cores were also compared with those from diver-operated hand cores and from sections of mud of 0·25 m$^2$ pumped from the loch bed. These gave similar estimates of density, showing that few larvae were missed by the corer. All larvae, except *C. plumosus* L. which was scarce in 1971–72, were restricted to the top 10 cm of mud and the sampler was weighted to penetrate greater than this depth, most cores reaching >15 cm.

The relationship between the horizontal dispersion of larvae in the mud and the numbers collected in Jenkin cores was assessed by measuring the variations in numbers from samples taken within areas of 10 m$^2$ and of 12·5 ha. In the summer of 1970, when these trials were conducted, the populations were unevenly dispersed, even within the smaller areas. To save time a number of bulked Jenkin cores taken around a point were used as the basic sampling unit when estimating mean densities with an area, thereby reducing the number of points to be sampled. This study allowed some tentative predictions to be made of accuracy of counts expected from different sampling efforts. The accuracy of results achieved during a 10-month sampling programme in 1970–71 were approximately as predicted and the current programme, which incorporated some practical and theoretical improvements, evolved from this work.

The objective was to measure the mean production of abundant Chironomidae within the study area through 1 year as accurately as possible relative to the time and labour available. It was hoped to keep confidence intervals on estimates of production to $<\pm 25$ per cent accepting that this figure would be higher for less common species and for estimates from individual strata within the mud zone. Six randomly sited points were sampled within each stratum during each sampling session. Six Jenkin cores were taken at each of the points within an area of 1 × 8 m; five cores were bulked and used for production measurements and one was retained for other purposes. Fifteen sets of samples were taken through the year, at fortnightly intervals between May and August, extending to 3-monthly intervals in winter when population changes were expected to be small. About 3750 cores were taken for this study.

Subsidiary measurements included emergence counts and collections of adults and eggs for taxonomic purposes to assist in determining life histories.

### *The Separation and Identification of Larvae*

The five bulked cores were sieved in mechanically operated baskets (Slack 1972) with mesh apertures of 175 microns. The use of smaller mesh would have led to difficulties in sieving and it was accepted that a few of the smallest larvae would be lost (Jonasson 1955). To reduce sorting all samples obtained between 30 April and 6 July, when many early instars were present, were subsampled. Two replicated subsamples were taken so that the efficiency of the process could be monitored; the degree of subsampling varied from 5 to 15 per cent of the total volume per replicate according to the numbers present. The larvae, together with other organic material, were separated from the mud residue by flotation using a sucrose solution with a s.g. of 1·12–1·15 (Anderson 1959). This process was used with live animals and trials showed that over 95 per cent of all small larvae and virtually all large larvae were separated. The samples were preserved in 5 per cent formaldehyde and after they had hardened for 24 hours they were stored in a deep freeze as a precaution against weight losses due to this preservative.

The samples were sorted using stereo-microscopes (×10–×40) and virtually all larvae over 4 mm in length could be identified at these magnifications. These were dried at 80°C and weighed individually on an electrobalance which weighed down to 1 $\mu$g: all values given in the results refer to oven-dry weights. Comparisons between larvae dried in desiccators and then dried at 80°C showed that 0–5 per cent of their dry weight was lost at the higher temperature. In all larvae $<4$ mm long, body lengths were measured and converted to estimated dry weights using regressions calculated from the weight of groups of measured animals. Many small individuals could not be identified from gross features. After measurements, their head capsules were removed and they were mounted in groups in D.M.H.F. resin which cleared them sufficiently for a detailed examination of mouth parts. Specific characteristics of first instar larvae differed from those described for later stages and these were therefore checked from reared material.

Samples of *C. anthracinus*, *Polypedilum* and *Limnochironomus* collected on six occasions during the sampling period were used to determine energy equivalents and ash contents of larvae. There was only sufficient material of *Glyptotendipes* to allow analyses from samples collected in March 1971. For this an adiabatic bomb calorimeter was used and because $>50$ mg of larvae were required for each measurement, replication was only possible in samples of *C. anthracinus*.

### *Analyses of Data*

Production of the four common univoltine species was estimated by numerical rather than graphical methods, as was the biomass of other types of larvae.

For the period between each sampling production was calculated from the average number of each species present multiplied by the weight increment of individuals (Edmondson and Winberg 1971).

This calculation could only be used for situations where a cohort could be followed from the start to the end of a period of measurement. Populations were increasing in the loch from the end of May until mid-July due to immigration of young larvae (table 3) and other methods had to be used to calculate production at these times. An account of the methods used to analyse the data is given in an appendix.

## RESULTS

### *Life Cycles*

A list of species recorded in the study area between March 1971 and March 1972 is given in table 2.

In *C. anthracinus* prepupating larvae were first noted in late March and pupae were present in the samples by late April, with emergence continuing until early June. Apparently all larvae had a life cycle of 1 year (cf. Jonasson 1972). First instar larvae colonised the mud from the end of May until mid-July (table 3), they probably spent some time in the water column (Davies 1974) and therefore had been exposed to the mixing action of the horizontal water movement (Smith 1974). Emergence in the other three species did not start until mid-May and was less protracted. There were apparently no large-scale movements of larvae between different sections of the loch once the initial colonisation was complete. There were two main growth periods, one in summer and the other during the following spring. Two events suggested that this pattern could vary markedly in this loch. In 1969 there had been a partial second emergence of *Glyptotendipes* in late August, and in 1971 about 5 per cent of the *Limnochironomus* population grew rapidly and emerged in late summer. Their numbers were too low to warrant separate treatment.

TABLE 2

*Chironomidae found in the mud zone at Loch Leven during 1971-72. 'Type' after the name indicates that identification was from larvae only, using the key quoted. Adults were identified by reference to Coe, Freeman and Mattingly 1950*

Tanypodinae
- *Pentaneura monilis* Linnaeus
- *Procladius simplicistilus* Freeman
- *Procladius crassinervis* Zetterstedt
- *Procladius choreus* Meigen
- *Psilotanypus rufovittatus* van der Wulp

Orthocladiinae

Chironominae
- *Chironomus anthracinus* Zetterstedt
- *Chironomus plumosus* Linnaeus
- *Limnochironomus pulsus* Walker
- *Cryptochironomus vulneratus* Zetterstedt
- *Cryptochironomus pararostratus* type (Chernovskii 1949)
- *Cryptochironomus pectinatellae* type (Mason 1968)
- *Glyptotendipes paripes* Edwards
- *Paratendipes albimanus* type (Bryce & Hobart 1972)
- *Microtendipes diffinis* type (Bryce & Hobart 1972)
- *Polypedilum nubeculosus* Meigen
- Tanytarsini (Chernovskii 1949)
- *Tanytarsus mancus* type (Chernovskii 1949)

TABLE 3

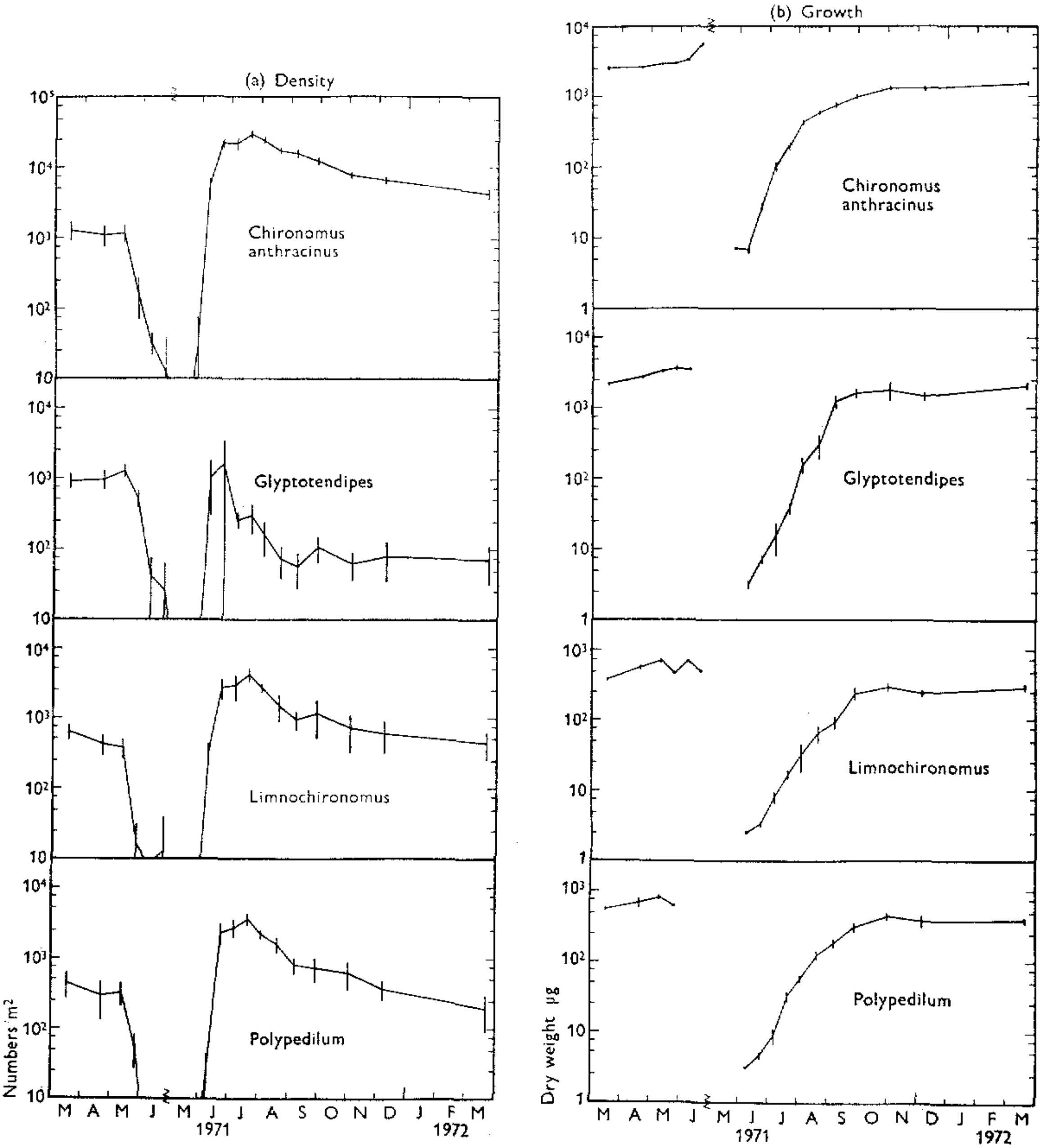
*The numbers and weight range of* Chironomus anthracinus *during the period when small larvae were immigrating to the study area*

| Weight (μg) groups | *Chironomus* Larvae/m² | | | | | |
|---|---|---|---|---|---|---|
| | 25 May | 8 Jun | 22 Jun | 6 Jul | 20 Jul | 3 Aug |
| 0–100 | 24 | 5,252 | 21,592 | 12,074 | 8,365 | 800 |
| 110–200 | — | — | 194 | 7,692 | 9,614 | 5,527 |
| 210–300 | — | — | — | 1,446 | 7,368 | 5,939 |
| 310–400 | — | — | — | — | 1,443 | 3,066 |
| 410–500 | — | — | — | — | 632 | 2,315 |
| 510–600 | — | — | — | — | 560 | 1,818 |
| 610–700 | — | — | — | — | 193 | 1,297 |
| 710–800+ | — | — | — | — | 496 | 2,872 |

Other large species followed the same pattern. Probably *C. plumosus*, which emerged from May to August, sometimes had a 2-year life cycle since large larvae were occasionally found throughout the summer. Young larvae from this species could not be separated from those of *C. anthracinus*, and based on the counts of the larger larvae it was assumed that they contributed less than 1 per cent to the combined populations. In the smaller species, emergence commenced in late March or April and continued with few breaks until September or October. Their communities were composed of a variety of instars at all seasons including the winter. Of these, only the Tanypodinae were abundant during 1971–72.

*Seasonal Fluctuations in Numbers*

Estimates of mean seasonal densities of *C. anthracinus*, *Glyptotendipes*, *Limnochironomus* and *Polypedilum* for the whole mud zone are given in text-fig. 2*a* and for



**TEXT-FIG. 2.**—Seasonal changes in (*a*) density and (*b*) mean weights of larvae for each generation within the whole study area: 95 per cent confidence intervals are shown.

*C. anthracinus* and *Limnochironomus* within each stratum in text-fig. 3*a*. In *C. anthracinus* there was a tenfold difference in densities between strata in March 1971, but a year later the ratio was about 2 : 1, which was less than the 95 per cent confidence intervals on these estimates. This pattern was reversed in *Glyptotendipes* which had almost disappeared from the southern section of the loch by the end of this study. *Polypedilum* and *Limnochironomus* behaved similarly throughout this period, their numbers varying by as much as 10 : 1 in different strata. From August 1971 to March 1972 shallow strata, particularly the west area, had the highest densities, while the central and east strata, which were deep areas, had the lowest densities.

### *Mean Weight and Growth*

Growth curves showing the mean estimates for the whole study area are given in text-fig. 2*b* and data from individual strata for *C. anthracinus* and *Limnochironomus* in text-fig. 3*b*.

The larval populations grew in a similar and consistent manner throughout the study area and the weight increases followed typical growth curves. However, rates were less regular in *Limnochironomus* than in other species; larvae from the north and east strata showed significant losses in weight between 20 August and 7 September and subsequently the overwintering larvae within these two areas were lighter than those in others. Because recruitment lasted for several weeks, incrementing populations were composed of increasingly wide ranges of weight groups in summer.

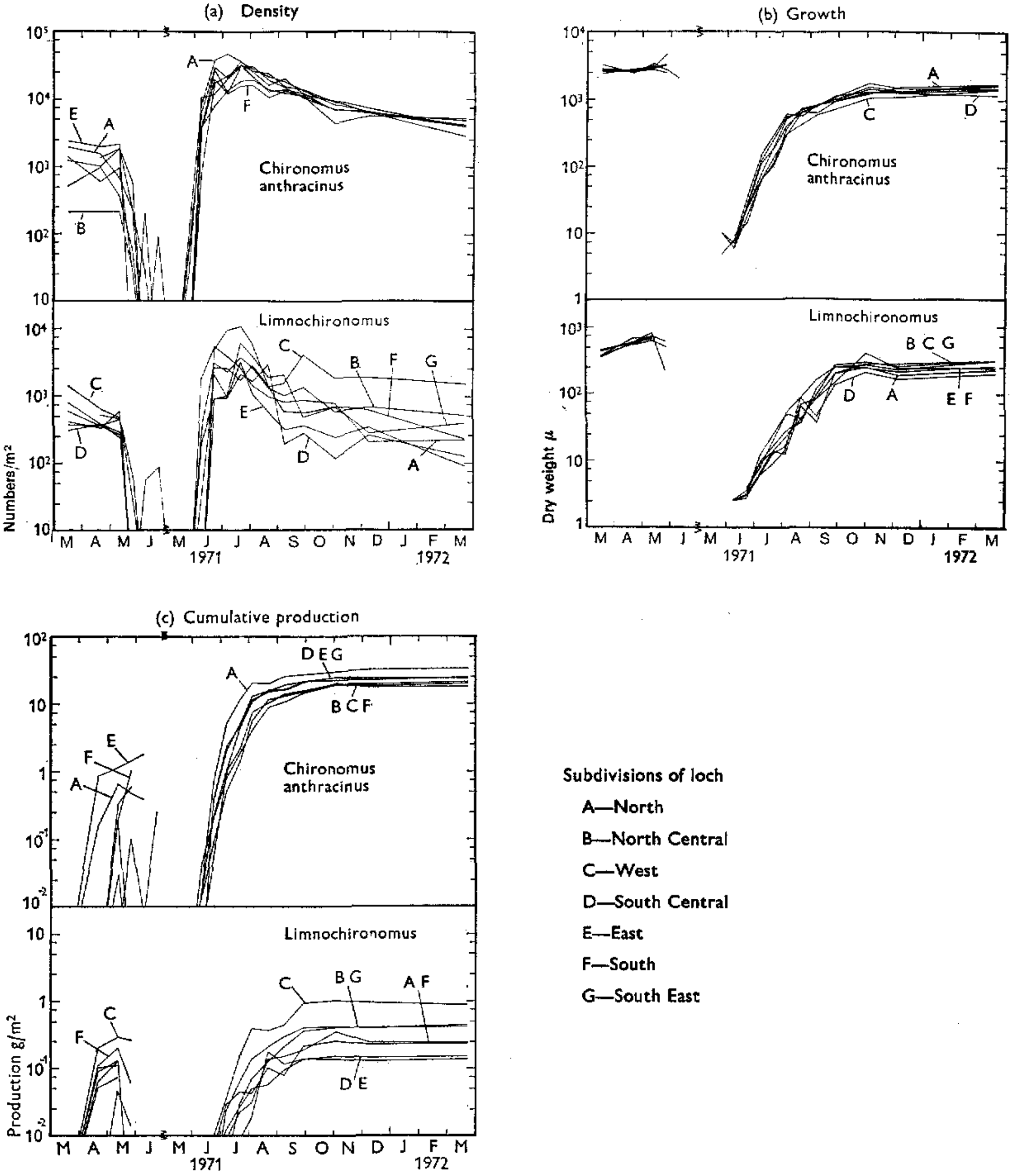
There were some marked differences between the two generations of larvae. The mean weights in the four species were significantly higher in March 1971 than in March 1972. When sampling commenced, weights were close to those normally attained prior to pupation and therefore there was little growth in the spring of 1971. During the following summer and autumn, young larvae only reached about 60 per cent of their expected maximum weights and this was maintained through to the following March, thus giving the low figures that were recorded.

### *Biomass*

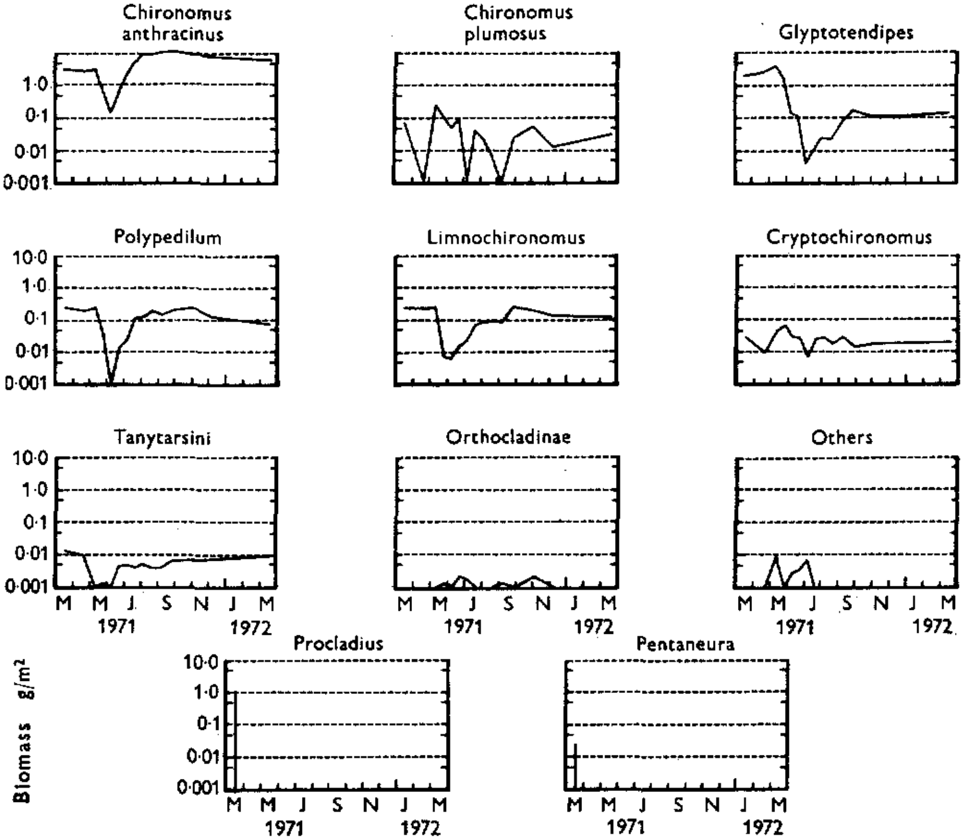
Seasonal estimates of mean biomass within the whole study area are given in text-fig. 4 for all larval Chironomidae, but those for the Tanypodinae are restricted to data collected in March 1971.

In the four species described in detail, seasonal differences in biomass between strata were generally similar to those already given for numbers. Between September 1971 and March 1972 biomass differed between strata by less than ×2 in *C. anthracinus* and by about ×12 in *Polypedilum* and *Limnochironomus*. Although the counts of larvae of less common species were low and variable they were all recorded from each stratum on one or more occasions during the year. Orthocladiinae are not usually found in this type of habitat and possibly they originated from the input streams or from shallow water and had been distributed round the loch in the water column. The Tanypodinae were abundant in all samples with a predominance of small larvae; probably their biomass exceeded 1 $g/m^2$ throughout the year.

These figures also show that the range in biomass between species or genera was very large. The maximum for *C. anthracinus* was about 170 times greater than that for the combined totals from three species of *Cryptochironomus*. Even so, the latter



TEXT-FIG. 3.—A comparison between *Chironomus anthracinus* and *Limnochironomus pulsus* showing seasonal changes within each stratum in (*a*) density (*b*) dry weights and (*c*) cumulative production by each generation of larvae. Some individual strata are labelled where differences are large.



TEXT-FIG. 4.—Seasonal changes in the biomass of the Chironominae and Orthocladiinae in the mud between March 1971 and March 1972, with an estimate for the Tanypodinae for March 1971.

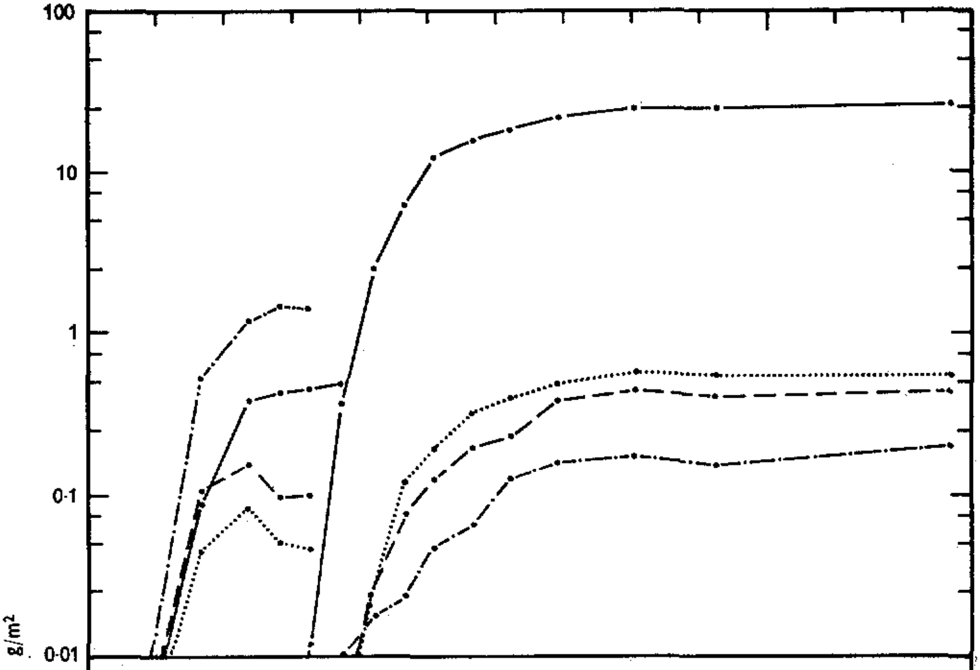
apparently maintained viable populations at least from 1968 (see later), though the more abundant species changed more through this period.

### *Production*

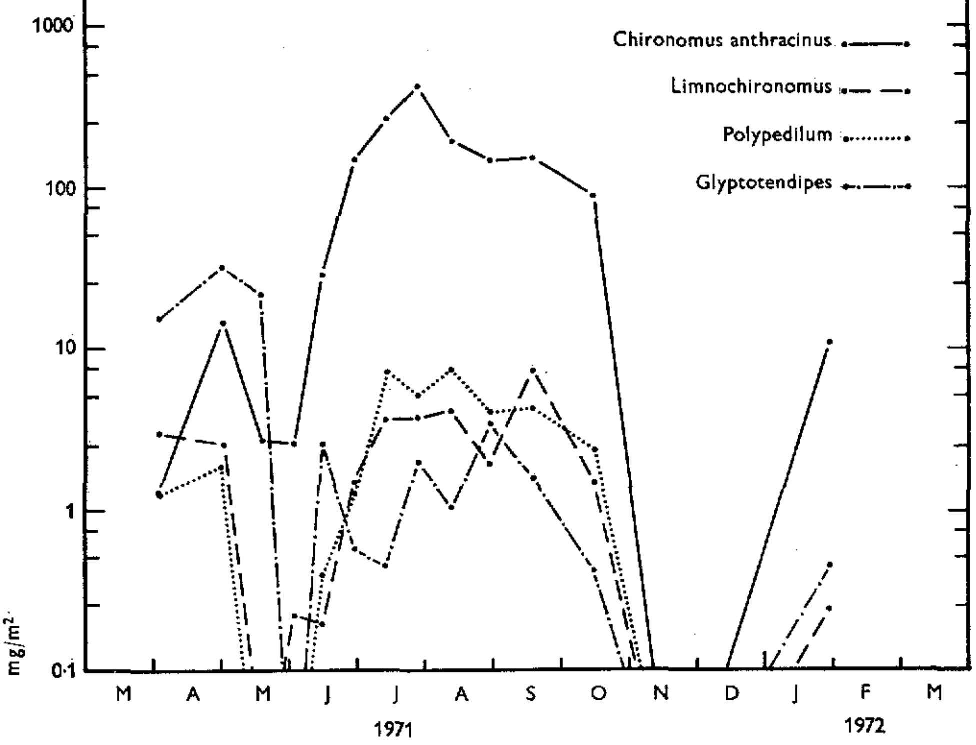
Cumulative production within each stratum by each generation of larvae is compared in *C. anthracinus* and in *Limnochironomus* (text-fig. 3*c*). Because there was little spring growth by the 1970–71 generation, there was also little production at that time. In most areas this phase was terminated by a period of negative production, probably as a result of larger larvae pupating so that the remaining populations had a lower mean weight. As predicted by data on numbers and weight for the 1971–72 generation, production by *C. anthracinus* was similar (19–35 g/m$^2$) between strata, but in *Limnochironomus* (0·14–1·0 g/m$^2$), differences were relatively greater. Equivalent figures for *Polypedilum* were 0·3–0·7 g/m$^2$ and for *Glyptotendipes* $<$0·01–0·5 g/m$^2$.

Over the whole study area most production was achieved in the summer by the 1971–72 population (text-fig. 5*a*). The exception was *Glyptotendipes* which, because of poor survival of larvae in this generation, produced most in spring 1971. Weight losses were recorded from all species from November to December, resulting in

(a) Cumulative production.



(b) Mean daily production



TEXT-FIG. 5.—(*a*) Cumulative production by each generation and (*b*) mean daily production by four dominant species of larvae within the mud zone between March 1971 and March 1972.

negative production. This had apparently been reversed by the following March, by which time spring growth had probably started.

Cumulative production increased exponentially during the first 6–8 weeks of growth by young larvae, with rates reaching peaks in July, August or September (text-fig. 5*b*). These occurred in each species just after most larvae had changed into fourth instars, which in *C. anthracinus* was in the second half of July but a little later in the other three species. The peak production rate in *C. anthracinus* was about 70 times greater than that reached by any of the other species.

Production estimates are summarised in table 4; these were calculated by summing the maximum cumulative figures reached by each generation. Meaningful 95 per cent confidence intervals can only be given for these estimates during part of the year.

TABLE 4

*Summary of production and component data for four important species of Chironomidae from March 1971 to March 1972 (P/B calculated from annual net production and from mean biomass/annum)*

| | Av. nos./m$^2$ | $\bar{w}$ dry (mg) (mean individual weight) | B dry (g/m$^2$) (mean biomass) | P dry (g/m$^2$/year) | P dry (mg/m$^2$/day) | Energy (kJ/m$^2$/year) | P/B |
|---|---|---|---|---|---|---|---|
| *Chironomus anthracinus* | 9,043 | 0·722 | 6·53 | 25·7 | 69·3 | 515 | 3·9 |
| *Glyptotendipes* | 368 | 1·774 | 0·653 | 1·66 | 4·46 | 38·0 | 2·5 |
| *Polypedilum* | 783 | 0·182 | 0·143 | 0·641 | 1·73 | 13·0 | 4·5 |
| *Limnochironomus* | 1,029 | 0·142 | 0·146 | 0·588 | 1·58 | 13·0 | 4·0 |

In the 1970–71 generation, production was only measured for a short time and rates were rather variable. Later, when young larvae were joining the second generation, mortality was estimated by indirect methods which precluded the calculation of confidence intervals. In *C. anthracinus* cumulative production between 20 July 1971 and 21 March 1972 was estimated as 19·1 g/m$^2$. An approximate 95 per cent confidence interval was $\pm$1·2 g/m$^2$ or $\pm$6 per cent, and therefore rather lower than the figure expected at the outset. The equivalent figures for the other species examined in detail were 0·44 g/m$^2$ $\pm$0·07 g ($\pm$15 per cent) for *Polypedilum*, 0·36 g/m$^2$ $\pm$0·09 g ($\pm$26 per cent) for *Limnochironomus* and 0·18 g/m$^2$ $\pm$0·04 g ($\pm$22 per cent) for *Glyptotendipes*. It is reasonable to assume that higher figures would apply to estimates of cumulative production given in table 4 for the whole period of measurement.

Estimates of ash-free energy values for the three species that were measured from material collected on six occasions (table 5) show that they were usually rather higher between May and September than at other times, but that they were similar in each species. In *C. anthracinus* and *Polypedilum* the percentage of ash in these samples was considerably higher in material from the 1971–72 generation than in samples from the previous generation, probably as a result of differences in feeding. In *Limnochironomus* ash content remained relatively low throughout. Energy equivalents for production given in table 4 were calculated in *Glyptotendipes* from energy values obtained by Maitland and Hudspith (1974).

Net annual production by the four species measured in this study totalled 29 g/m$^2$ (579 kJ/m$^2$). The standing crop of Tanypodinae did not differ much throughout the year from the figures quoted for March 1971. Assuming that the relationship between biomass and production is similar in all species (and this is likely to be an underestimate in multivoltine types), net production for all Chironomidae between March 1971 and March 1972 was very approximately 34 g/m$^2$ or 682 kJ/m$^2$.

TABLE 5

*Energy and ash values for* Chironomus anthracinus, Polypedilum nubeculosus, Limnochironomus pulsus *and* Glyptotendipes paripes *between March 1971 and March 1972*

| | Energy kJ/g (ash free) | | | | | |
|---|---|---|---|---|---|---|
| | 1971 Mar | 1971 May | 1971 Aug | 1971 Sep | 1971 Dec | 1972 Mar |
| *Chironomus anthracinus* | 23·7 | 24·7 | 23·7 | 23·5 | 23·3 | 23·4 |
| *Polypedilum* | 23·6 | 24·6 | 24·3 | 23·4 | 22·8 | 22·5 |
| *Limnochironomus* | 24·4 | 24·5 | 23·4 | 24·8 | 23·3 | 23·4 |
| *Glyptotendipes* | 25·4 | — | — | — | — | — |
| | Percentage ash | | | | | |
| *Chironomus anthracinus* | 7·7 | 9·6 | 13·6 | 14·3 | 16·7 | 15·0 |
| *Polypedilum* | 9·1 | 9·0 | 14·4 | 14·5 | 13·7 | 13·7 |
| *Limnochironomus* | 6·6 | 6·3 | 7·7 | 8·1 | 6·0 | 8·5 |
| *Glyptotendipes* | 3·7 | — | — | — | — | — |

## DISCUSSION

Estimated 95 per cent confidence intervals on mean numbers and weights within the whole sampling area were usually ±5–20 per cent, but often much wider in individual strata. Although the major sources of error are covered by these analyses, there were also some others such as the losses of larvae during sieving and flotation, that were not taken into account. Estimates for *C. anthracinus* were the most precise because it was a more abundant and evenly dispersed species than the other three species studied intensively. This study, which occupied four biologists for 4 years, was carried out in a water body which presented few practical sampling difficulties. In more varied habitats it would be even more time consuming to obtain meaningful estimates of production of the zoobenthos. If in future, production is to be used to assess and compare the dynamics of freshwater benthic populations, it is to be hoped that continuing efforts will be made to devise reliable short-cut methods of measurement.

Although in this study an attempt was made to measure the production of all larvae in the populations, one frequently adopted short cut is to measure only the larger larvae. Jonasson (1955) showed that the densities of some benthic populations have been seriously underestimated because too coarse sieves were used for sorting. However, Maitland *et al.* (1970) confirmed the suggestion by Kajak (1967) that small larvae contribute little to annual production. When using a sieve with a mesh of 0·5 mm rather than 0·125 mm, the loss of this fraction only reduced the estimates of annual production in *Stictochironomus* by 2·7 per cent. This figure will vary between species of larvae, and substrates, and according to growth rates and the amount of sieving, etc. Preliminary estimates of the maximum production attributable to small larvae that could pass through a 0·5 mm sieve have been calculated from our data and show that they contributed over 5 per cent to net annual production. More accurate estimates will be given later for each of the four common species. The identification of small larvae more than doubled the time required for sorting. Although these figures are much higher than the earlier estimate, they are of the same magnitude as numerous other errors affecting estimates of production. Unless there is unlimited manpower available, some errors are almost inevitable when estimating production. In many instances it may be preferable to subjectively estimate production by small larvae, and use the time saved to improve other aspects of sampling.

It was reported above that the mean weights in all species of larvae were greater in March 1971 than in March 1972. *C. anthracinus* showed the greatest relative difference of 2·6 mg to 1·5 mg and *Glyptotendipes* showed the least difference with 2·2 mg to 2·1 mg. Spring weights were probably determined by the amount of growth during the preceding summer and autumn, the weight remaining relatively static between November and March. In 1970 all four species sampled within a section of the mud zone had reached high mean weights by November (Charles in press), whereas in the autumn of 1971 they were considerably lighter. Thus in years when spring weights were low, production by larvae prior to pupation in May was probably high and *vice versa*. Since most species were similarly affected, some general factor such as the availability of food, crowding or changes in oxygen levels may influence growth. For example, the phytoplankton were dominated by larger species in the later part of 1971 compared with earlier years (Bailey-Watts pers. com.) and this could have influenced the performance of larvae. These differences had a marked effect on P/B ratios. In 1970–71 when larvae grew rapidly, the mean annual biomass was relatively high since larvae were close to their maximum weight for most of the year. Biomass was relatively lower, however, when growth was delayed, as was the case in 1971–72. The mean weight of *C. anthracinus* was 1·9 mg during the former period and 0·7 mg during the latter period. As a result P/B ratios ranged from 1·1 to 1·7 in 1970–71 and from 2·5 to 4·5 in 1971–72. Therefore, in this case these indices were influenced more by standing crop than by the efficiency of production. Annual production is almost certainly underestimated in this study since in the 1970–71 generation production was low between March and May and low summer growth by the 1971–72 generation reduced production during the period of measurement. Short-term production estimates for univoltine Chironomidae are probably more meaningful if they cover the life span of one generation rather than part of two generations.

The data show that there were changes in the composition of the larval community through 1 year of measurement which were part of more substantial changes proceeding during the IBP study (table 6). The initial measurements in the mud by Morgan (pers. com.) during 1967 showed *C. plumosus* to be dominant in respect to the standing crop. By 1968 *C. anthracinus* was increasing, and the former species became scarce, a trend which continued until 1972 or later. *Glyptotendipes* was abundant in the shallow part of the mud zone but a marked decline was noted in the populations during 1970, which continued in 1971. In both years there was a heavy mortality among young larvae of this species during July and August. Other changes include the loss of *Endochironomus* and of *Harnischia* and a marked reduction in the numbers of *Cryptochironomus* and of the Tanytarsini. It appears that Loch Leven is either an unstable system which possibly has cyclic changes in its communities or is permanently changing in its status.

The annual production by the Chironomidae alone which was estimated at 34 g/m$^2$ or 682 kJ/m$^2$ was roughly equal to or above those for the total macrobenthos reported from other temperate lakes (Jonasson 1972; Kajak 1972). McLusky (1974) has calculated the energy intake needed for respiration by *C. anthracinus*, *Glyptotendipes* and *Polypedilum* as 1069·7 kJ/m$^2$/year. He applied the formula of McNeil and Lawton (1970) and estimated annual production as 353·2 kJ/m$^2$, which is reasonably close to our estimate of 565·5 kJ/m$^2$ for these species. On the assumption that other non-predatory Chironomidae have similar requirements for respiration relative to temperature and biomass, a speculative estimate of assimilation by the predominantly phytophagous larval community is 1692 kJ/m$^2$/year. This is 12 per cent of the net production of phytoplankton (Bindloss 1974), which of course excludes benthic algae that may also be assimilated.

TABLE 6

*The density of larvae sampled at three points in autumn 1968 compared with mean density in autumn 1971*

| | Larvae/m$^2$ | |
|---|---|---|
| | Oct–Nov 1968 | Nov 1971 |
| *Chironomus anthracinus* | 267 | 7,386 |
| *C. plumosus* | 281 | 9 |
| *Glyptotendipes* | 1,017 | 61 |
| *Polypedilum* | 1,025 | 587 |
| *Limnochironomus* | 546 | 705 |
| *Cryptochironomus* | 189 | 15 |
| *Endochironomus* | 111 | 0 |
| *Harnischia* | 412 | 0 |
| Tanytarsini | 17,254 | 589 |
| Tanypodinae | 20,189 | 9,474 |

## ACKNOWLEDGEMENTS

It is with pleasure that we acknowledge the help received from the Supervisory Committee for Loch Leven (Chairman Dr J. W. G. Lund, F.R.S.) and from our colleagues in the research team. In particular we are indebted to Mr N. C. Morgan for his advice when planning this study, and for access to his unpublished data on the mud zone at Loch Leven, and to Dr P. S. Maitland for his guidance and encouragement throughout the programme. We wish to acknowledge the assistance given by Mr P. McDonald, Mr K. Morris and Mr D. Scrimgeour, and by Mrs I. Wildman in preparing the map. We are grateful to Mr S. Allen for carrying out energy determinations. We wish to thank these and all others who have helped us through this study.

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## APPENDIX

### Methods of Analysis By David Brown

Estimates of mean density and biomass per square metre (and their standard errors) were obtained for each species and each occasion using standard methods for stratified sampling schemes (Sukhatme 1954, 83–86). Separate ratio estimates of the mean individual weight for each species within each stratum were calculated, and then combined into a single ratio estimate for the whole sampling area for each species. This overall estimate is biased, but the bias is expected to be small compared with the standard error (Sukhatme 1954, 166–178).

During the part of the year when immigration appeared relatively small, production between times $t_i$ and $t_j$ was estimated using the formula:

$$\hat{P}_{i,j} = \tfrac{1}{2}(\bar{n}_i + \bar{n}_j)(\bar{w}_j - \bar{w}_i), \qquad (1)$$

where $\bar{n}_i$, $\bar{w}_i$, $\bar{n}_j$, $\bar{w}_j$ are estimated mean densities and individual weights at $t_i$ and $t_j$ respectively (Edmondson and Winberg 1971, 300). Approximations to the variance of this estimator and that of cumulative production were made by Taylor series expansion methods. The variance of $\hat{P}_{i,j}$ was estimated by:

$$\hat{V}(\hat{P}_{i,j}) = \tfrac{1}{4}(\bar{n}_i+\bar{n}_j)^2\{\hat{V}(\bar{w}_i)+\hat{V}(\bar{w}_j)\}+\tfrac{1}{4}(\bar{w}_j-\bar{w}_i)^2\{\hat{V}(\bar{n}_i)+\hat{V}(\bar{n}_j)\}$$
$$+\tfrac{1}{2}(\bar{n}_i+\bar{n}_j)(\bar{w}_j-\bar{w}_i)\{\widehat{\text{cov}}\,(\bar{n}_j,\bar{w}_j)-\widehat{\text{cov}}\,(\bar{n}_i,\bar{w}_i)\}, \quad (2)$$

where the covariance between $\bar{n}_j$ and $\bar{w}_j$ was estimated as follows:

$$\widehat{\text{cov}}\,(\bar{n}_j,\bar{w}_j) = \frac{1}{\bar{n}_j}\{\widehat{\text{cov}}\,(\bar{n}_j,\bar{b}_j)-\bar{w}_j\hat{V}(\bar{n}_j)\}, \quad (3)$$

$\bar{b}_j$ is the estimated mean biomass per square metre; $\widehat{\text{cov}}(\bar{n}_j, \bar{b}_j)$ was estimated directly from biomass and density data within each stratum. Cumulative production to occasion m was estimated by $\hat{C}_m$ where

$$\hat{C}_m = \sum_{i=1}^{m-1}\hat{P}_{i,i+1} \quad (4)$$

and its variance by:

$$\hat{V}(\hat{C}_m) = \sum_{i=1}^{m-1}\hat{V}(\hat{P}_{i,i+1})+2\sum_{i=2}^{m-1}\widehat{\text{cov}}\,(\hat{P}_{i,i+1},\hat{P}_{i-1,i}). \quad (5)$$

The covariance term was estimated:

$$\widehat{\text{cov}}\,(\hat{P}_{i,i+1},\hat{P}_{i-1,i}) = \tfrac{1}{4}[\widehat{\text{cov}}\,(\bar{n}_i,\bar{b}_i)\{\bar{n}_{i-1}(\bar{w}_{i+1}+\bar{w}_i)+\bar{n}_i(\bar{w}_{i-1}+\bar{w}_{i+1})+\bar{n}_{i+1}(\bar{w}_i+\bar{w}_{i-1})\}$$
$$-\hat{V}(\bar{n}_i)\{\bar{n}_{i-1}\bar{w}_i\bar{w}_{i+1}+\bar{n}_i\bar{w}_{i-1}\bar{w}_{i+1}+\bar{n}_{i+1}\bar{w}_{i-1}\bar{w}_i\}$$
$$-\hat{V}(\bar{b}_i)\{\bar{n}_{i-1}+\bar{n}_i+\bar{n}_{i+1}\}$$
$$-\bar{n}_{i-1}\bar{n}_i\bar{n}_{i+1}\hat{V}(\bar{w}_i)]. \quad (6)$$

All the estimates for the whole sampling area were assumed to be normally distributed in calculating confidence intervals from the standard errors; this is probably a reasonable approximation as each estimate is based on seven strata each with six independent samples. The standard errors refer only to errors due to spatial sampling, not to sampling in time or non-sampling errors, and so the confidence intervals quoted should only be taken as rough indicators of errors due to sampling in space.

For the period when immigration was appreciable, mean individual growth and survival cannot be directly estimated, and so formula (1) cannot be applied. Instead the survival rate was assumed to be the same during the period of immigration and for the few weeks immediately afterwards; and mean individual growth was estimated separately for each of up to five cohorts: cohort 1 entering before the first sampling occasion, cohort 2 between the first and second occasion, and so on until the end of the period. The data for the few weeks immediately after the period of immigration were used to estimate the survival rate by regression of the logarithm of mean density on time. Let $\hat{N}_1, \hat{N}_2, \ldots, \hat{N}_5$ be the estimated mean total densities on occasions 1, 2, . . ., 5 and $\hat{\lambda}$ be the estimated survival rate per week; then estimates of the densities on occasions 1, 2, . . ., 5 of individuals entering the population during the immediately preceding time interval were given by solving the following equations for $\hat{B}_1$, $\hat{B}_2$, . . ., $\hat{B}_5$:

$$\begin{aligned} \hat{N}_1 &= \hat{B}_1 \\ \hat{N}_2 &= \hat{B}_2+\hat{N}_1\hat{\lambda}^2 \\ &\cdots\cdots\cdots\cdots \\ \hat{N}_5 &= \hat{B}_5+\hat{N}_4\hat{\lambda}^2. \end{aligned} \tag{7}$$

The sampling occasions were 2 weeks apart. From $\hat{B}_1$, $\hat{B}_2$, . . ., $\hat{B}_5$, estimates of the density of each cohort at each sampling occasion were made, and the weight distributions on each occasion were apportioned between the cohorts in the ratio of the estimated densities, the heaviest individuals being regarded as the oldest. This procedure produced an estimated mean weight for each cohort at each time. Formula (1) was then used to estimate production of each cohort separately, except for the period of initial appearance of each cohort; then the following estimator was used:

$$\hat{P}_{i-1,i} = \hat{B}_i(\bar{w}_i-\bar{w}_o), \tag{8}$$

where $\hat{B}_i$ is as above, $\bar{w}_i$ is the estimated mean weight of the individuals in the $i$th cohort on occasion $i$, and $\bar{w}_o$ is the estimated mean weight of a larva entering the benthic population. The graph of mean density (that is of $\hat{N}_i$) against time over the period of immigration was smoothed by eye, before making these calculations, to produce a more realistic pattern of immigration; however, working with the unsmoothed data gave a very similar estimate of production over this period.

This procedure probably underestimates production in two ways: (1) production of larvae which enter the population and die between two sampling occasions was not included, but this would probably increase the production estimates only slightly (e.g. for *Chironomus anthracinus*, if the mortality estimate is correct, by at most 1 per cent of annual production); (2) mortality during the early stages is possibly higher than that estimated; some idea of possible underestimation is given by the fact that if mortality for *Chironomus anthracinus* during the early stages were 25 per cent per week rather than the 8 per cent used, the annual production estimate would be increased by about 10 per cent. It is recognised that the cohort method used involves a number of arbitrary elements, but it is less misleading than applying formula (1) directly to all the data. It increased the estimates of production by the latter method for this period by between 40 per cent and 60 per cent.