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10.—Production of Larval Tanypodinae (Insecta: Chironomidae) in the Mud at Loch Leven, Kinross.* By W. Nigel Charles, Kenneth East and Thomas D. Murray, The Institute of Terrestrial Ecology, † Edinburgh. Communicated by Dr J. Morton Boyd. (With 6 figures and 2 tables)

(MS received 9 June 1975. Read 27 October 1975)

SYNOPSIS

Life histories and production of the five common species of Tanypodinae (*Pentaneura monilis*, *Procladius simplicistilus*, *P. crassinervis*, *P. choreus* and *Psilotanypus rufovittatus*) in the mud at Loch Leven were measured from March 1971 to March 1972. The methods used to identify each species of larva are described. All were univoltine except *Pentaneura monilis* which had two generations per year, but the seasonal patterns of the life cycles were different. The average density of third and fourth instar Tanypodinae was 3100/m² and densities of individual species exceeded 2500/m² for short periods in *Procladius crassinervis* and *P. choreus*. Net annual dry weight production by this subfamily was 2.6 g/m² (57 kJ/m²), with individual species ranging from 1.1 g/m² (*P. crassinervis*) to 0.16 g/m² (*Pentaneura monilis*). These results are discussed briefly and compared with production estimates for other zoobenthos.

INTRODUCTION

This study contributed to an IBP project at Loch Leven in central Scotland that measured production through food chains leading to fish and wildfowl. Chironomidae were the most abundant macrobenthos in the mud (Maitland and Hudspith 1974). The life cycles and production of five species of larval Tanypodinae (*Pentaneura monilis* Linnaeus, *Procladius simplicistilus* Freeman, *P. crassinervis* Zetterstedt, *P. choreus* Meigen and *Psilotanypus rufovittatus* van der Wulp) in this substrate, measured between March 1971 and March 1972, are described here. The production of four species of Chironominae, also present in the samples, has already been described (Charles *et al.* 1974a). These were secondary producers, whereas the Tanypodinae were mainly tertiary producers.

STUDY AREA

Loch Leven has a surface area of 1331 ha, and mud covers 57% of the loch bed (Calvert 1974). Areas greater than 10 m deep were excluded from this study and the remaining area of mud was divided geographically into seven strata for sampling, each of 94.5 ha (fig. 1). To reduce the number of samples to be sorted, Tanypodinae were only analysed from the four hatched strata shown on the map.

Within the study area the bed sloped gently towards deeps in the north and south of the loch; it usually had a flat or slightly undulating surface and macrophytes were absent. The mud was flocculent, particularly in the deeper parts of the area. Cores of

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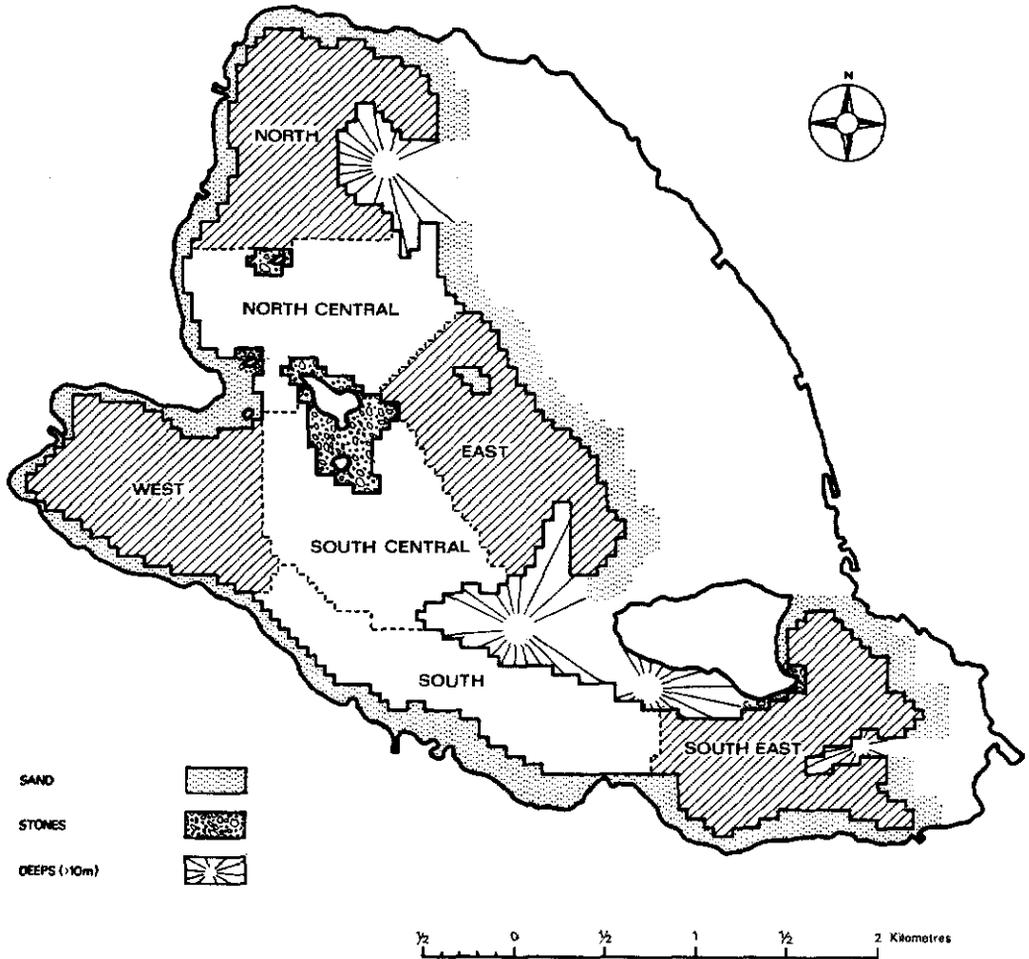


FIG. 1.—Loch Leven showing the mud zone divided into seven strata and the characteristics of adjoining areas. Samples of Tanypodinae were examined from the four hatched strata.

15 cm depth from shallow areas were mainly oxidised mud, but those taken at 10 m contained mostly black reduced mud. There was little thermal stratification in the study area in 1971-72.

METHODS

Emergence Traps

Samples of emerging adults were taken from each stratum from June to October 1971. To obtain these, undisturbed mud samples of 0.25 m² and 20 cm deep were removed with a pneumatic grab and sited in shallow water and adults caught in attached funnel traps (Murray and Charles 1975). There were no measurements of emergence early in the year.

Sampling and Sorting Larvae

Methods were developed between 1968 and 1971 (Maitland *et al.* 1972) and those used for this study have already been described (Charles *et al.* 1974*a, b*) and will only be mentioned briefly here. Samples of larvae were taken with Jenkin mud corers (Mortimer 1941) collecting 6.9 cm diameter cores, usually to a depth of more than 15 cm. Each set of samples consisted of five cores taken at each of six randomly chosen points within each stratum. The cores taken at each point were bulked and sieved, using a mesh aperture of 175 microns, which retained most first instar larvae. Initial separation of living larvae was by flotation in a sucrose solution (Anderson 1959). Later, after preservation in 5% formalin, larvae were extracted from the organic residue by hand and identified and measured using a stereoscopic microscope. They were dried at 80°C and weighed singly or in groups on an electro-balance. Energy equivalents were calculated for two grouped samples, each of 100 mg, using an adiabatic bomb calorimeter.

Larvae were examined from 14 sets of samples during the year, taken at fortnightly intervals between May and August, extending to 3 months in winter. To reduce the amount of sorting when larvae were most abundant, samples collected from 10 May to 19 July 1971 were subsampled and 10–25% of their volume examined. Thus data for this study were derived from 336 sampling points comprising 1680 cores.

Identification of Larvae

Larval Tanypodinae from Loch Leven could only be separated into two groups by gross morphological characters. Three additional methods were used to separate the five common species known to be present in the samples from the identification of adult midges:

1. Measurements of head capsules and mouth parts had previously separated some other species in the subfamily (Macdonald 1956). We measured the length of each head capsule longitudinally from the tip of the labrum to the posterior rim. Some second instars and most third and fourth instar larvae could be separated by these measurements.
2. Two species with morphologically similar larvae emerged at different times during the summer. They were separated by individually weighing all fourth instar larvae from each set of samples and plotting their frequency distribution.
3. Two types of larvae were separated by the shape and colour of their head capsules.

Initial identifications of fourth instar larvae were made by associating each group of prepupating larvae (distinguished by their swollen thoraxes) with adults of equivalent size, which were emerging at the time. Partly moulted larvae, which had two head capsules, together with data on seasonal abundance and the relative size of larvae, were used to trace the cohorts back to identify third instar and some second instar larvae. First instars were too small to measure and identify in the time available.

Analyses of Data

No confidence intervals are given for these results because the division of larvae into species and instars was sometimes conducted on grouped data and these divisions could not be allotted to individual samples. Production was estimated using the

methods applied to the Chironominae (Charles *et al.* 1971a), but these calculations could only be used on third and fourth instar larvae because many smaller larvae could not be separated. The cohort method used there to estimate production of incrementing populations was particularly applicable here, because periods of population increase were longer than in the Chironominae.

RESULTS

Identification and Emergence of Adults

Most adults were readily identified (Coe 1950), but one type from the subgenus *Procladius* proved difficult. The characters of the male genitalia were variable and most were intermediate between those of *Procladius choreus* and *P. sagittalis* Kieffer. Thus these adults could not be distinguished by this character. We therefore measured the leg ratios of animals caught between June and September and the frequency distributions of these indices were unimodal. We concluded that this material was from *P. choreus* alone, since this is the most abundant species in similar water bodies in mid-summer (Mundie 1957). It is still possible, however, that there were two species present or that this species was *P. sagittalis*. Either way, these errors would have little effect on the main findings on production.

The emergence rates of adult males caught in funnel traps between 1 June and 11 October 1971 are given in table 1. This shows that *P. choreus* (as here defined)

TABLE 1
Numbers of male Tanypodinae emerging per m² per week during the sampling periods shown, from 1 June to 11 October 1971
(Data from five emergence traps each enclosing 0.25 m² of substrate)

	Sampling periods							
	1/6 16/6	16/6 29/6	29/6 26/7	26/7 9/8	9/8 24/8	24/8 30/8	30/8 21/9	21/9 11/10
<i>Pentaneura monilis</i>	0	1	11	1	16	7	1	0
<i>Procladius simplicistilus</i>	0	1	1	0	0	0	0	0
<i>Procladius crassinervis</i>	24	6	2	5	2	2	1	0
<i>Procladius choreus</i> *	31	33	30	42	76	122	175	2
<i>Psilotanypus rufovittatus</i>	0	3	2	4	2	2	1	0

* and/or *P. sagittalis*.

was the most abundant species in these traps, and was present throughout the sampling period. *P. crassinervis* was abundant in the first samples in June, while *Pentaneura monilis* and *Psilotanypus rufovittatus* apparently emerged in the middle of the sampling period. Very few *P. simplicistilus* were caught and all were in the earlier samples.

Identification of Larval Instars

Larvae of *Pentaneura monilis* were distinguished from other Tanypodinae by their narrow head capsules. Only a few first instar larvae were found, but the remaining instars, together with prepupating larvae, were frequent in the samples. Each instar was clearly separated by capsule length as shown in fig. 2, where they occur in size classes 2, 4 and 6.

Species	Instar	Number measured
<i>Psilotanypus rufovittatus</i>	2nd	96
<i>Procladius</i> spp.	2nd	206
<i>Pentaneura monilis</i>	2nd	43
<i>Psilotanypus rufovittatus</i>	3rd	80
<i>Procladius</i> spp.	3rd	271
<i>Pentaneura monilis</i>	3rd	59
<i>Procladius simplicistilus</i>	3rd	67
<i>Psilotanypus rufovittatus</i>	4th	41
<i>Psilotanypus rufovittatus</i>	4th pre-pupating	17
<i>Procladius</i> spp.	4th	277
<i>Procladius</i> spp.	4th pre-pupating	26
<i>Pentaneura monilis</i>	4th	40
<i>Pentaneura monilis</i>	4th pre-pupating	3
<i>Procladius simplicistilus</i>	4th	29
<i>Procladius simplicistilus</i>	4th pre-pupating	16

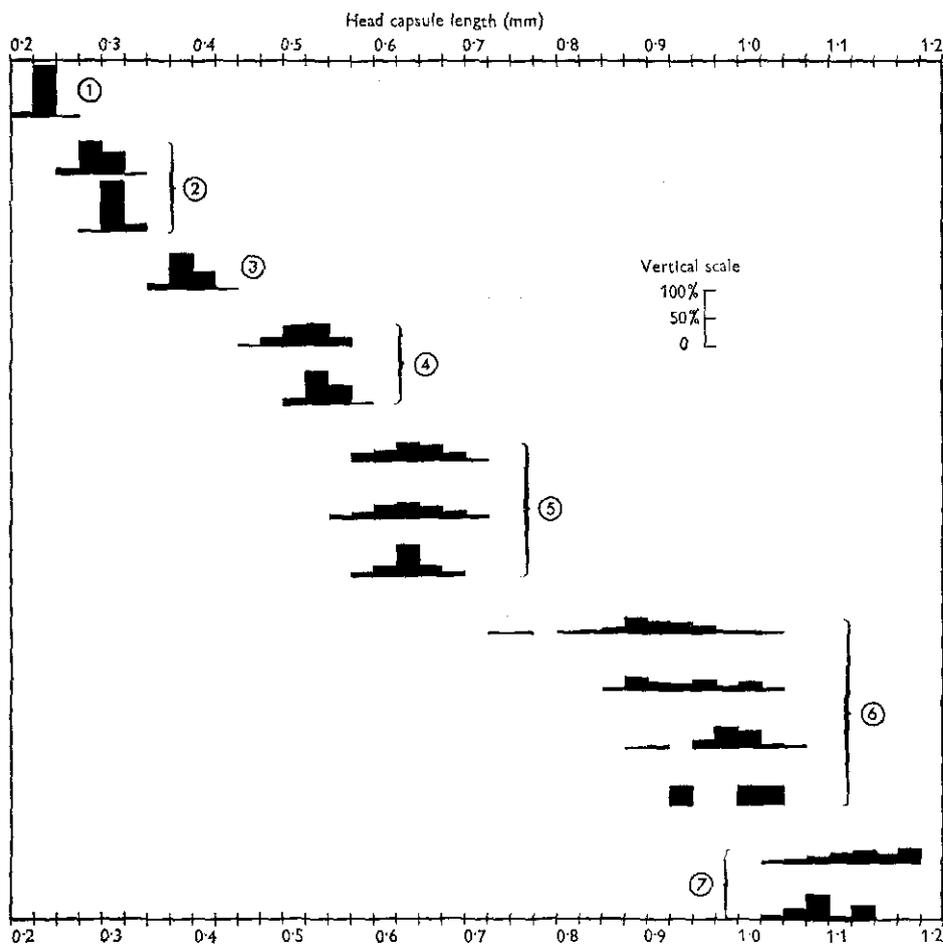


FIG. 2.—Head capsule length frequency distributions of some instars from five species of Tanypodinae showing seven size classes of larvae. *Procladius* spp. was composed of *P. crassinervis* and *P. choreus*.

Head capsule lengths from 1350 of the remaining larvae were also measured, covering a range of sizes drawn from each set of samples. They fell into seven size classes by these measurements (fig. 2), plus first instar larvae which had capsule lengths of about 0.15 mm. Three of the former classes also included prepupating larvae on some occasions. Each had a relatively small size spread with little overlap between neighbouring classes and they remained constant throughout the year. For example, mean capsule lengths of fourth instar larvae of *P. crassinervis* and *P. choreus* measured

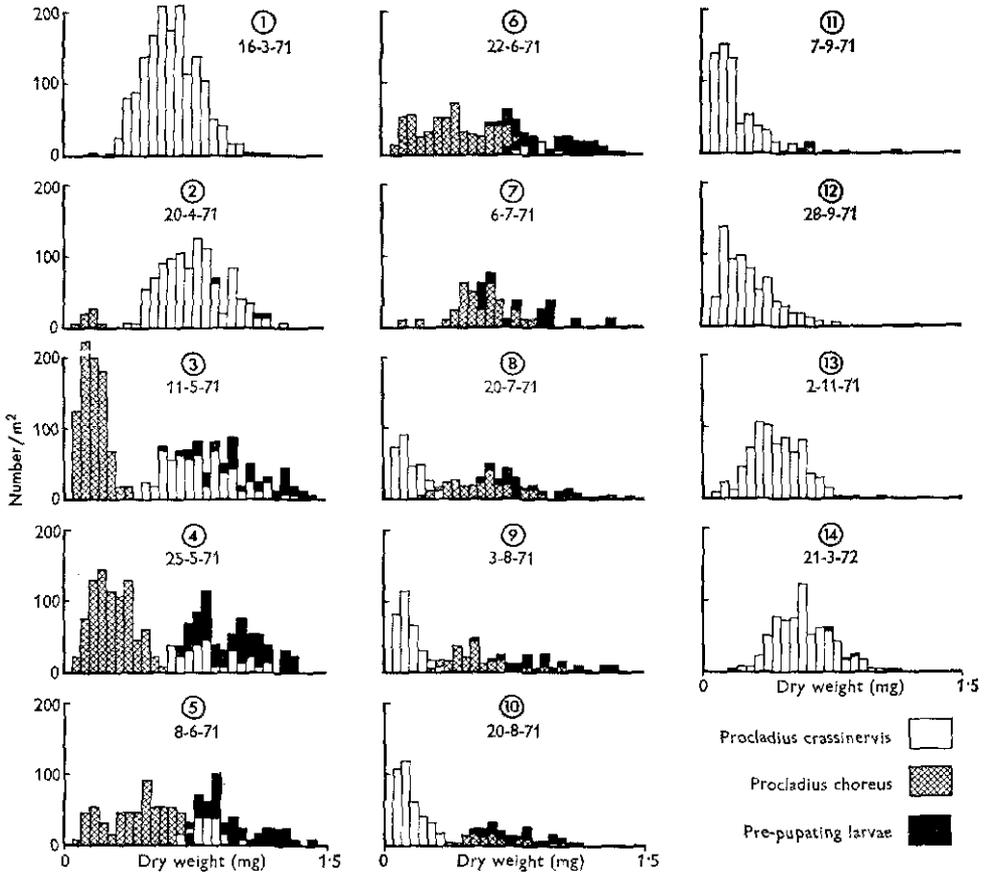


FIG. 3.—Weight distributions of fourth instar larvae of *Procladius crassinervis* and *P. choreus*, two morphologically similar species, with an interpretation of their life histories from fourteen sets of samples taken from March 1971 to March 1972.

from seven sets of samples only varied from 0.89 mm to 0.92 mm and did not differ significantly. Differences in size between species of Tanypodinae are shown by third instar larvae of *P. simplicistilus* and fourth instars of *Psilotanypus rufovittatus* which had similar head capsule lengths.

Emergence data suggested that apart from *Pentaneura monilis*, the sixth class of head capsules was composed of *P. crassinervis* and *P. choreus*. When the weight frequency distributions were plotted for these groups of larvae (fig. 3), they showed

that the two species could be separated throughout most of the year, each with a life cycle that agreed with emergence data. During June–August, however, there was some overlap between these distributions, but they only included a small proportion of each population of larvae. Third instar larvae from these species occur together in size class 4, but they could be separated because they mostly occurred at different seasons. In June and in August and September when both species had third instar larvae, this division was subjective and no attempt was made to separate their second instar larvae. The only remaining size class that needed separating to species was the fifth, in which fourth instar larvae of *Psilotanytus rufovittatus* had greenish rather flat head capsules and third instars of *P. simplicistilus* had brown and more rounded capsules.

Seasonal Life Cycles of Larvae

The seasonal densities of fourth, third and some second instar larvae are given for each of the five species in fig. 4 and the average densities of third and fourth instar larvae summarised in table 2. These show that *P. crassinervis* and *P. choreus* were the most numerous species with third and fourth instar larvae reaching up to 2500/m². *P. simplicistilus*, the least abundant species, only reached 450/m². The course and timing of the life cycles differed between species throughout the year. *Pentaneura monilis* had two generations but all other species only one. *P. simplicistilus* and *P.*

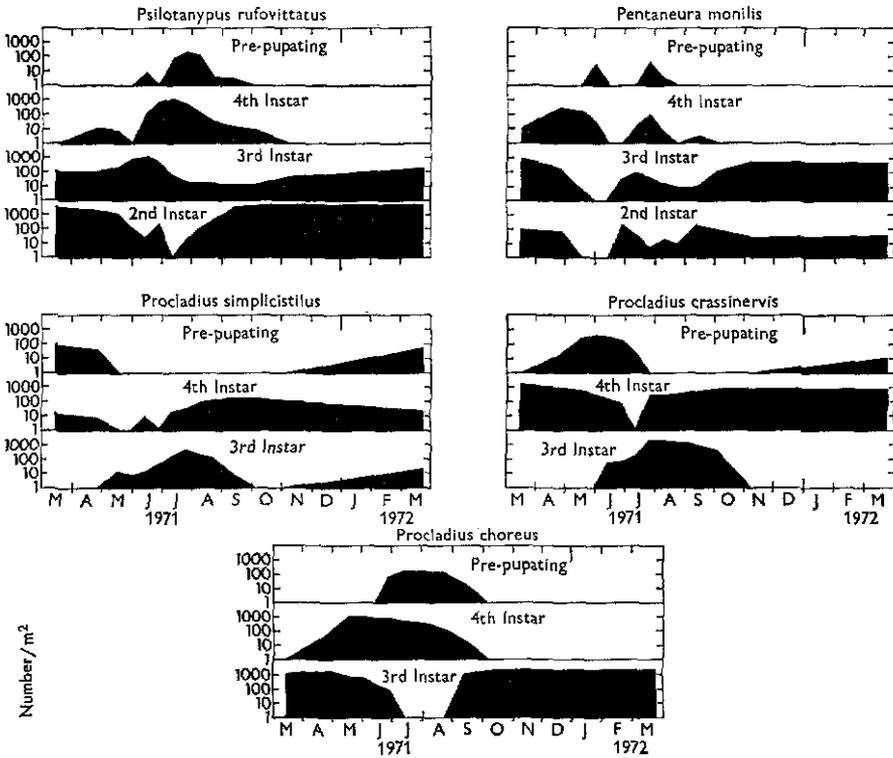


FIG. 4.—Changes in the density of some instars and of prepupating larvae from five species of Tanypodinae between March 1971 and March 1972.

crassinervis overwintered as fourth instar larvae and pupated in spring and early summer, while other species overwintered as earlier instars and pupated and emerged as adults later. Growth rates and progress through the life cycle were often rapid in summer, as shown by the first and second generations of *Pentaneura monilis* between May and August. The populations remained static through the winter and few larvae changed from one instar to the next between November and March.

TABLE 2

Summary of production and component data for five species of Tanypodinae from March 1971 to March 1972 estimated from 3rd and 4th instar larvae

	Av. no./m ²	\bar{w} dry (mg) (mean individual weight)	B dry (mg/m ²) (mean biomass)	P dry (mg/m ² / year)	P dry (mg/m ² / day)	Energy* (kJ/m ² / year)
<i>Pentaneura monilis</i>	285	0.063	17.9	163	0.430	3.55
<i>Procladius simplicistilus</i>	104	0.657	68.3	166	0.440	3.63
<i>Procladius crassinervis</i>	1027	0.474	487	1059	2.80	23.1
<i>Procladius choreus</i>	1419	0.191	271	896	2.37	19.6
<i>Psilotanypus rufovittatus</i>	268	0.093	24.9	263	0.701	5.75

* Estimated from energy and ash values from mixed samples of 4th instar larvae of *Procladius crassinervis* and *P. choreus*.

Biomass of Larvae

Seasonal changes in the biomass of third and fourth instar larvae are shown for each species in fig. 5, which also gives the biomass of all first and second instar larvae. The latter groups accounted for between 0.1 and 7.5% of the biomass of all Tanypodinae in each set of samples and averaged 3% of the total. Seasonal changes in biomass varied markedly between species. In *Pentaneura monilis*, *P. simplicistilus* and *Psilotanypus rufovittatus* there was a sharp drop between generations, but in *P. crassinervis* and *P. choreus*, which had long emergence periods, the corresponding drop was less. The estimates of mean annual biomass for each species (table 2) were influenced by the timing of the life cycle. They were relatively low for species that overwintered as second or third instar larvae compared with those that overwintered as fourth instar larvae. This accounted for *P. crassinervis* having a considerably higher mean annual biomass than *P. choreus*.

The total biomass for the Tanypodinae dropped from 1.2 g/m² (dry weight) in March 1971 to 0.7 g/m² in March 1972. This drop was mostly attributed to a decline in *P. crassinervis*. It was not general, however, since in two of the remaining species, *P. choreus* and *Psilotanypus rufovittatus*, this was reversed. The mean annual biomass for all Tanypodinae, including first and second instar larvae, was 0.896 g/m².

Production of Larvae

Estimates of cumulative and mean daily production of third and fourth instar larvae (fig. 6) show that the five species also had varied seasonal production cycles. In *P. simplicistilus* and *Psilotanypus rufovittatus* most production within a generation occurred during the summer. In *P. crassinervis* and *P. choreus* production occurred in autumn, with a second phase the following spring. In *Pentaneura monilis*, with two

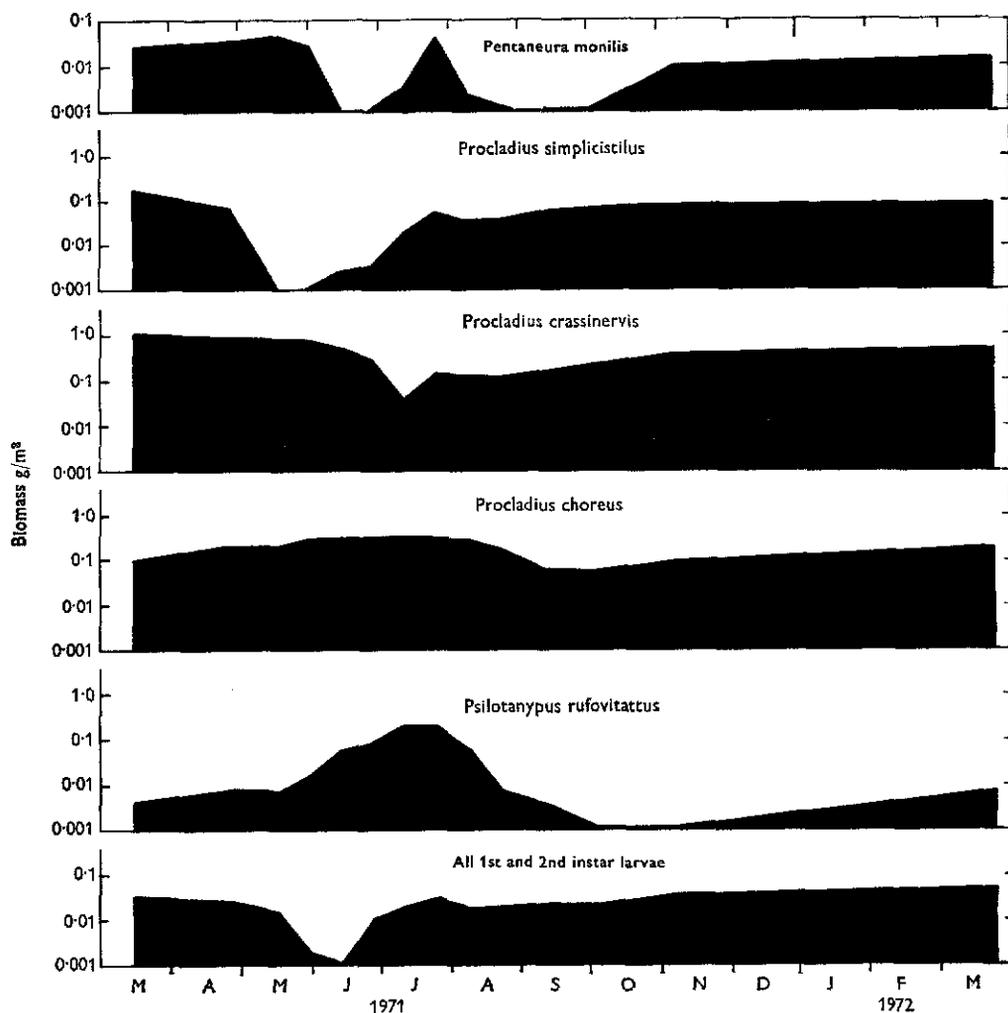


FIG. 5.—Changes in biomass of third and fourth instar larvae of five species of Tanypodinae between March 1971 and March 1972 and the combined biomass of first and second instar larvae of these species.

generations per year, there was a short production period by one generation in summer and production by the other generation spanned the winter.

Maximum daily rates of production were often similar in species with widely different annual production. For example, in *Psilotanytus rufovitatus*, the daily production reached $6.54 \text{ mg/m}^2/\text{day}$, but high rates were only recorded for two months. In *P. crassinervis* the peak production rate was only a little higher at $7.08 \text{ mg/m}^2/\text{day}$, but cumulative annual production was four times greater than the previous species, because a high rate was sustained for most of the year. Samples of fourth instar larvae of *P. crassinervis* and *P. choreus* were bulked for energy determinations to give sufficient material for analysis. Two sets of samples were used, one from July 1971 had an ash-free value of 24.0 kJ/g with 6.8% ash and the second from November 1971 with

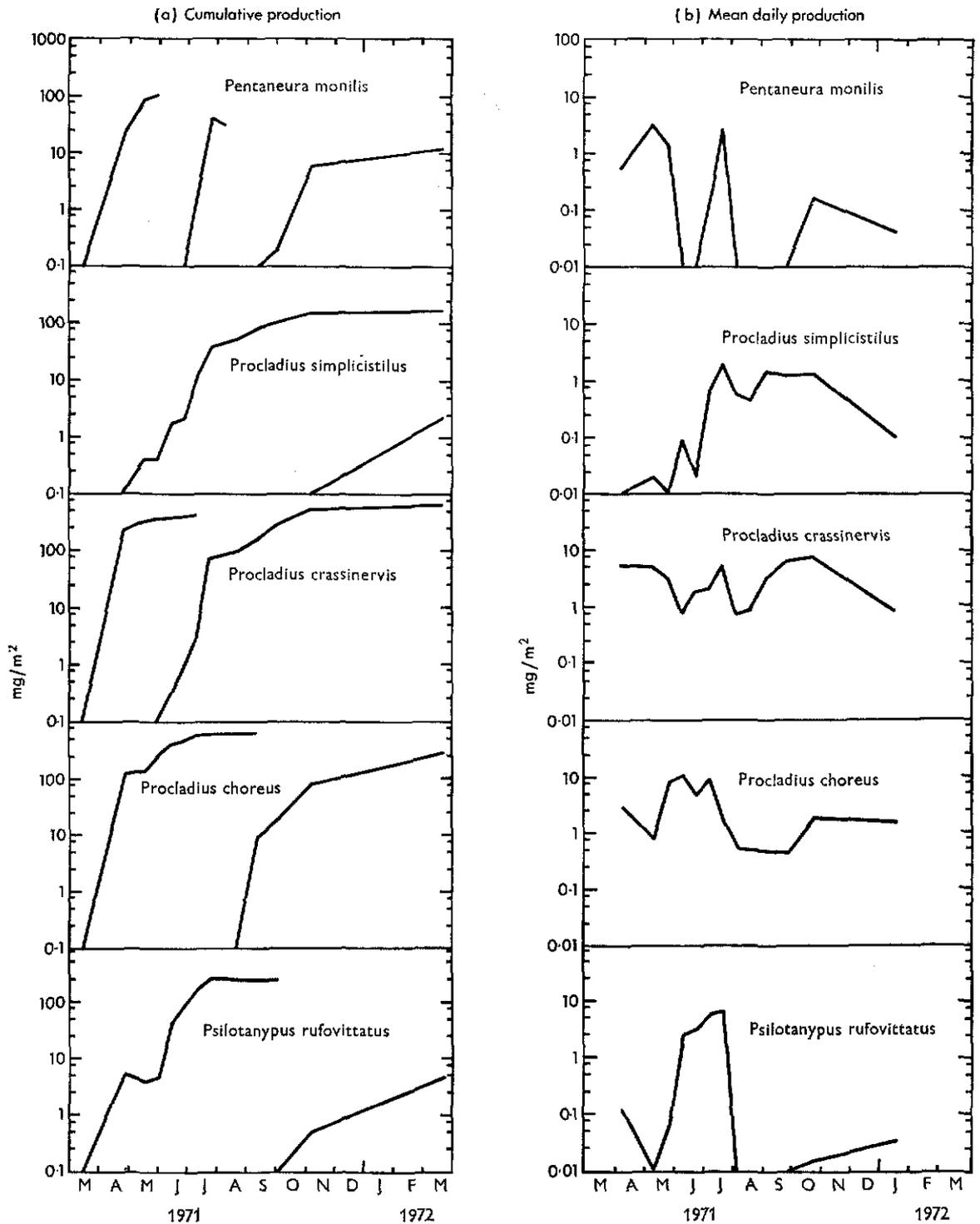


FIG. 6.—(a) Cumulative production by each generation and (b) mean daily production of five species of third and fourth instar Tanypodinae, between March 1971 and March 1972.

figures of 22.6 kJ/g and 5.8% ash. The energy estimates given in table 2 were derived from the means of these analyses and it was assumed that the values for the other three species were similar.

The summarised production data in table 2 show that net annual production by individual species ranged from 0.2 g/m² to 1.0 g/m². The latter figure, however, was only 4% of the total estimated for *Chironomus anthracinus* (Charles *et al.* 1974a) for the same period. Total net production by third and fourth instar larval Tanypodinae was 2.55 g/m²/year (55.6 kJ/m²/year). With the addition of first and second instar larvae, assuming that they had a similar P/B ratio, net production by all Tanypodinae in the mud was 2.62 g/m²/year (57.3 kJ/m²/year).

DISCUSSION

The data were obtained from only four out of the seven strata that formed the mud zone sampled in Loch Leven. Earlier results for the Chironominae (Charles *et al.* 1974a) were obtained from all strata, however. These two sets of data were therefore compared to see if the estimates for the Tanypodinae were representative of the whole zone. The first analysis compared the relative densities of individual species of larvae from 14 sets of samples in each of the four selected strata. The numbers of Tanypodinae varied less between strata than the Chironominae, averaging $\pm 45\%$ in each set of samples and ranging from $\pm 20\%$ to $\pm 67\%$ in individual species. The Chironominae varied $\pm 50\%$ with a species range of $\pm 29\%$ to $\pm 75\%$. The production estimates for Chironominae in these four strata were then compared with those from the whole mud zone. Net production by each species varied by an average of $\pm 4\%$ between the two areas and ranged from -4% to $+8\%$. It is concluded that the estimates of production by the Tanypodinae given here are likely to be within 10% of the figure for the whole mud zone and therefore they are assumed to be representative.

The identification of the five species of larval Tanypodinae was based on the length, shape and colour of head capsules. *P. crassinervis* and *P. choreus*, however, were morphologically similar and could only be separated from larval weight frequency distributions which involved time-consuming measurements. It is not certain that Tanypodinae from other water bodies could be identified using these methods, particularly if different species were present or if they were multivoltine. The measurements of head capsules did, however, give some confirmatory information which could be used elsewhere. In this study partly moulted larvae, with head capsules from two instars, were used to identify different instars of the same species, but other workers have applied Dyar's rule for this purpose. Macdonald (1956) found that head capsule lengths varied by a factor of 1.63 between different instars of *Procladius umbrosus* Goetghebuer. Ford (1959) quoted a coefficient of 1.57 based on mandible lengths of *P. choreus*. Our results show that the coefficient calculated from head capsule lengths was 1.76, ranging from 1.68 to 1.80 in individual species. This range was rather wide and the mean differed from earlier estimates. However, most larval Tanypodinae from Loch Leven, down to second instars, would be correctly identified to one of the seven groups based on head capsule length by applying a factor of 1.76 to prepupating larvae. Thus this method could be used to separate some groups of larvae but it would not necessarily separate all species. All species, except *Pentaneura monilis*, were univoltine. This had not been expected since both the long emergence

periods and the seasonal spread of relatively small larvae had suggested that these species were multivoltine. The emergence of some Tanypodinae at Loch Leven was similar to that in other British lakes. Thus Mundie (1957) found that *Pentaneura monilis* had two generations in southern England and Macan (1949) showed two peaks of emergence by this species in a moorland lake. Morgan and Waddell (1960) found that *Procladius simplicistilus* emerged in late April in a Scottish loch and Macan recorded a single short emergence for this species in May. In *Procladius crassinervis*, however, Mundie showed that there were two distinct peaks of emergence in southern England. The second occurred in August–September when little emergence of this species was found at Loch Leven.

Since the seasonal timing of the larval cycle and of emergence differed between species at Loch Leven, first to fourth instar larvae were present in the community throughout the year. Because different species complemented each other in this way the mean biomass of the Tanypodinae only varied from 0.3 to 1.2 g/m² in each set of samples. It is also possible that larvae exploited a wider range of food resources than would have been the case if life cycles were synchronised, so that all potential food sizes were always utilised to some degree.

Measurements of the Chironominae from 1968 to 1972 showed that there were marked changes in the composition of the community. Less information is available for the Tanypodinae, but measurement suggested that their density had halved between November 1968 and November 1971 (Charles *et al.* 1974a). There was a drop in the mean biomass between March 1971 and March 1972, with a maximum of a twofold difference within each species. This was small when compared with a tenfold drop in density by *Glyptotendipes paripes* Edwards during this period.

A short study at Loch Leven showed that although *Procladius* spp. fed partly on algae, they were mostly carnivorous (Maitland *pers. comm.*) and therefore we class them as tertiary producers. If certain assumptions are accepted, some general comparisons can be made between secondary production by the zoobenthos and tertiary production by the Tanypodinae in the mud. Firstly, a survey during 1968 showed that the Chironominae accounted for about 50% of the biomass of the zoobenthos in the mud (Maitland and Hudspith 1974) and this figure was applied to calculations on the 1971–72 data. Secondly, it is assumed that the P/B ratios for all benthic fauna were similar to the figure for the Chironominae (Charles *et al.* (1974a) and that their respiratory requirements relative to temperature and biomass, were also similar to those calculated for the Chironominae (McLusky and McFarlane 1974). Thus net production by the Chironominae was calculated as 680 kJ/m²/year and therefore if these constituted 50% of the zoobenthos, total secondary net production was equivalent to 1360 kJ/m²/year. Assimilation by the Tanypodinae equals the measured net production of 57.3 kJ/m²/year, plus an estimated 82.3 kJ/m²/year used for respiration. This total of 140 kJ/m²/year is equivalent to 10% of net production by the zoobenthos in the mud.

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