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THE COLONIZATION OF CALIFORNIA RICE PADDIES BY CHIRONOMID MIDGES

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SUMMARY

Temporal changes in the population structure of the colonist species of chironomids were determined from replicated rice plots flooded at two different times. These studies were conducted in 1974 and 1975 at the Rice Research Facility, University of California, Davis Farm and the Co-operative Rice Research Station, Biggs, California. The chironomid community consisted of larvae from *Paratanytarsus* n.sp., *Tanytarsus* n.sp. 6, *Cladotanytarsus* n.sp., *Cricotopus sylvestris*, *C. bicinctus* spp., *Paralauterborniella* spp. and *Procladius* spp. Most samples were usually characterized by one predominant species (Davis plots) or one to three co-dominant species (Biggs plots). Previously reported species of economic importance, *Cricotopus sylvestris*, *Paralauterborniella* spp. and *Paratanytarsus* n.sp. were usually recorded in intermediate abundance but the latter species assumed dominant status in some 1974 Biggs samples. While species richness was similar in both localities, the Davis plots supported greater numbers of larvae. Diversity (\tilde{D}) and rank correlation (γ) patterns were usually similar between plots flooded at different times at the same locality. Dissimilar abundance-rank patterns existed between localities at comparable sampling intervals.

INTRODUCTION

Rice paddies are flooded each spring in California in preparation for the rice growing season. They form an ideal habitat for observing the colonization of a temporary manmade agro-ecosystem by aquatic insect populations. Immediately on flooding, these rice paddies are invaded by numerous species of ovipositing chironomid females that most likely come from nearby pools and drainage ditches, where larvae can usually be found throughout the year. Planting of rice seed customarily takes place within a few days of the initial flooding date and the potential then exists for injury to rice by chironomid larvae. This injury in initiated shortly after planting and occasionally the larvae reduce the stand in a given field to the extent that reseeding is necessary. Larvae damage rice by consuming portions of the germinating seed and by feeding on all parts of the young seedlings (Darby 1962; Lange & Grigarick 1970).

A two-year study was therefore conducted to identify the conditions associated with rice injury by midge larvae. In this paper we discuss one facet of the study: the structure of the colonizing chironomid community during the three to four week period that rice is susceptible to damage. In particular, information was collected to describe the dominance and relative abundance patterns of *Cricotopus sylvestris* (Fabr.), *Paratanytarsus* n.sp. (= *Tanytarsus* n.sp. 5), and *Paralauterborniella* spp., the species that Darby (1962) and Lange & Grigarick (1970) considered were economically important. However, this paper examines changes in the community structure of the entire chironomid taxocene.

METHODS

Sampling

Studies were conducted during the spring of 1974 and 1975 in a series of six rice plots (each 3.7×4.6 m) at the Rice Research Facility at the University of California, Davis Farm and six plots at the Co-operative Rice Research Station, Biggs, California. In order to relate colonization patterns to the time of flooding, three plots at each site were flooded first and the other three ten days later. Flooding times within a rice growing area vary depending on weather, land preparation and the availability of water. Water at Davis was pumped from a well and transported about 0.4 km down newly constructed ditches into the plots. At Biggs, water was transported down several established ditches from a large reservoir about 8–9 km from the study site, before flowing into the experimental plots.

The shallow-water benthic sampler designed by Kellen (1954) to sample an area of 225 cm^2 was used for collecting the larvae since they were limited principally to the surface of the soft bottom. This apparatus originally penetrated the mud bottom to a depth of 5 cm and collected an excessive volume of mud and debris so two lateral aluminium flanges were attached to limit penetration to 2.5 cm. Water depth in the plots ranged from 10.2–17.8 cm.

A stratified random sampling procedure (Southwood 1966) was employed. In 1974, each plot was divided into two quadrats $(1.85 \times 2.3 \text{ m})$ and one subsample per quadrat was taken (totaling 0.045 m² per plot). Samples were taken ten, twenty and thirty days after flooding. In 1975, each plot was divided into three quadrats $(1.23 \times 1.53 \text{ m})$. On the first sampling data two subsamples were taken per quadrat but thereafter three randomly collected subsamples were taken per quadrat (totaling 0.2025 m² per plot). Samples this year were taken at seven, fourteen, twenty-one and twenty-eight days after flooding.

Each subsample was lifted slowly from the water and transferred to a large plastic bag which was then tied, placed on ice, and transported to a glasshouse for sieving through screens with mesh sizes of 4, 2 and 0.42 mm. Tap water was used to rinse material through the screens. The residue on the smallest screen which contained larvae was transferred with water into 560 ml plastic containers and brought to the laboratory for immediate examination. The larvae collected were primarily third and fourth instars. Most of the first and second instar larvae pass through a 0.42 mm opening but the use of a smaller mesh slows down the sieving of mud and other debris so much as to make it impractical.

The live larvae were floated from the debris with 96% glycerin (Mulla *et al.* 1971). Approximately 30–40 ml of glycerin was added to 200 ml of the sample and this floated more than 90% of the larvae within 10 min.

Larvae were preserved in 70% ethyl alcohol until slide mounts could be made by mounting them directly into Hoyer's solution. The larvae 1.5-4.0 mm in length were identified using the keys of Darby (1962). Unidentified specimens never reached 1% of the total of any sample and these were excluded from population analyses.

Analysis of population data

Diversity was calculated in order to examine temporal variations in this component at the community level. An unbiased version of Simpson's (1949) index produces values on a probability scale from 0.0-1.0 in ascending order with increased diversity (Pielou 1969; DeJong 1975). This probability is calculated as —

$$\tilde{D} = 1 - \sum_{i=1}^{S} \frac{n_i (n_i - 1)}{N (N - 1)}$$

where S is the number of species, n_i is the number of individuals of the *i*th species and N is the total number of individuals in the sample. This index was selected for use because it expresses the dominance or concentration of abundance of the two or three most abundant species in a community (Whittaker 1972; Poole 1974; DeJong 1975) and it is considerably more influenced by its evenness component than is the Shannon-Weaver index, the most frequently used measure of species diversity (DeJong 1975).

When species were ranked by their numbers in samples, the Kendall coefficient of rank correlation (Ghent 1963; Sokal & Rohlf 1969) was used to compare the species composition of these samples. This nonparametric test is sensitive to changes in rankings among species.

Physical-chemical measurements

For the duration of the sampling period, water samples were collected weekly or biweekly from the surface layer of one randomly selected plot from each flooded block.

 Table 1. Ranges of certain environmental factors, Davis and Biggs, 1974 and

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| | | 1975 | | | |
|---------------------------------|---------|----------|---------|------------|--|
| | D | avis | Biggs | | |
| | 1974 | 1975 | 1974 | 1975 | |
| Soil pH | 6.6-2.2 | 7.0–7.8 | 4.0-4.5 | 4.4-4.7 | |
| Water pH | 7.5-8.5 | 7.5-8.6 | 6·6–7·0 | 6·2–7·9 | |
| Total water hardness | | | | | |
| (CaCO ₃) | 269-310 | 250-320 | 36-46 | 28-42 | |
| Water conductivity | | | | | |
| $(\mu mhos/cm at 25^{\circ} C)$ | - | 529-630 | - | 59.5-110.4 | |
| S-R phytoplankton counts | | | | | |
| (no./ml) | - | 360-6048 | - | 108-4680 | |
| | | | | | |

The Hach Kit DEL/2 (Hach Chemical Co., Ames, Iowa) was used to analyse the water samples for total hardness (CaCO₃), conductivity (μ mhos/cm at 25° C) and dissolved oxygen (diurnal; modified Winkler method). Water pH was measured with a Beckman model SS-2 pH meter. In 1975, water samples were collected weekly from each plot for counting phytoplankton in accordance with the Sedgwick-Rafter (S-R) counting cell technique (Taras *et al.* 1971). Prior to flooding, the soil pH of each plot was determined. A thermograph was used at each locality to provide a record of water temperature midway (*c.* 7.5 cm) between the water surface and the mud-water interface.

RESULTS

Physical-chemical conditions

Water pH, conductivity, total hardness and soil pH were all higher at Davis than at Biggs (Table 1). Lower soil pH readings at Biggs may be the consequence of leaching of alkaline salts from the soil since rice had been grown in these plots for a number of years prior to this study. At Davis leaching is less a factor because rice had only been grown twice with a one-year fallow period between the plantings. Furthermore, irrigation of these previous plantings was by periodic flushing rather than continuous flooding. Higher water pH, conductivity, and total hardness values at Davis reflected the qualities of the well water at this locality. The Davis plots also exhibited higher phytoplankton counts (Table 1). At both sites, dissolved oxygen readings were uniformly high (>9.2 mg/ l). The shallow water temperatures recorded in 1974 and 1975 followed fluctuations in air temperatures. In general, water temperatures in the Davis plots fluctuated more widely than those in the Biggs plots (Fig. 1).



FIG. 1. Daily maximum and minimum water temperatures in experimental rice plots.

Midge colonization of the Biggs plots

Examination of 1974 data (Table 2) reveals the relative dominance of *Tanytarsus* n.sp. 6. In the later flooded plots, the parthenogenetic species, *Paratanytarsus* n.sp., assumed a position of dominance. Very few (≤ 1 larvae/0.045 m²) *Cricotopus sylvestris* (Fabr.) were recovered and predatory larvae in the genus *Procladius* were not collected in the first samples.

Generally similar patterns were observed in 1975 in all plots (Table 3) with larvae of *Paratanytarsus* n.sp. and *Tanytarsus* n.sp. 6 as the predominant forms. Larvae in the genus *Chironomus* were occasionally as or more abundant than one or both of the

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preceeding species. Cricotopus sylvestris, Paralauterborniella spp. and Procladius spp. were recorded in intermediate abundance. The two species, Cladotanytarsus n.sp. (= Tanytarsus viridiventris (Malloch)) and Cricotopus bicinctus (Meigen) were infrequently collected.

Table 2. Numbers of larvae $(\bar{x} \pm S.E./0.045 m^2)$ sampled at ten-day intervals following two flooding periods at Biggs, 1974

| a 11 | Firs | st flooding (18 | Second flooding (28 May) | | |
|--------------------------|-----------------|-----------------|--------------------------|-----------------|---------------------------|
| days after flooding) | 10 | 20 | 30 | 10 | 20 |
| Paratanytarsus n.sp. | 1.0 ± 1.0 | 1.0 ± 0 | 15.0 ± 4.4 | 21.3 ± 26.9 | 46.7 ± 28.4 |
| Tanytarsus n.sp. 6 | 18.0 ± 12.5 | 55.7 ± 26.6 | 15.7 ± 4.1 | 133·3±113·6 | 43·3±19·9 |
| Cladotanytarsus n.sp. | - | _ | - | | - |
| Cricotopus sylvestris | - | | 0.7 ± 0.6 | - | 1.0 ± 0 |
| C. bicinctus | - | - | - | - | - |
| Chironomus spp. | 19.3 ± 15.0 | 11.0 ± 10.5 | 1.3 ± 1.5 | 1.3 ± 0.6 | 1.3 ± 1.2 |
| Paralauterborniella spp. | 1.3 ± 1.5 | 9·7±11·7 | 1.7 ± 2.9 | 2.7 ± 2.9 | 1.3 ± 0.6 |
| Procladius spp. | - | 1.0 ± 0 | 5.3 ± 2.5 | - | $2 \cdot 3 \pm 1 \cdot 2$ |

Table 3. Numbers of larvae $(\bar{x} \pm S.E./0.2025 m^2)$ sampled at seven-day intervals following two flooding periods at Biggs, 1975

| ~ | First flooding (18 May) | | | | | | | |
|--|--------------------------|---------------------------|------------------------------|-----------------|--|--|--|--|
| Sampling interval (in days after flooding) | 7* | 14 | 21 | 28 | | | | |
| Paratanytarsus n.sp. | 3.7 ± 3.2 | 747·3±118·0 | $832 \cdot 0 \pm 43 \cdot 2$ | 56·7 ± 10·0 | | | | |
| Tanytarsus n.sp. 6 | 43.3 ± 26.5 | 704·0±36·6 | 82.7 ± 32.5 | 15·3±6·5 | | | | |
| Cladotanytarsus n.sp. | - | _ | 10.3 ± 0.6 | 2.3 ± 1.5 | | | | |
| Cricotopus sylvestris | 1.3 ± 1.5 | 36.0 ± 6.6 | 29.0 ± 10.5 | 7.0 ± 3.0 | | | | |
| C. bicinctus | - | $4 \cdot 3 \pm 2 \cdot 5$ | 7.0 ± 6.9 | 2.0 ± 1.0 | | | | |
| Chironomus spp. | 26.3 ± 7.8 | 93.0 ± 2.0 | 64.0 ± 26.9 | 26.7 ± 8.6 | | | | |
| Paralauterborniella spp. | 4.3 ± 4.1 | 50.0 ± 26.9 | 18.3 ± 6.1 | 3.0 ± 2.7 | | | | |
| Procladius spp. | _ | 5.3 ± 2.9 | 16.0 ± 1.7 | 17·7±4·5 | | | | |
| | Second flooding (28 May) | | | | | | | |
| Sampling interval (in | | | | | | | | |
| days after flooding) | 7* | 14 | 21 | 28 | | | | |
| Paratanytarsus n.sp. | 216.3 ± 161.4 | 556.0 ± 241.5 | 219.3 ± 51.6 | 73·0±19·1 | | | | |
| Tanytarsus n.sp. 6 | 696·3±544·6 | 142·3±109·9 | 146.3 ± 76.1 | 74·7±25·6 | | | | |
| Cladotanytarsus n.sp. | 2.3 ± 0.6 | 4.0 ± 6.1 | 1.7 ± 1.5 | 16·7±4·0 | | | | |
| Cricotopus sylvestris | 15.0 ± 6.1 | 17·0±14·1 | 31.3 ± 14.7 | 15·7±6·1 | | | | |
| C. bicinctus | - | 0.7 ± 1.2 | $2 \cdot 3 \pm 1 \cdot 5$ | - | | | | |
| Chironomus spp. | 142.3 ± 38.0 | 244.3 ± 41.0 | 162.7 ± 70.3 | 72.0 ± 30.5 | | | | |
| Paralauterborniella spp. | 14.0 ± 10.2 | 23.3 ± 13.4 | 9.0 ± 8.5 | 1.3 ± 0.6 | | | | |
| Procladius spp. | - | 9·0±6·3 | 15.0 ± 7.6 | 21.3 ± 2.1 | | | | |
| | * Comm | 11 | | | | | | |

* Sampling area was 0.135 m².

Although larval densities were greater in 1975, the data presented in Tables 2 and 3 are not strictly comparable because of differences in the sample size. Two subsamples were taken in 1974 v. six or nine subsamples in 1975. Thus, the detection of *Cladotanytarsus* n.sp. and *Cricotopus bicinctus* larvae in 1975 might be attributed to the larger sample size. Nevertheless, the discernable pattern that emerges for both years is the relative dominance of *Tanytarsus* n.sp. 6, *Paratanytarsus* n.sp. and, to a lesser extent, the genus *Chironomus*. Chironomid midge colonization in rice paddies

The data in Tables 2 and 3 also show that the population densities at comparable sampling times were consistently higher for the second flooding period each year. Water temperatures were higher in the later flooded plots and laboratory studies on development indicate that midges develop more rapidly at higher water temperatures.

Table 4. Numbers of larvae $(\bar{x} \pm S.E./0.045 \text{ m}^2)$ sampled at ten-day intervals following two flooding periods at Davis, 1974

| G | First flooding (6 May) | | | Second | Second flooding (16 May) | | |
|--------------------------|------------------------|-----------------|---------------------------|---------------|-----------------------------|-----------------|--|
| days after flooding) | 10 | 20 | 30 | 10 | 20 | 30 | |
| Paratanytarsus n.sp. | 0.7 ± 1.2 | 10.0 ± 3.5 | 31·7±19·8 | 5.3 ± 2.5 | $38 \cdot 3 \pm 22 \cdot 5$ | 5.7 ± 1.5 | |
| Tanytarsus n.sp. 6 | 40.3 ± 37.9 | 28.0 ± 13.5 | 861.0 ± 349.4 | 18·7±17·7 | 428.7 ± 161.0 | 50.3 ± 12.5 | |
| Cladotanytarsus n.sp. | _ | 2.3 ± 0.6 | 0·7±0·6 | | | 2.0 ± 2.6 | |
| Cricotopus sylvestris | 3.3 ± 2.1 | 0.7 ± 0.6 | 16.3 ± 10.2 | 0·7±0·6 | 7.7 ± 2.5 | 0 ·3±0·6 | |
| C. bicinctus | 4.0 ± 2.7 | _ | 13.3 ± 10.4 | 4.7 ± 2.9 | 11.3 ± 3.8 | 1.0 ± 1.0 | |
| Chironomus spp. | 1.0 ± 1.0 | 3.0 ± 2.7 | 9.3 ± 6.0 | 3.7 ± 2.9 | 4.0 ± 1.0 | 13.3 ± 7.5 | |
| Paralauterborniella spp. | 0.7 ± 0.6 | 23.3 ± 8.3 | 99·3 ± 38·0 | 4.3 ± 1.2 | 60.3 ± 22.5 | 2.0 ± 1.0 | |
| Procladius spp. | | | $2 \cdot 3 \pm 1 \cdot 5$ | | 2.0 ± 2.7 | - | |

Table 5. Numbers of larvae $(\bar{x} \pm S.E./0.2025 m^2)$ sampled at seven-day intervals following two flooding periods at Davis, 1975

| | First flooding (12 May) | | | | | | |
|--|-------------------------------|---------------------------|------------------------------|-----------------------------|--|--|--|
| Sampling interval (in days after flooding) | 7* | 14 | 21 | 28 | | | |
| Paratanytarsus n.sp. | | 225.7 ± 34.5 | $351 \cdot 3 \pm 30 \cdot 7$ | $201{\cdot}3\pm46{\cdot}5$ | | | |
| Tanytarsus n.sp. 6 | - | 405·0±69·5 | 2977.8 ± 725.9 | 4429.7 ± 673.8 | | | |
| Cladotanytarsus n.sp. | | | 11·3 <u>+</u> 10·1 | 103.7 ± 25.4 | | | |
| Cricotopus sylvestris | | 154.3 ± 43.0 | 670·7±112·4 | 47.7 ± 26.1 | | | |
| C. bicinctus | - | 31.0 ± 8.9 | 44.3 ± 32.5 | 13·7±13·3 | | | |
| Chironomus spp. | - | 43·7±59·2 | 41.3 ± 14.0 | 8·3±5·0 | | | |
| Paralauterborniella spp. | | 48·0±13·0 | 271.0 ± 13.0 | 11 3·3 <u>+</u> 46·1 | | | |
| Procladius spp. | - | $5 \cdot 3 \pm 4 \cdot 1$ | 130.7 ± 38.7 | 208.0 ± 17.1 | | | |
| | , | | | | | | |
| Sampling interval (in | | | | | | | |
| days after flooding) | 7* | 14 | 21 | 28 | | | |
| Paratanytarsus n.sp. | 112.7 ± 21.5 | 412·0±157·9 | 85·7±19·0 | 18.0 ± 1.0 | | | |
| Tanytarsus n.sp. 6 | $424 \cdot 3 \pm 161 \cdot 5$ | 1207.7 ± 596.9 | 970·3 ± 232·3 | 378.0 ± 71.7 | | | |
| Cladotanytarsus n.sp. | _ | - | 19·3 ± 7·5 | 12.3 ± 3.5 | | | |
| Cricotopus sylvestris | 118.3 ± 67.3 | 405·0±157·9 | 56·7±18·8 | 2.7 ± 2.1 | | | |
| C. bicinctus | _ | 36.0 ± 22.3 | 10.0 ± 2.0 | 2.0 ± 1.0 | | | |
| Chironomus spp. | 29.3 ± 8.2 | 110·7 ± 32·7 | 47.7 ± 12.1 | 5.7 ± 2.5 | | | |
| Paralauterborniella spp. | 11.3 ± 5.8 | 155.7 ± 107.3 | 24.0 ± 6.1 | 15·0±8·5 | | | |
| Procladius spp. | _ | 67·0±29·6 | 129.0 ± 12.8 | 46.7 ± 3.2 | | | |

* Sampling area was 0.135 m²

Midge colonization of the Davis plots

Numerically dominant species in 1974 were *Tanytarsus* n.sp. 6, *Paralauterborniella* spp. and *Paratanytarsus* n.sp. (Table 4). These species were followed in abundance by *Cricotopus sylvestris*, *C. bicinctus*, *Chironomus* spp., *Procladius* spp. and *Cladotanytarsus* n.sp. In 1975, the same general patterns were observed (Table 5) except that *Cricotopus*

sylvestris assumed greater dominance the second year. As at Biggs, population levels at comparable sampling times were higher for the later flooded plots.

Between-locality comparisons

Contrasting 1974 patterns between localities reveals the stronger dominance of *Para-lauterborniella* and *Cricotopus sylvestris* in the Davis plots; *Chironomus* and *Paratany-tarsus* larvae were usually more abundant in the Biggs plots. Similar dominance patterns occurred once again at both study sites in 1975, but in each year more larvae were recovered from the Davis plots. As mentioned earlier, unlike the Biggs experimental acreage, rice had not been previously grown under continuous water at Davis. The 'newer' Davis rice plots supported greater populations of midge larvae apparently because of higher phytoplankton levels (Table 1). Darby (1962) observed similar trends where an apparent good correlation existed between first-year rice fields and the greater number of midges produced. He concluded that the more fertile first-year fields provided more larval food than did the older fields.

Table 6. Species richness (s) and diversity (\bar{x}) values $(\tilde{D} \pm S.E.)$ for Davis and Biggs, 1975

| Sampling in | terval | | | | | | | |
|---------------------------|-----------------|-----------------------------|-----------------------------------|-----------------------------------|-----------------------------|---------------------------|---------------------------|---------------------------|
| (in days afte | r | 7 | 1 | .4 | 2 | 1 | 2 | 28 |
| flooding) Flooding tin | ne 1 | 2 | 1 | 2 | 1 | 2 | 1 | 2 |
| (a) Davis | | | | | | | | |
| S | - | 5 | 7 | 7 | 8 | 8 | 8 | 8 |
| \widetilde{D} | - | 0.56 ± 0.12 | $\textbf{0.71} \pm \textbf{0.02}$ | $\textbf{0.68} \pm \textbf{0.05}$ | $0{\cdot}53\pm0{\cdot}04$ | 0.46 ± 0.08 | $0{\cdot}25\pm0{\cdot}02$ | $0{\cdot}37\pm0{\cdot}07$ |
| (b) Biggs | | | | | | | | |
| S | 5 | 6 | 7 | 8 | 8 | 8 | 8 | 7 |
| $	ilde{D}$ | 0.58 ± 0.06 | $0{\cdot}56{\pm}0{\cdot}08$ | $0{\cdot}60\pm0{\cdot}01$ | $0{\cdot}58\pm0{\cdot}03$ | $0{\cdot}37 \pm 0{\cdot}06$ | $0{\cdot}70\pm0{\cdot}01$ | 0.73 ± 0.05 | $0{\cdot}80\pm0{\cdot}02$ |

Population analysis

.. .

Diversity (\tilde{D}) and rank correlation (γ) measurements were computed only for the 1975 data since the collections of that year extended over a greater sampling area and thus provide a more representative indication of changes in the chironomid community as a whole. Identification to species was not possible for members of the genera *Chironomus*, *Paralauterborniella* and *Procladius*. Consequently, these three provisional species groups were treated as separate 'functional units' in the calculation of \tilde{D} and γ . Although the number of species present was underestimated by the failure to identify to species the larvae in these three genera, the \tilde{D} and γ statistics were adequately estimated because the composition of the chironomid communities at each study site was similar. In addition, \tilde{D} responds more to patterns in relative abundance of the dominant forms than to species richness.

Table 6 presents the species richness or the number of species present (s), and diversity data for Davis and Biggs. Mean \tilde{D} values were calculated from replicate plot values (n = 3) and, in general, indicate the occurrence of similar relative abundance patterns amongst the dominant species at comparable sampling times in the early and late flooded plots for each study site. The data range from values of 0.25-0.46 with a single species strongly dominant, through values of 0.53-0.60 in which one species is less dominant or in which two species usually share dominance, to values of 0.68-0.80 in collections with dominance generally shared by three species. Species richness patterns were similar in both areas.

Chironomid midge colonization in rice paddies

A visible representation of temporal abundance and rankings of species is obtained when relative abundance-rank curves are drawn (Fig. 2). With this technique it is possible graphically to identify the numerical positions of the species by labelling each point on the curves. Murdoch, Evans & Peterson (1972) previously illustrated the use of relative abundance-rank curves in comparisons of plant and insect evenness patterns.



FIG. 2. Labelled relative abundance-rank curves for plots at flooding time 1 (---) and flooding time 2 (----) at 7, 14, 21 and 28 day sampling periods after initial flooding, Biggs and Davis, 1975. The proportion that each species forms of the total abundance in the pooled samples from each sampling date is located on the log scale against species' rank. *Tanytarsus* n.sp. 6 (A), *Paratanytarsus* n.sp. (B), *Cricotopus sylvestris* (C), *Paralauterborniella* spp. (D), *Chironomus* spp. (E), *Procladius* spp. (F), *Cladotanytarsus* n.sp. (G) and *Cricotopus bicinctus* (H).

The changes in species diversity with flooding time and locality were evaluated by analysis of variance. All data were normally distributed. The results of these tests and rank correlation comparisons are provided in Table 7. The Kendall rank correlation test requires equal pairings of items for comparisons so whenever a species was absent it was listed as zero frequency and assigned last rank (Ghent 1963). Absent species were usually paired with the least abundant species of other samples.

The first type of analysis looks at within-locality comparisons (Table 7(a) and (b)). In only one of seven \tilde{D} comparisons between flooding time 1 and flooding time 2 plots at

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identical sampling intervals was a difference (P < 0.05) detected in the dominance patterns. There were positive correlations in rank and abundance (P < 0.05 or P < 0.01) for all three sampling periods at Davis and two of the four at Biggs.

The second analysis compares between-locality \tilde{D} and γ values (Table 7(c)). In all but one instance, \tilde{D} values were significantly different (P < 0.01), indicating differential dominance patterns between Davis and Biggs. Correlations of abundance and rank were non-significant. Similar flooding times were contrasted here because in each locality most comparisons of the two flooded blocks provide no statistical differences between \tilde{D}

Table 7. F-ratios for species diversity (\tilde{D}) and rank correlation coefficients (γ) for comparisons between flooding time measures at comparable sampling times within and between localities, 1975

| Sampling interval (in days after flooding) | 7 | 14 | 21 | 28 |
|--|--------------------------|----------------------------------|-------------------------------|------------------------------|
| Within-locality comparisons (a) Davis | | | | |
| F (\tilde{D}) | - | 0.28 | 1.74 | 4.29 |
| (y)† | - | 0.91 (N = 38)** | 0.65 (N = 36)* | 0.86 (N = 48)** |
| (b) Biggs | | | | |
| Flooding time 1 v. flooding time 2 $F(\tilde{D})$ (γ) | 0.17 0.40 (N = 18) | 1.23 0.91 (N = 38)** | 83·67** 0·79 (N = 44)** | $4.88 \\ 0.52 \\ (N = 22)$ |
| Between-locality comparisons | | | | |
| (c) Davis v. Biggs Elocding time 1 v. flooding time 1 | | | | |
| $F(\tilde{D})$ (7) | - | 40.56^{**} 0.52 (N = 22) | 15.14* 0.50 (N = 28) | 319.44** 0.21 (N = 12) |
| Flooding time 2 v . flooding time 2 | | | | |
| F(D) | 0.001 | 9·56* | 21.78** | 73.26** |
| (7) | (N = 12) | (N = 22) | (N = 28) | (N = 18) |

* P<0.05; ** P<0.01.

† The limits for γ are: +1, a perfect positive correlation; -1, a perfect negative correlation and 0, the complete absence of correlation. A special table provided by Sokal & Rohlf (1969) was consulted for critical values of N (count of ranks) because n (sample size) was < 10.

values; plus rank correlations were generally significant, an indication of the good consistency in the chironomid assemblages.

DISCUSSION

California rice fields can not technically be classified as shallow ponds or lakes because of the continual water movement during the growing season. They may be considered as intermediate to a shallow pond or lake and a sluggish stream. Water depth is usually kept below 18 cm except in bordering borrow pits where it is deeper. These depressions are created when soil is removed to form levées

After flooding, seral succession proceeds quite rapidly; within two or three weeks

young rice plants start to emerge from the surface of the water and aquatic weeds fill the gaps between the rice plants. It is within this three-week period that colonist species of chironomids establish high numbers and become economically important. Margalef (1958, 1962, 1968) stated that in aquatic ecosystems, rapidly growing, early successional algae are the most palatable and support the highest numbers of zooplankton in early spring in temperate lakes. Recently, Cates & Orians (1975) have provided evidence for the higher palatability qualities of some species of early successional primary producers and suggest that this phenomenon is widespread in both terrestrial and aquatic communities. Perhaps a similar pattern occurs in rice fields where early successional species of algae and diatoms account for the enormous populations of benthic chironomids. Results of this study suggest that newer rice fields (Davis plots) support greater numbers of midges than do older rice fields (Biggs plots).

The separate variables \tilde{D} and γ were used to detect temporal changes in the community structure of benthic midges during the initial development of a freshwater agro-ecosystem. As noted earlier, this study (1975 data) illustrates the strong similarity in \tilde{D} and γ patterns in plots at the same locality but flooded at different times. The data suggest that for a particular set of environmental factors, similar and predictive seral changes may occur with regard to dominance and species rankings during the initial development of the chironomid community. Goulden (1969) discussed the apparent similarity, and therefore predictability, that occurred in changes in the diversity patterns of chydorid Cladocera in lakes. It appears, as Goulden suggested, that other organisms (e.g. chironomids in rice fields) may exhibit similar seral changes during the early developmental phases of an aquatic community.

The importance of dominance and diversity in discussions of the structure of plant and animal communities has been stressed by Whittaker (1965) and McNaughton & Wolf (1970). During the time this study was undertaken, dominance was a characteristic of the organization of the chironomid communities at Davis and Biggs. However, the \tilde{D} and γ statistics revealed that significantly different patterns occurred at the two study sites.

For practical purposes, however, it was desirable to observe the specific dominance and abundance-rank patterns of the economic species. These patterns were easily revealed by labelled abundance-rank curves (Fig. 2). *Paratanytarsus* n.sp. assumed dominant status in some 1975 Biggs collections while the other economic species, *Cricotopus sylvestris* and *Paralauterborniella* spp., were often recorded in intermediate abundance at both localities. *Tanytarsus* n.sp. 6 was usually the single most commonly encountered species.

ACKNOWLEDGMENTS

We thank the staff and personnel of the Rice Research Facility, Davis Farm and the Rice Research Station, Biggs for land and technical assistance to undertake this study. The constructive criticisms and comments of the manuscript by Drs W. R. Cothran and R. K. Washino are appreciated. Without taxonomic assistance from Drs R. E. Darby and J. E. Sublette this study could not have been completed. We also thank R. Harris, S. Scott and Dr M. Sears for technical assistance. This research was supported by a grant awarded to Dr A. A. Grigarick from the California Rice Research Advisory Board.

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(Received 13 October 1976)