THE MICRODISTRIBUTION OF MAYFLIES (EPHEMEROPTERA) IN MYRIOPHYLLUM BEDS IN PENNINGTON CREEK, JOHNSTON COUNTY, OKLAHOMA

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Abstract

I studied the population densities and the microdistributions of the four most abundant mayfly (Ephemeroptera) nymphs in *Myriophyllum heterophyllum* beds in Pennington Creek, Johnston County, Oklahoma, from May to December, 1977. The section of the stream studied has relatively constant flow rates and temperatures throughout the year due to continuous inflow from groundwater. This uniform physical environment allows the plant beds to grow throughout the year and provide a permanent habitat. The four mayflies are *Tricorythodes fictus* (Tricorythidae), *Caenis delicata* (Caenidae), *Baetis flavistriga* and *B. quilleri* (Baetidae). All four species are of similar size and feed by scraping periphyton from the surface of the *Myriophyllum*. *T. fictus* and the two species of *Baetis* have overlapping microdistributions in the leafy, upper one-half of the plant bed. *T. fictus* and *C. delicata* have overlapping microdistributions in the lower portion of the plant bed and roots. Each species has similar population densities where their distributions overlap. There is no significant selection for position with respect to current flow in the *Myriophyllum* for any of the species. Food and space are always abundant, especially in the top one-half of the *Myriophyllum*. There are no major changes in these trends over the year.

Introduction

Aquatic vascular plants serve as excellent habitats for many aquatic macroinvertebrates. The submerged leaves and roots serve as a substrate for periphyton, provide a refuge and a food source for some macroinvertebrates (Berg, 1949, 1950a, 1950b; McGaha, 1952; Rosine, 1955; Frohne, 1956; Hynes, 1970; Cummins, 1973). Percival and Whitehead (1929) found a large number of

species of benthic macroinvertebrates in beds of *Potamogeton* in a stream. Krecker (1959) found a similar situation in beds of *Myriophyllum* in Lake Erie. He expressed the density of the macroinvertebrate population in terms of number of organisms per unit length of plant stem. This type of expression does not lead to a valid comparison with other plant species having different morphologies. Rosine (1955) suggested that plant surface area is important in determining the number of organisms. Harrod (1964) carried out a study of the benthos of several different species of macrophytes in a small limestone stream. The plants did not die back in winter, providing a permanent habitat. She expressed population densities in terms of number of organisms per unit of plant surface area. She found that some invertebrates prefer specific plants while others are generalists, found on all plants in similar densitites. Population densities appeared to be proportional to plant surface area.

Plant beds in streams can form different microhabitats within their boundaries due to direction of current flow and other factors. I studied the microdistribution of mayfly (Ephemeroptera) nymphs in solitary beds of *Myriophyllum heterophyllum* in the headwater region of Pennington Creek, Johnston County, Oklahoma. The mayfly nymphs are among the more abundant members of the plant bed community. There are four very common ones: *Tricorythodes fictus* (Tricorythidae), *Caenis delicata* (Caenidae), *Baetis flavistriga* and *B. quilleri* (Baetidae). These nymphs are about the same size and could possibly compete for the same food source because they all scrape periphyton from the plant surface.

In this paper I will answer the following questions. Do any of the mayflies maintain a specific non-overlapping

microdistribution within a plant bed? Does this distribution change temporally? What factors are responsible for determining the microdistribution of these organisms in the plant bed?

Methods

I chose a site in the headwater region of Pennington Creek. *Myriophyllum heterophyllum* occurs in solitary beds 1-3 m wide and 1-4 m long, growing in depressions or on snags on the limestone stream bottom. These plants do not die back in the winter.

I divided the beds into three vertical strata based on plant morphology (Fig. 1A). The top half of the bed consists of leafy stem sections. The bottom half of the bed consists of stem sections which are almost devoid of leaves. Light penetration is greatly reduced by the top half. The roots make up the third stratum and occur in the mud substrate above the limestone bedrock. I also determined five horizontal positions with respect to current flow (Fig. 1B). The front of the bed is where the current strikes it. The two sides of the bed are on the east and west with respect to stream flow. The rear of the bed experiences reduced flow and the middle of the bed is most protected from the current. This configuration allows for the definition of 15 distinct positions within any plant bed.

Flooding and scouring are negligible throughout the year. Flow and temperature in the stream are very stable due to the ample supply of groundwater in the form of springs and seeps. Flow patterns within the plant beds were observed by injecting drops of fluorescein dye into the water upstream of the plant beds and visually following the movement of the dye. Flow rates were measured with a propeller-driven flow meter. Measurements were made in the central channel of the stream and are equivalent to the rate of flow of the water striking the front of the plant bed.

Air and water temperatures were measured with a mercury thermometer. All water samples for chemical analysis were taken from the center of the stream. The pH and conductivity were measured *in situ*. Calcium and dissolved oxygen (Winkler titration) were determined as described by Lind (1974); however, 0.0250 N phenylarsine oxide (Anonymous, 1973) was used in the Winkler titration instead of 0.0125 N sodium thiosulfate. Ortho-phosphate, nitrate and turbidity were determined in the laboratory within 24 hrs. of sampling.

I removed duplicate plant sections from each of the 15 positions in the plant beds on a sampling day. I sampled two beds each time, resulting in four replicates for each position. Stem sections of 10-15 cm were cut and removed in a net to guard against loss of invertebrates. A handful of roots was dislodged and placed in a net for removal. Invertebrates were washed off the plant sections and counted. Surface area was determined by weighing the water that would cling to the plant surface after soaking. The weight of the water adsorbed is proportional to the plant surface area (Harrod and Hall, 1962). A detailed account of the procedure for determining surface area is given in Magdych (1978).

The mayfly nymphs were counted and then placed in an oven at $100°C$ for 24 hours to dry prior to weighing. Weights were measured with a Cahn Electrobalance model G. I divided the nymphs into two size classes during enumeration. This separation allowed for estimating approximate age distribution. The small size class included nymphs < 2.0 mm and the large size class included those > 2.0 mm. The raw data were expressed in terms of number and dry biomass of nymphs per cm^2 of plant surface area. Presence of other invertebrates was also recorded.

I monitored the emergence of adult mayflies by collecting adult insects with an ultraviolet light trap. I used this trap for two hours after sunset at least once each month during the sampling period. I also collected by net any adult mayflies that I could in the mornings of sampling days.

Statistical analyses were carried out as described by Sokal and Rohlf (1969). The computer program for the factorial analysis of variance (referred to as ANOVA in the remaining text) given by these authors was used to determine differences in nymphal densities with respect to the position in the plant bed, the stratum of the plant bed, the time of year and the differences between population densities for each species.

Results and discussion

Physical – Chemical Data
The temperature of Pennington Creek is relatively constant (approximately 19°C) through most of the year at this site. In December the temperature dropped to 15°C. The major spring feeding the stream dried up and the only visible groundwater entering the stream was from seep action. Groundwater maintains the constant tem-
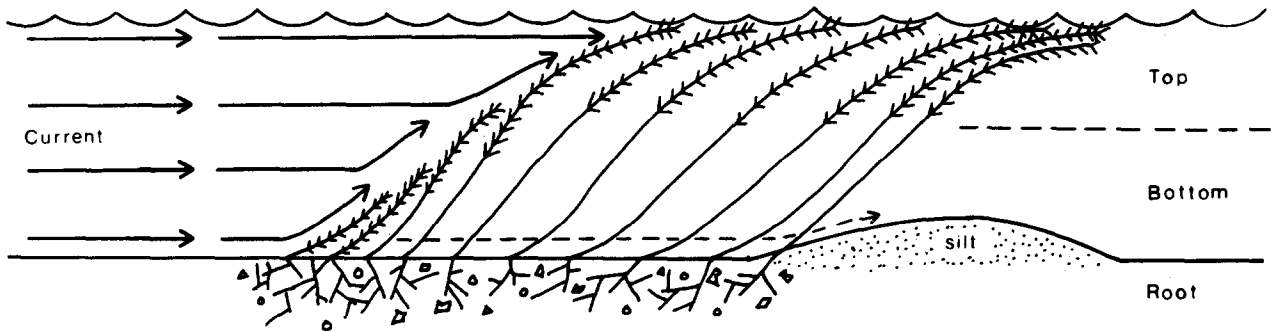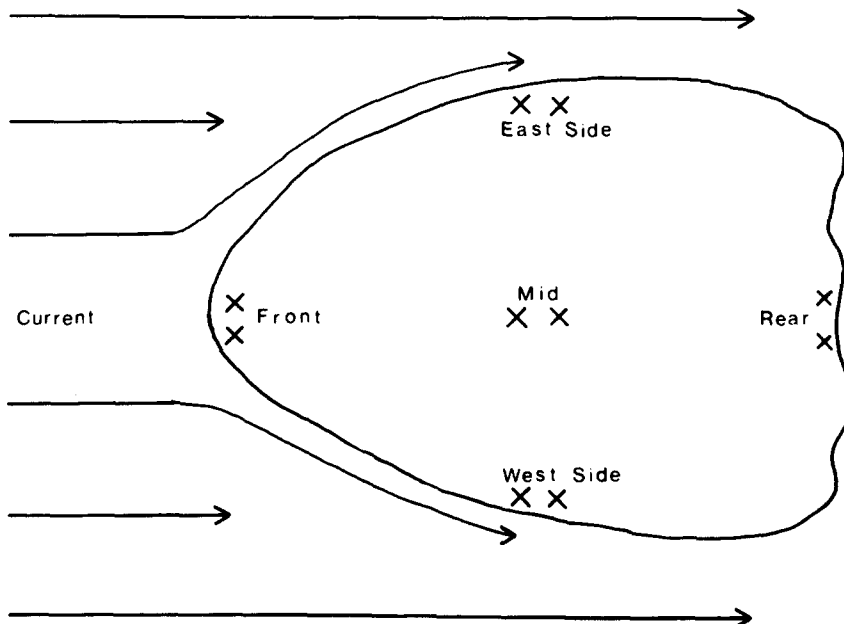
Fig. 1A & B. A schematic diagram of the *Myriophyllum heterophyllum* beds as they occur in the stream. The 3 vertical strata are shown in cross-section in 1A. The 5 horizontal positions are shown in 1B. Major current patterns are shown by the arrows in both parts.

Table 1. Results from the 3-factor analysis of variances for each species of mayfly. The data analyzed are based on numbers of organisms/cm^2 surface area. The three factors are: (1) position in plant, (2) stratum in plant, and (3) day of sampling.

Factor	T. fictus			C. delicata		
	Small size class	Large size class	Total number	Small size class	Large size class	Total number
Position	**	ns	**	ns	ns	ns
Stratum	***	***	***	ns	***	***
Day	***	***	***	ns	ns	ns
Position X Stratum	*	ns	ns	ns	ns	ns
Position X Day	*	ns	ns	ns	ns	ns
Stratum X Day	***	***	***	ns	ns	*

Factor	Baetis sp. 1			Baetis sp. 2		
	Small size class	Large size class	Total number	Small size class	Large size class	Total number
Position	*	*	**	ns	ns	ns
Stratum	***	***	***	***	***	***
Day	***	***	***	***	***	***
Position X Stratum	*	*	ns	ns	ns	ns
Position X Day	ns	ns	ns	ns	ns	ns
Stratum X Day	***	***	***	***	***	***

perature. Full groundwater flow was restored in the early spring of the following calendar year. Even though the water temperature decreases for a few months in winter, the water never approaches freezing. This allows for the plants to persist through the year and provide a permanent habitat for invertebrates. Growth of the plant beds is held back by lack of suitable substrates for attachment.

Pennington Creek has a high calcium content (51.82 ± 11.27 mg/l) and is slightly alkaline (pH = 7.66 ± 0.40). Conductivity remains relatively constant (500 ± 77 μmhos) and the turbidity is usually zero. Turbidity increases after hard rains and usually remains high for several days after the rain.

The dissolved oxygen concentration (8.00 ± 0.82 mg/l) remained at or near saturation levels (Lind, 1974) through-

out the study period. I compared dissolved oxygen concentrations in the center of the *Myriophyllum* beds to that of the open stream water during the beginning of the study. I found no significant difference, so all dissolved oxygen samples were taken from the open water and were assumed to be the same within the plant beds. There was no evidence of large diurnal dissolved oxygen changes.

Major nutrients are not limiting in Pennington Creek. The stream is surrounded by lightly grazed cattle pastures at the sampling site and by woodland at approximately 1 km upstream. Runoff after rains is high and seepage provides the predominantly groundwater-fed stream with a supply of nutrients for plant growth.

The velocity of the current striking the *Myriophyllum*

Table 2. Results from the 3-factor analysis of variances for each species of mayfly. The data analyzed are based on dry weight of organisms/cm^2 surface area. The three factors are: (1) position in plant, (2) stratum in plant, and (3) day of sampling.

Factor	T. fictus			C. delicata		
	Small size class	Large size class	Total number	Small size class	Large size class	Total number
Position	***	ns	ns	ns	ns	ns
Stratum	***	***	***	***	***	***
Day	***	***	***	ns	ns	ns
Position X Stratum	**	ns	ns	ns	ns	ns
Position X Day	*	ns	ns	ns	ns	ns
Stratum X Day	***	***	***	**	*	*

Factor	Baetis sp. 1			Baetis sp. 2		
	Small size class	Large size class	Total number	Small size class	Large size class	Total number
Position	*	ns	*	ns	ns	*
Stratum	***	***	***	***	***	***
Day	***	***	***	***	***	***
Position X Stratum	ns	ns	ns	ns	ns	*
Position X Day	ns	ns	ns	ns	ns	ns
Stratum X Day	***	***	***	***	***	***

beds is low (0.31 ± 0.12 m/s) and relatively constant through the year. It does increase during periods of flooding, but generally not enough to destroy the plant beds. During average current conditions, most of the water flows around the sides or over the top of the beds as seen in Fig. 1A & B. Some water does flow through the center of the bed. This movement is slow and was measured at a rate of 0.017 m/s when the upstream current velocity outside of the bed was approximately 0.2 m/s. There is also a weak, secondary current which flows along the interface of the bottom and root strata of the *Myriophyllum* (Fig. 1A). Therefore, the invertebrates that inhabit these plant beds are protected from the stream flow.

Distribution of the Mayfly Nymphs

The densities of the nymphal populations were monitored with respect to the mean number of organisms per cm^2 of plant surface area (referred to below as number/cm^2) and with respect to the mean dry weight of organisms per cm^2 of plant surface area (referred to below as weight/cm^2) for separate size classes and totals for each species. Three-way factorial ANOVAs were performed on these data for each size class of each species and for the totals of each species of mayfly. The three main factors of the ANOVAs are: (1) the position in the plant beds, (2) the strata in the plant beds and (3) the day of sampling. The results of these ANOVAs are given in Table 1 for the data on number/cm^2 and in Table 2 for the data on weight/cm^2. Four-way factorial ANOVAs were performed on
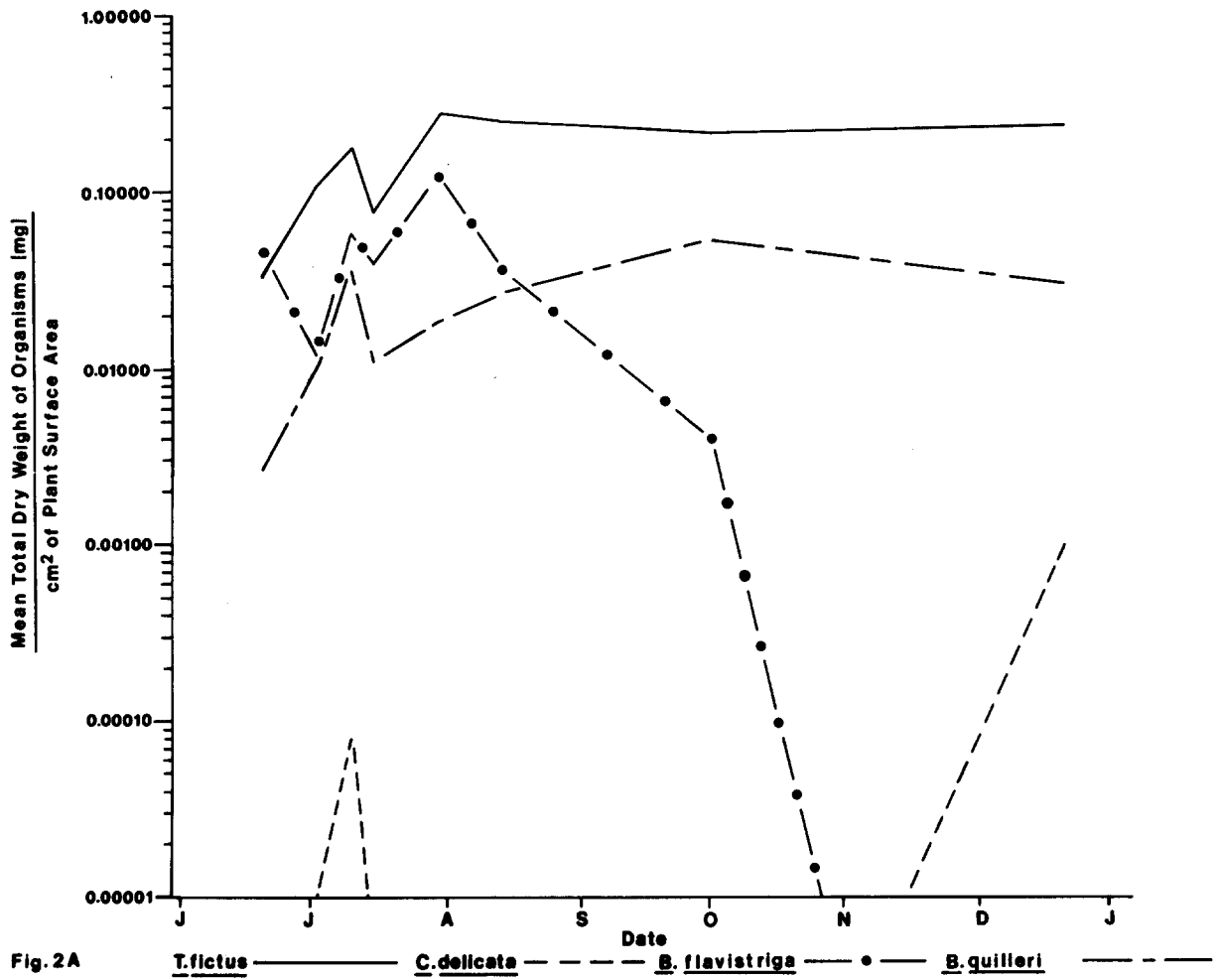
Fig. 2A-E. The average total dry weight (mg) of each species of mayfly per cm² of *Myriophyllum* surface area. 2A is for the top stratum, front position; 2B is for the bottom stratum, front position; 2C is for the root stratum, front position; 2D is for the top stratum, mid position; 2E is for the top stratum, east side position.

these data to determine trends in the entire community of mayflies and resulted in four ANOVAs (Table 3). The four main factors of these ANOVAs are: (1) the position in the plant bed, (2) the strata in the plant bed, (3) the day of sampling and (4) the organism sampled.

Tricorythodes fictus, Baetis flavistriga and *B. quilleri* follow the same trend in Tables 1 and 2. *Caenis delicata* tends to deviate from this pattern. Each of the four species selects for a particular stratum (Fig. 2A-C). *T. fictus* reaches greatest densities in the top stratum of the *Myriophyllum* although it is common in the other strata. *B. flavistriga* and the small size class of *T. fictus* do show a significant selection of position and a positive interaction

between position and stratum in Table 1. This relationship is probably due to the tendency for these individuals to occur in relatively large densities in the bottom stratum in the front and side positions in the plant beds. In these positions, the bottom stratum is usually composed of very leafy stems (at least in the front position) which provide a favorable substrate.

There are other trends that can be seen from the results of the four-way ANOVAs in Table 3. There is a highly significant selection for stratum. This selection would be expected since three of the four species of mayflies reach very high densities in the top stratum of the plant beds.

There is a highly significant difference between den-

166

Fig. 2B   T. fictus ——————— C. delicata — — — — B. flavistriga —— • —— B. quilleri —— - ——
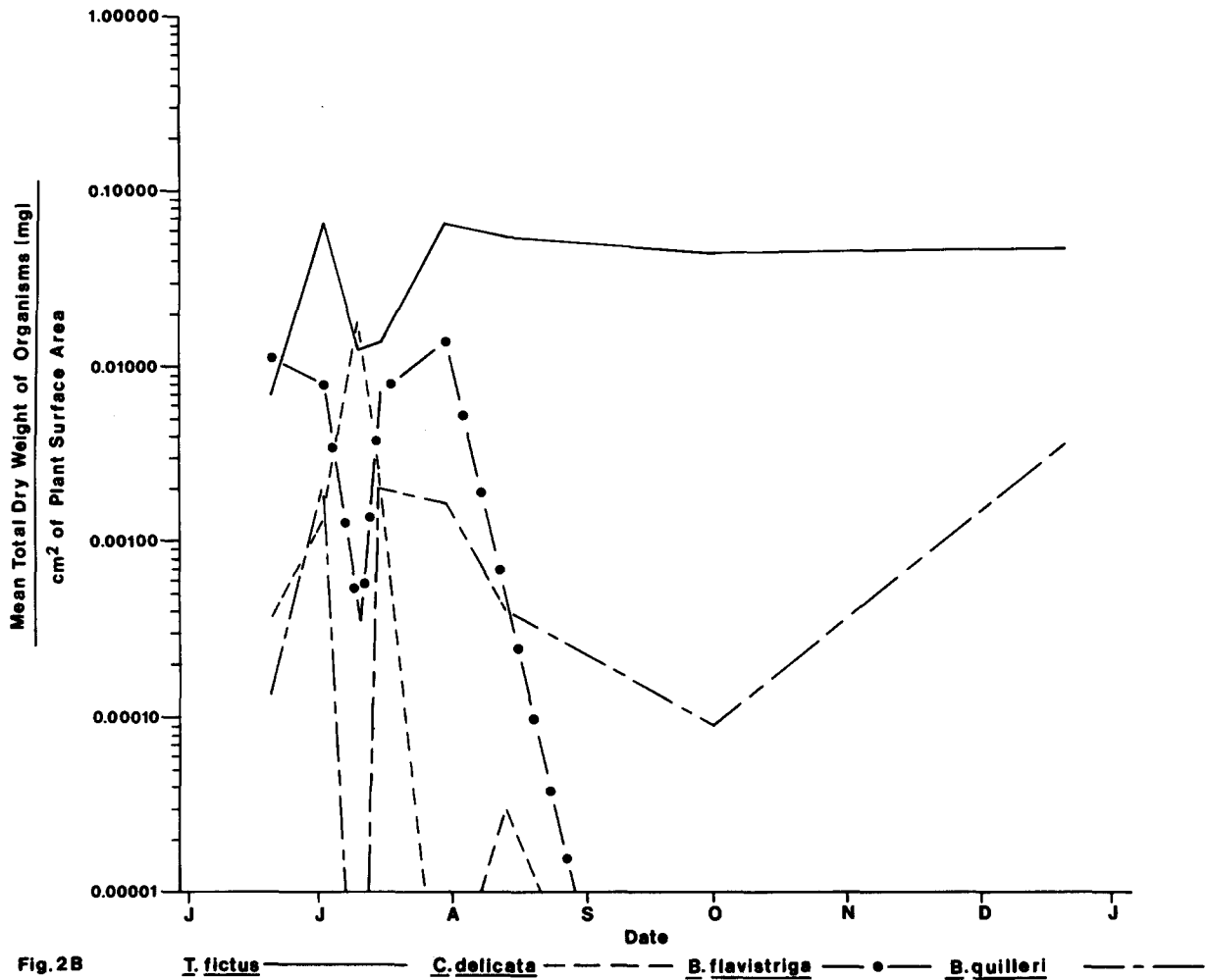
Bottom Stratum   Front Position

sities of organisms based on weight/cm^2 and total number/cm^2. Dominance in the mayfly nymphal communities in the plant beds can be ranked as:

T. fictus > *B. quilleri* = *B. flavistriga* > *C. delicata*. This ranking can be seen in Fig. 2A-C. This relationship does not hold for separate size classes when they are based on number/cm^2. Densities fluctuate and overlap in these organisms throughout the year so that there is a lack of significance for differences in this parameter (Fig. 3A & B).

There is a highly significant change in the densities of all organisms over time. This change is due to the general cyclic fluctuation of the population densities as seen in Fig. 2A, D & E. This significance is also lost when the data are expressed as the number/cm^2 for the separate size

classes. Again, this is due to the random fluctuations of population densities over the year when the data are expressed in this manner.

The position factor produces a perplexing situation in Table 3. Selection for position is marginally significant. There is a high degree of interaction between position and organism. This interaction indicates that one or more organisms are selecting for a particular position in the plant bed. There are no obvious trends among any of the mayflies in this manner. However, *B. flavistriga* may be able to account for this significance. In early spring it was present in relatively high densities. It completely left the *Myriophyllum* after August and did not show up through December. It may have moved to a different habitat in the stream during this time or else the last cohort of
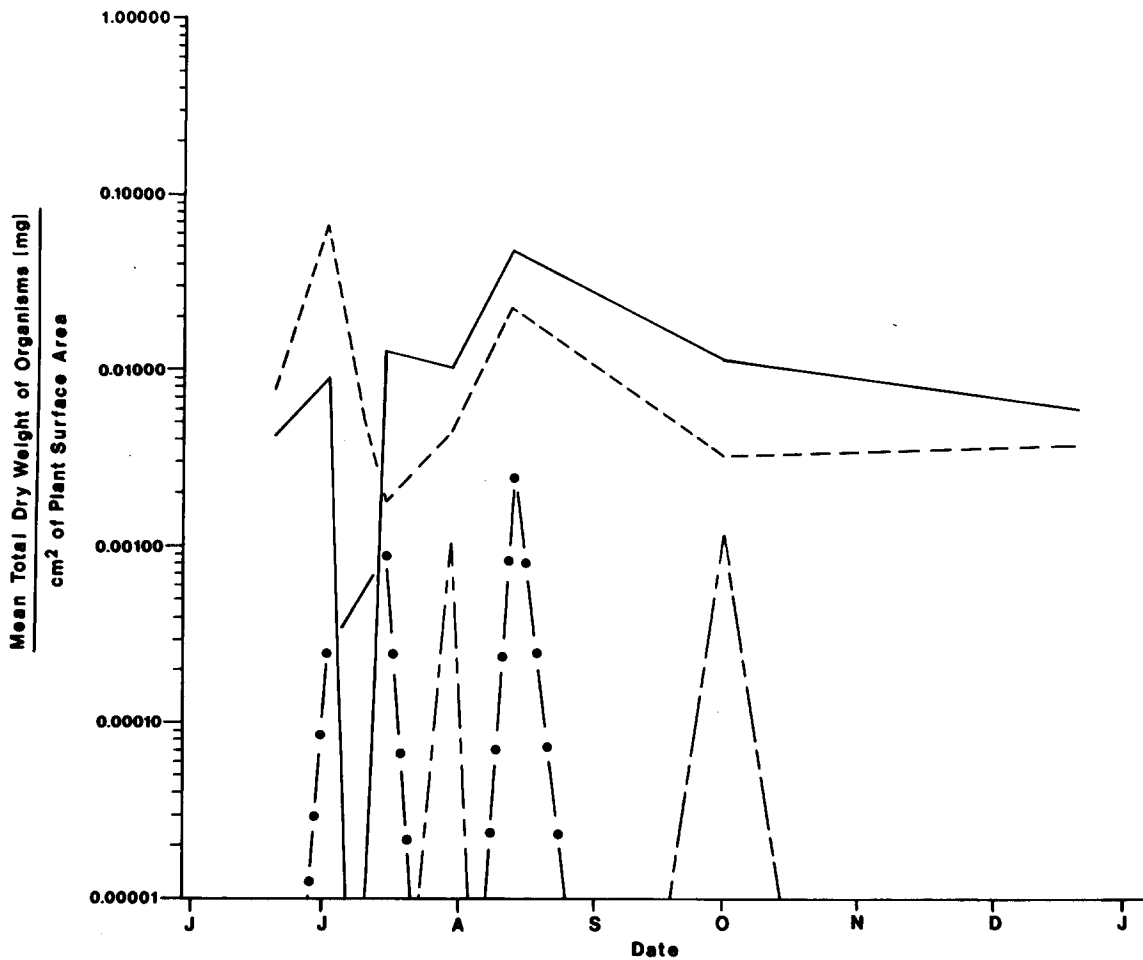
Fig. 2C   T. fictus ————   C. delicata — — — — —   B. flavistriga — • ——   B. quilleri —— - ——

Root Stratum Front Position

adults emerging in August laid eggs that overwinter in a state of diapause. I did not find *B. flavistriga* existing anywhere else and the latter explanation may be more probable (Fig. 3A and 4). The eggs would be scattered throughout the stream and they would not hatch until spring. The newly hatched nymphs may move toward favorable habitats. The movement may be mostly in the downstream direction for these small nymphs. The nymphs would encounter the *Myriophyllum* from the front and be able to climb to the favorable top stratum by going up the leafy bottom which exists in the front position of the plant beds. This interpretation is supported by the significant interactions between position and organism, between stratum and day, and between day and organism, and by the marginal significance of the interaction between position, stratum and organism and the interaction

between position, day and organism in Table 3. The significant interaction between stratum and organism is due to the isolation of *C. delicata* from the other species.

T. fictus and *C. delicata* adults appear to emerge constantly from June through September. *C. delicata* was very abundant in ultraviolet light traps that were run in the evenings just after sunset. *T. fictus* was not, but occurred in large mating swarms over the water in the mornings. Adults of the genus *Baetis* were rarely observed and those few that were captured could not be linked with the nymphs in the plant beds.

The dominant invertebrates that would be potential predators of the top stratum are *Hydra* sp., planaria and the trichopteran, *Cheumatopsyche*. Odonates are more prevalent in the bottom and root strata of the *Myriophyllum* beds. They may exert some pressure in determining
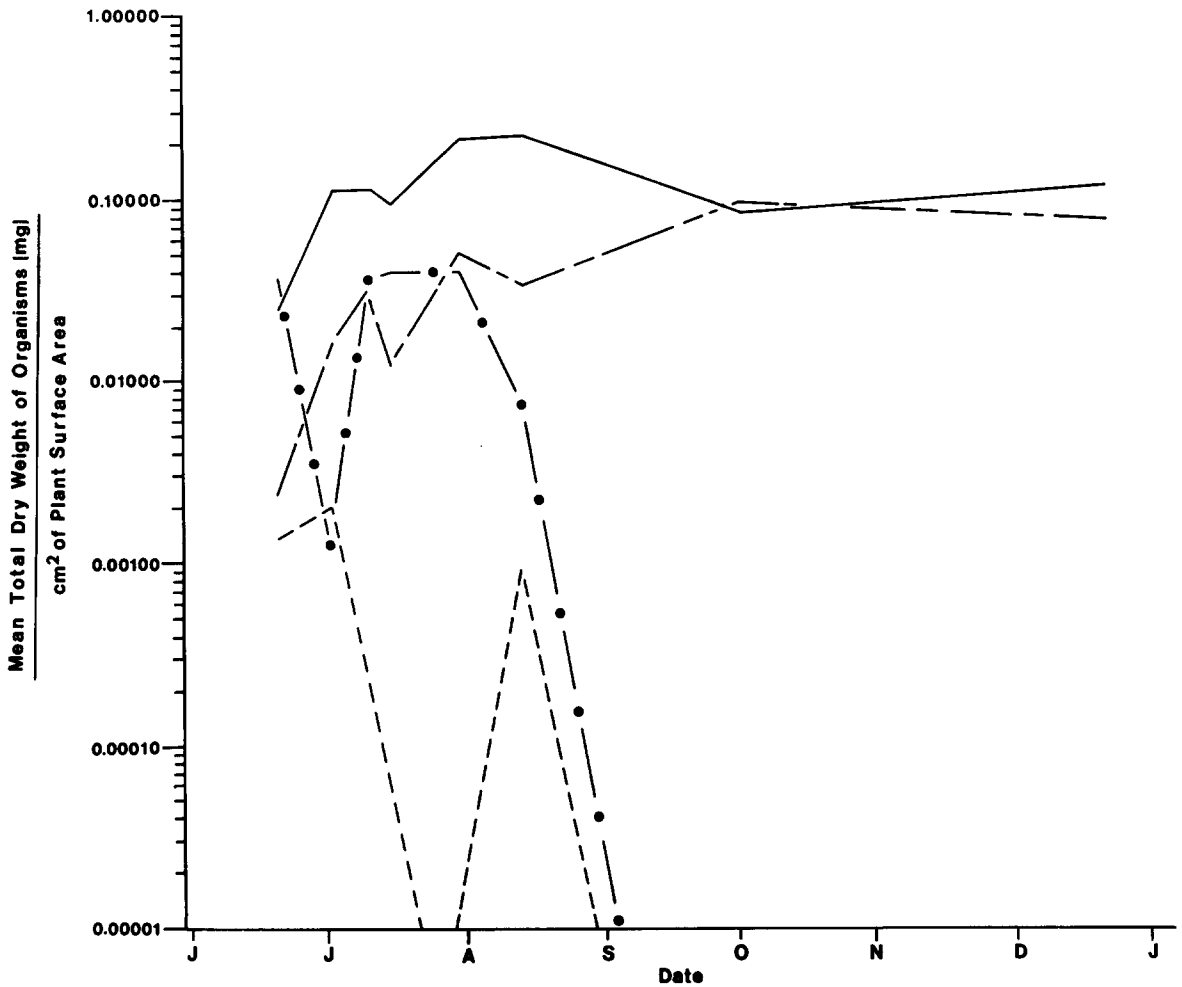
Fig. 2D T. fictus ———— C. delicata — — — — B. flavistriga ——— • ——— B. quilleri — — • — —

Top Stratum   Mid Position

the densities of the mayflies in these strata. A total of more than 50 species of invertebrates were encountered throughout the course of the study.

Conclusions

Baetis flavistriga and *B. quilleri* are almost identical morphologically. The major difference between these two nymphs is color patterns on the legs, abdomen and tails. Species of *Baetis* tend to prefer open flowing water or the edges of plant beds in streams (Edmunds, Jensen and Berner, 1976). *Tricorythodes fictus* and *Caenis delicata* are also very similar morphologically. Both of these have operculate gill covers, are slow moving and are

adapted to silted substrates according to Edmunds, Jensen and Berner (1976). These authors state that *Tricorythodes* and *Caenis* are commonly found in the roots of aquatic plants and that *Caenis* is capable of withstanding stagnant conditions and pollution. All four species of mayflies are very similar in that they are the same size and utilize the same food source (periphyton on the surface of the *Myriophyllum*).

T. fictus reaches its highest densities in the top stratum of the *Myriophyllum* and *B. flavistriga* and *B. quilleri* appear to be almost completely confined to the top stratum. *C. delicata* is almost completely restricted to the bottom and root strata. There are no trends indicating that the different species inhabit different positions within any stratum. Therefore, the microdistribution of *T.*

Fig. 2E   T. fictus ——————   C. delicata — — — —   B. flavistriga — • —   B. quilleri — — —

Top Stratum   East Side Position
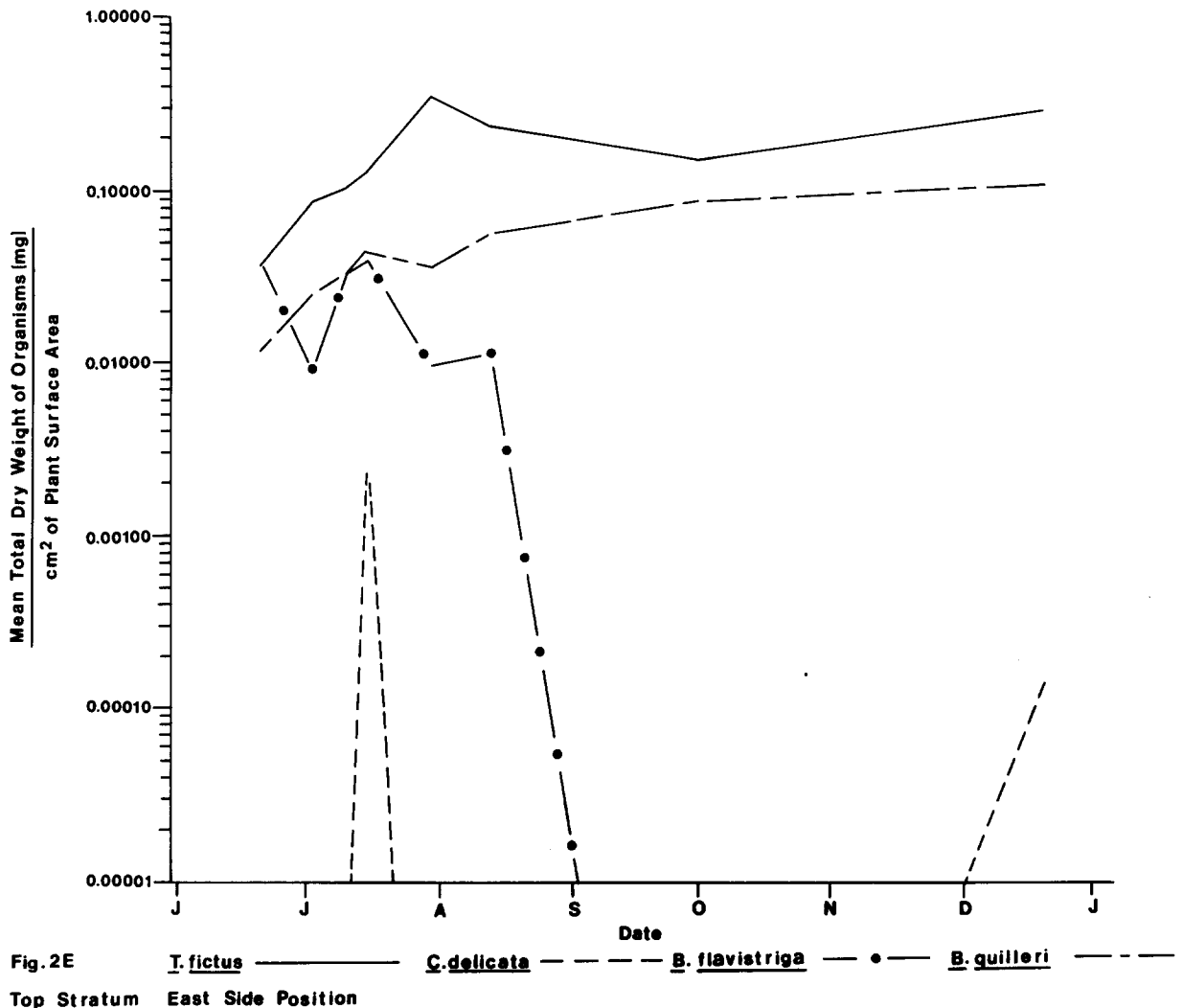
fictus, B. flavistriga and *B. quilleri* overlap significantly. *T. fictus* also overlaps the microdistribution of *C. delicata*. The overlapping microdistributions of these species do not change temporally with the exception of *B. flavistriga* which was absent from the plant beds from September through December. These species have very similar population densities where their microdistributions overlap (Fig. 2A-E). *T. fictus* is slightly more abundant than *B. flavistriga* and *B. quilleri* which are equally abundant when they are both present. *C. delicata* is the least abundant.

The top stratum of the *Myriophyllum* is the most favorable stratum for insect herbivores. The plant stem sections are exposed to sunlight and support a large amount of periphyton. The food source is probably not limiting. Grazing often stimulates primary production (Cooper, 1973) and the surface area for attachment of periphyton is very great in an average *Myriophyllum* bed. Also, the finely dissected leaves probably provide surfaces for periphyton that are relatively inaccessible to macroinvertebrates. It seems more likely that space would be limiting before food. The two species of *Baetis* are probably restricted to the top stratum because of their behavior to orient themselves into water currents and to lift their abdominal gills up into the current (Edmunds, Jensen and Berner, 1976). They would be able to orient most readily in the top stratum which is exposed to strong currents. It is unlikely that *C. delicata* is being forced into the lower strata by some form of competitive exclusion (Pielou, 1974). For competition to exist, a

Table 3. Results from the 4-factor analysis of variances for all species of mayflies. The data analyzed are based on number of organisms/cm² surface area and dry weight of organisms/cm² surface area. The four factors are: (1) position in plant, (2) stratum in plant, (3) day of sampling, and (4) organism (species or size class) sampled.

Factor	Mean number of organisms/cm² of plant surface area		Mean dry weight of organisms/cm² of plant surface area	
	Number of organisms for separate size classes of each species	Total number of organisms for each species	Weights for separate size classes of each species	Total weights for each species
Position	ns	*	**	ns
Stratum	**	***	***	***
Day	ns	***	***	***
Organism	ns	***	***	***
Position X Stratum	ns	ns	*	ns
Position X Day	ns	ns	ns	ns
Position X Organism	ns	***	**	**
Stratum X Day	ns	***	***	***
Stratum X Organism	ns	***	***	***
Day X Organism	ns	***	***	***
Position X Stratum X Day	ns	ns	ns	ns
Positon X Stratum X Organism	ns	*	***	ns
Position X Day X Organism	***	ns	***	ns
Stratum X Day X Organism	ns	***	***	***
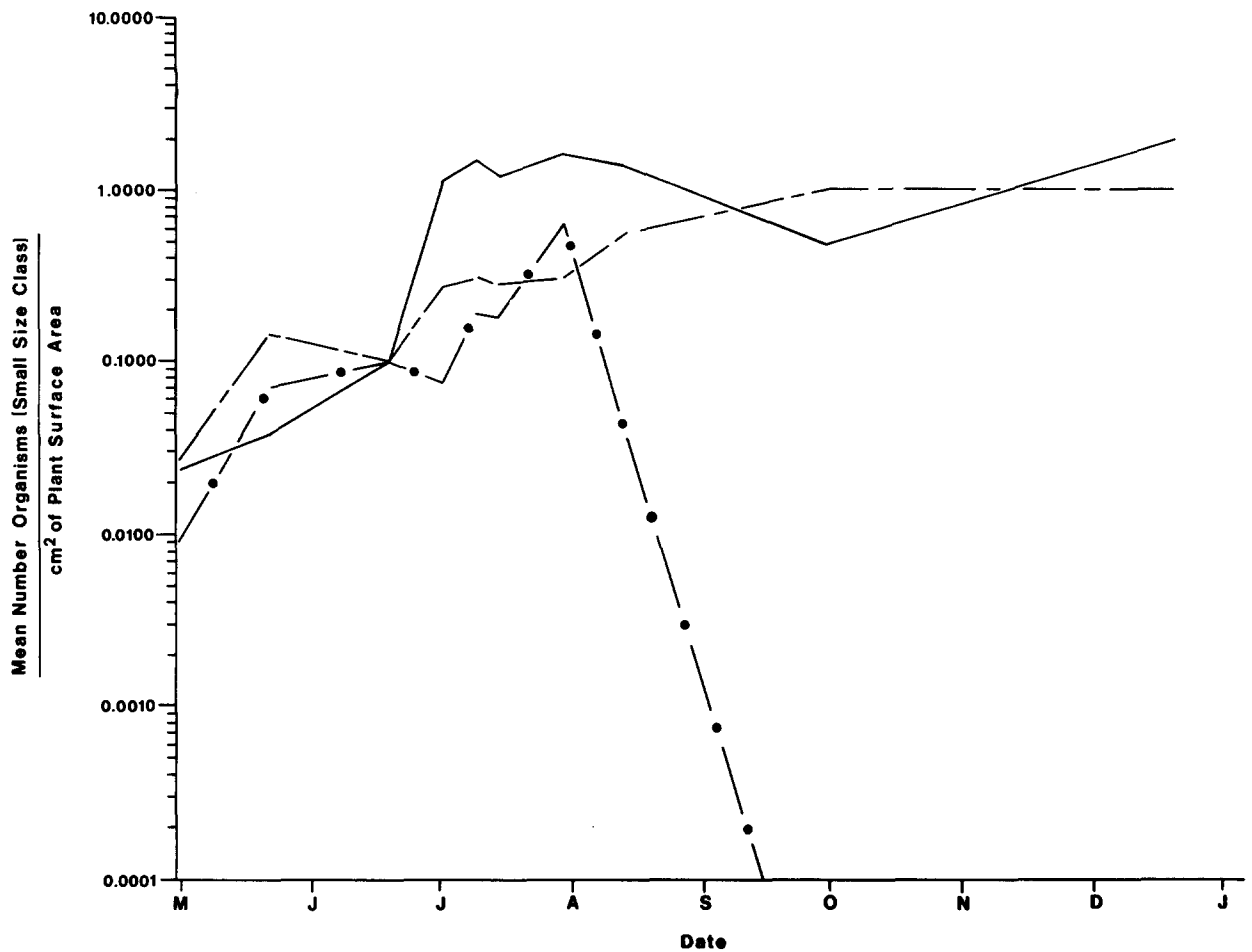
Fig. 3A **T. fictus** —————— **C. delicata** — — — — **B. flavistriga** —— • —— **B. quilleri** ——— - ———

Top Stratum   Mid Position

Fig. 3A & B. The average number of each species of mayfly per cm² of *Myriophyllum* surface area. 3A is for the small size class of each species and 3B is for the large size class of each species. Both are for the top stratum, mid position.

common resource must be limited in supply (Andrewartha, 1971). *C. delicata* seems as well adapted morphologically as *T. fictus* and should have no physical problem in entering the top stratum and taking up space. I have observed *C. delicata* at high densities in groundwater-fed pools that co-occur with high densities of *T. fictus* in the upper strata of the plant beds. There may be some physiological or behavioral basis for preference of stratum in *C. delicata*.

Hynes (1970) states that competitive exclusion of similar species usually holds in streams and that similar species are generally separated ecologically by having different life histories. This pattern may not be the case for these mayflies. Streams can be classified as 'nonequili-

brium' communities (Hutchinson, 1953) and should show a high degree of niche overlap. The overlapping microdistributions of the mayflies in the *Myriophyllum* in this section of Pennington Creek tend to support this interpretation. But this section of the stream exhibits relative thermal constancy through the year and may not be a 'nonequilibrium' community (Ward, 1976). Ward (1976) produced a model describing the effect of thermal constancy on stream invertebrates with particular reference to sites below dams with water released from the hypolimnion. He suggested that thermal constancy would produce an equilibrium community which would result in reduced niche overlap and finally result in reduced species diversity. This situation is not the case in the
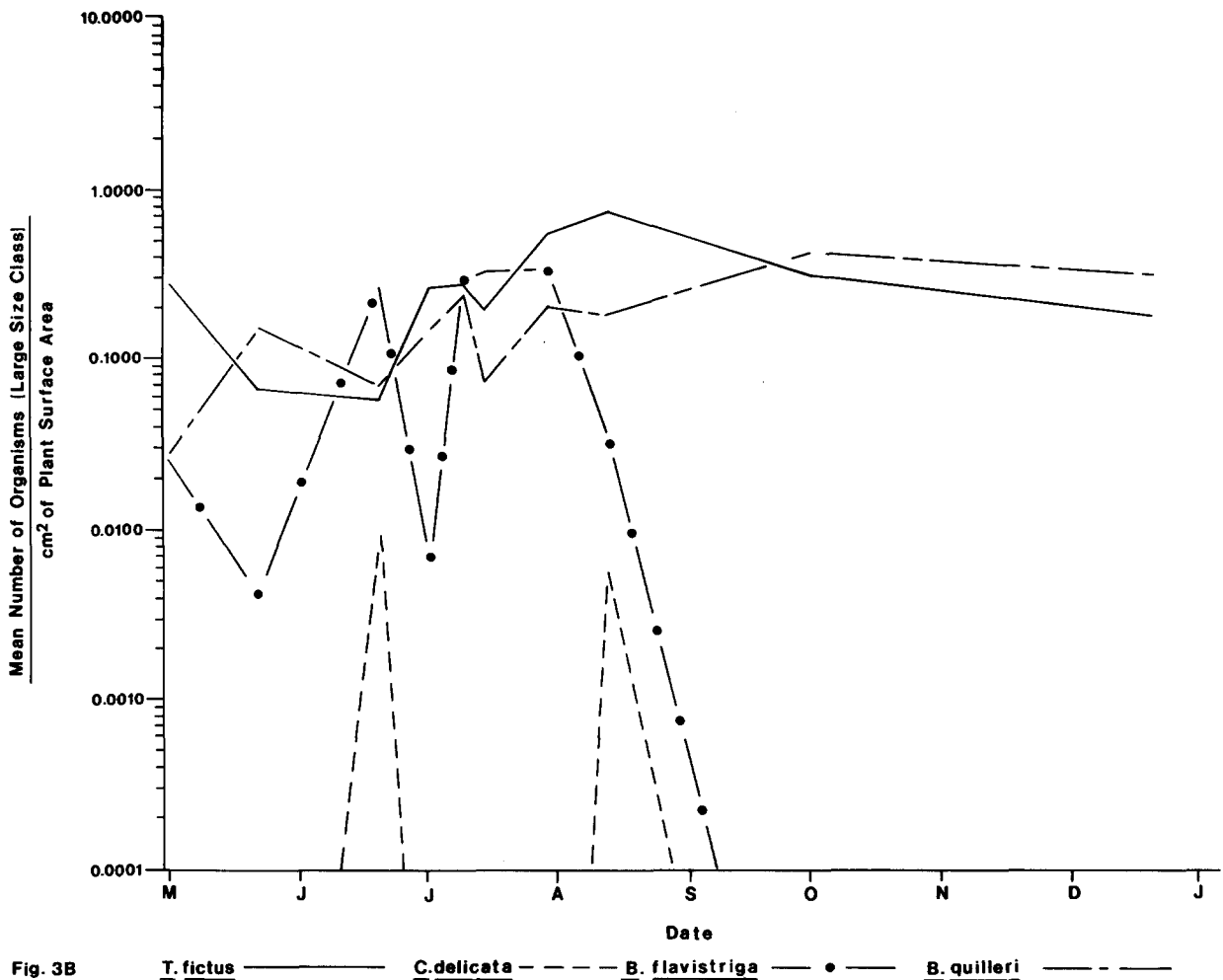
Fig. 3B   T. fictus ———————   C. delicata — — — —   B. flavistriga ——— • ———   B. quilleri ——— - ———

Top Stratum   Mid Position

community of mayflies in the *Myriophyllum* beds.

I propose that the constant temperature and the constant flow conditions enhance the stable growth of *Myriophyllum* in this section of Pennington Creek. The plant beds provide a nearly optimum habitat for the mayflies. The four species of mayflies are very similar and food and space are probably not in short supply. Therefore, they apparently do not compete sufficiently to prevent overlapping microdistributions and population densities throughout the year.

Acknowledgements

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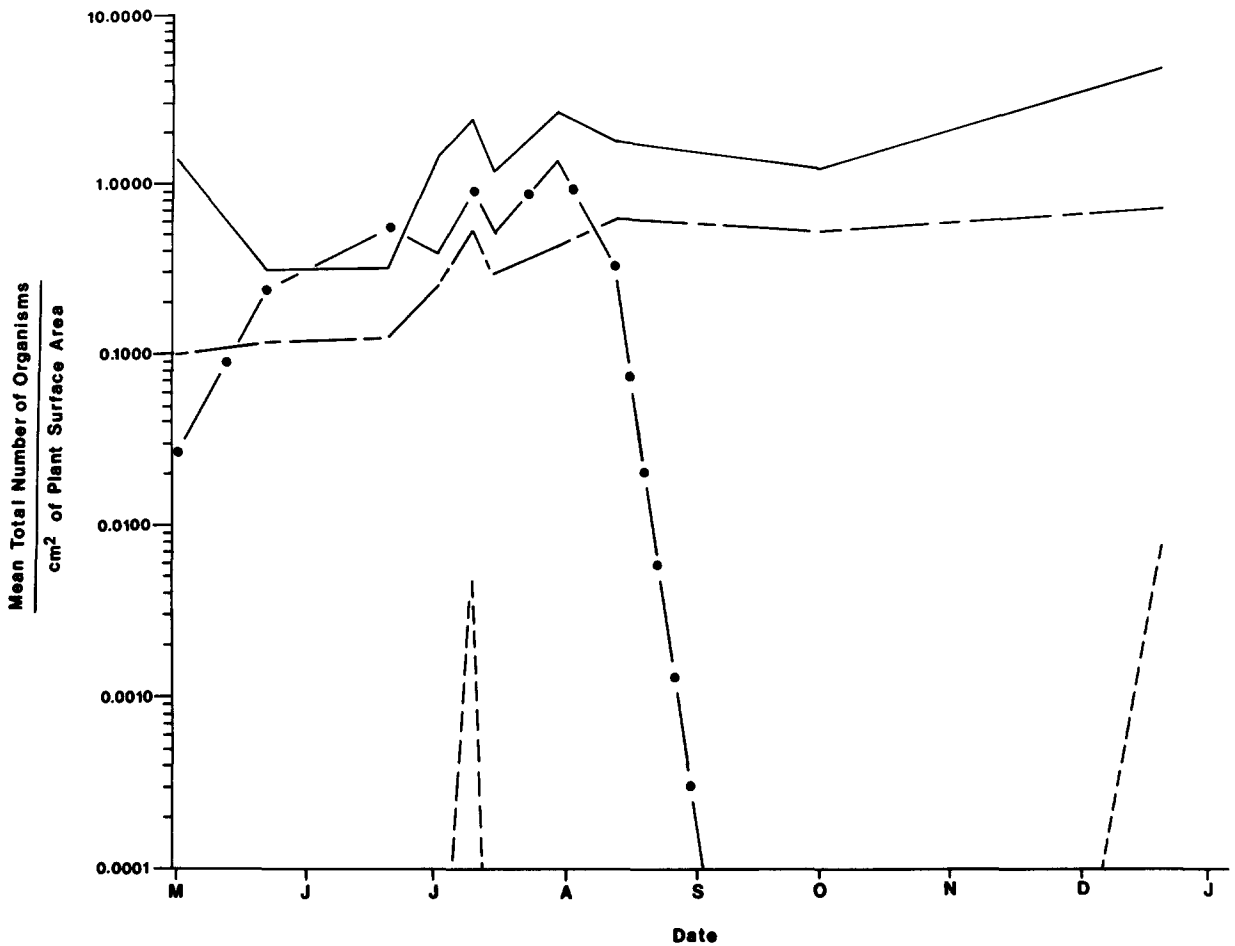Berg, C. O. 1950a. Biology of certain Chironomidae reared from

Fig. 4

Top Stratum   Front Position

T. fictus —————— C. delicata — — — — B. flavistriga ———•——— B. quilleri —— — ——

Fig. 4. The average total number of each species of mayfly per cm² of *Myriophyllum* surface area for the top stratum, front position.

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