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Seasonality and Diversity of Mayfly Adults (Ephemeroptera) in a "Nonseasonal" Tropical Environment[1]

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ABSTRACT

Fluctuations in abundance of adult Ephemeroptera were analyzed from a year of daily light-trap collections made at Miramar, a relatively nonseasonal locality on the Atlantic coast of northwest Panama. Most taxa occurred year-round and some of these showed within-year fluctuations in abundance that may be seasonal. The species in the genus *Leptohyphes* showed a pronounced lunar periodicity. A comparison of this sample with other samples of Ephemeroptera suggests that mayflies in the tropics may not be more diverse than in the temperate zone.

SEASONAL FLUCTUATIONS IN THE ABUNDANCE of tropical insect populations have been systematically investigated only in recent years. The absence of a cold season allows many species to be present during much of the year, although the alternation of wet and dry seasons imposes its own constraints. Seasonal fluctuations in terrestrial tropical insect populations have been documented in a number of studies (Galindo *et al.* 1956; Owen 1969; Owen and Chanter 1970, 1972; Wolda 1979b, 1980a, b, 1982, 1983a; Denlinger 1980); for further references see Wolda (1978). It has been shown that the seasonal range—the length of time per year that a species is present as an active adult (Wolda 1979a)—is, on the average, longer in the tropics than in the temperate zone. A number of cases of insect population fluctuations have been documented in "nonseasonal" tropical habitats (Wolda and Fisk 1981, Wolda and Galindo 1981)—that is, in habitats without a clear alternation of wet and dry seasons. Insect species in such areas with a less seasonal weather pattern tend to be less seasonal, but not necessarily aseasonal (Wolda 1983a).

Studies of seasonal fluctuations in the abundance of tropical Ephemeroptera and other aquatic insects are scarce. Most have been done in African lakes (Hartland-Rowe 1958; Tjønneland 1960, 1961; Chutter 1970; Corbet *et al.* 1974) and streams (Hynes 1975, Zwick 1976, Statzner 1976, Kopelke 1981), some in Asian streams (Bishop 1973, Bright 1982), and one in Panama (McElravy *et al.* 1982). Although studies of life histories and seasonal patterns of temperate Ephemeroptera are numerous (see Clifford 1982 for review), work on tropical members of this important part of the aquatic fauna has only recently begun. To date, seasonality studies have been published on the mayflies of the Ethiopian region (Tjønneland 1960, 1961; Corbet *et al.* 1974; Kopelke 1981) and Malaya (Bishop 1973). All were conducted in areas with a distinct alternation of wet and dry seasons; this paper presents the first data on seasonality of mayflies in a tropical area which lacks a distinct dry season.

The diversity of aquatic tropical insects, relative to their temperate counterparts, is a subject of controversy (Stout and Vandermeer 1975, Stanford and Ward 1983). Tropical Trichoptera seem to be slightly more diverse than temperate ones (McElravy *et al.* 1982). The available information on Ephemeroptera will be discussed in this paper.

STUDY SITE AND METHODS

The study site was near the village of Miramar (9°N, 82°15'W) in the province of Bocas del Toro, Republic of Panama. Miramar is on the Atlantic coast in the southwest corner of the Laguna de Chiriqui. Insects were collected with a light-trap, Pennsylvania type, with a 15-W blacklight. The insects fell through a funnel in a collector with preservative (FAA, a mixture of alcohol, formaldehyde, and acetic acid). The trap was located in a row of trees among pastures, at the foot of a wooded slope. A small stream traversed the pastures about 50 m from the light-trap. The trap was operated nightly from 6 to 10 P.M. from 15 November 1978 to 13 November 1979. Local help was hired to collect the daily samples, which were then taken to the Smithsonian Tropical Research Institute where they were sorted to order. Due to logistic problems data are missing from 12–30 June, from 12–25 July, and from 28–31 July 1979; therefore, in this

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TABLE 1. *List of genera, number of individuals in each genus, and, among the males, number of species of mayflies caught in a light-trap during one year in 1978/79 in Miramar, Panama.*

Taxa	Species	Individuals
Baetidae		
Apobaetis	1	6
Baetis	3	36
Baetodes	3	117
Dactylobaetis	1	91
Pseudocloeon	5	145
New Genus	1	2
Leptophlebiidae		
Farrodes	1	581
Hermanella	1	1
Traverella	1	1
Terpides sp. A	1	11
Terpides sp. B	1	11
Terpides sp. C	1	2
Thraulodes	1	11
New Genus 1	1	6
New Genus 2	1	3
Tricorythidae		
Haplohyphes	1	48
Leptohyphes sp. A	1	21,266
Leptohyphes spp.	2	6366
Tricorythodes	1	270
Euthyplociidae		
Euthyplocia hecuba	1	104
Polymitarcidae		
Campsurus	>1	42

paper, which presents data per week, weeks 24, 25, 28, and 29 are missing, and weeks 26 and 30 are based on only 3 and 2 daily samples, respectively. Also, data for the final two weeks have been combined since the trap was emptied only at the end of that period.

Although no weather records are kept for Miramar, those available for other sites in the province of Bocas del Toro all demonstrate a bimodal seasonal rainfall pattern. The town of Changuinola, some 50 km from Miramar, experiences no dry season: rainfall in February or March and August or September drops to 100 mm, but it peaks to 400 mm during April and December (Wolda and Galindo 1981; Fig. 1). Villagers in Miramar claim a similar general pattern. The total annual rainfall for Miramar is estimated at 3000 mm based on interpolation of data from a variety of other sites. Monthly examination of the stream near the light-trap showed no obvious variation in water level or stream velocity.

The mayflies were shipped to Flowers for determination and tabulation. They were determined to genus and where possible to species; for most adult neotropical mayflies, reliable determination of species is not possible at this time since most of the fauna is undescribed or known only from nymphs. Even the simpler task of separating different species is complicated by the fact that in many genera only male imagos can be distinguished from each other at the species level. All the Miramar samples contained genera with large numbers of females and subimagos which could not be correlated with any males; hence that part of each sample could not be sorted to species. Voucher specimens are deposited in the Ephemeroptera collection of Florida A&M University.

RESULTS

The almost 30,000 mayflies caught belonged to the 18 genera listed in Table 1. On the basis of the males, the minimum number of species present was determined in each genus except *Campsurus*; this widespread neotropical genus contains 27 known species identifiable only by the male imago, but all *Campsurus* trapped in Miramar were female.

The samples were dominated by the genus *Leptohyphes*, L. sp. A, representing 73 percent of the individuals and 94.8 percent of the genera. The minimum number of species present was 30, but it is conceivable that the actual number was as high as 35. When using a diversity index, it is generally advisable to use the alpha of the log series distribution (Fisher *et al.* 1943, Wolda 1983b). This index for the present sample is somewhere between 3.3 and 3.9, using the extremes given above for the number of species. Table 2 presents the diversity of adult mayflies in a number of samples from both the temperate zone and the tropics, including an unpublished Panamanian sample. These data suggest that samples taken by light-traps or by sweeping the vegetation were more diverse than samples from emergence traps. Tropical samples were not conspicuously more diverse than temperate ones.

During the year of study the total number of individuals caught decreased dramatically (Fig. 1), mostly because of a decrease in the most common species (Fig. 3A). The numbers caught fluctuated dramatically over a period of about four weeks, especially in the months before the missing samples. Again, these fluctuations occurred especially in the genus *Leptohyphes*. The number of individuals in that genus caught per week is plotted against the phase of the moon in Figure 2 for the first seven mooncycles of the study period. The number in the week with a new moon is set at 100 percent, and the numbers in the other weeks are expressed as a percentage of that. The number of *Leptohyphes* caught during the full moon was only 10 percent of that during the new moon, and the numbers caught during the first and last quarters averaged 50 percent. The large variation during

TABLE 2. *Diversity of some tropical and temperate samples of adult Ephemeroptera. Em = emergence traps, LT = light-traps, Ns = net samples. Var = a combination of different methods.* N = *number of individuals,* S = *number of species, alpha = diversity index with standard deviation.* MC *is the number of individuals in the most common species as a percent of the total number in the sample. Data ordered according to the value of alpha. In some cases the samples are from the same area but collected with a different technique (Ulfstrand 1969) or in different years (Illies 1978, 1982).*

Source	Method	Country	*N*	*S*	*MC*	Alpha
Jazdzewska (In press)	Var	Poland	349	25	22.7	5.93 ± 1.19
Carlson 1971	Var	USA, SC	11,815	45	37.4	5.92 ± 0.88
Peters and Warren 1966	LT	USA, AR	3456	34	60.7	5.21 ± 0.89
Ulfstrand 1969	LT	Sweden	532	17	63.3	3.36 ± 0.81
Ulfstrand 1969	Ns	Sweden	2915	22	13.7	3.24 ± 0.69
Present paper	LT	Panama Mir	29,120	30–35	73.–	3.30 ± 0.60–3.92 ± 0.66
Flowers and Wolda (Unpubl.)	LT	Panama CG	7178	24–30	69.2	3.10 ± 0.63–4.00 ± 0.73
Kopelke 1981	Em	Zaire	29,892	21	29.5	2.21 ± 0.48
Langford 1975	Em	England	2620	15	37.8	2.10 ± 0.54
Illies 1980	Em	Austria Tb	17,737	12	48.4	1.26 ± 0.36
Flannagan and Lawler 1972	Em	Canada	193	5	49.2	0.94 ± 0.42
Illies 1980	Em	Austria Sb	1725	7	81.1	0.93 ± 0.35
Brittain 1978	Em	Norway	3071	7	53.6	0.86 ± 0.32
Illies 1982	Em	Germany	127,744	9	84.–	0.70 ± 0.24
Illies 1978	Em	Germany	67,730	7	79.4	0.60 ± 0.23

the first and last quarters could be related to the cloud cover during those weeks. There is no clear evidence that the phases of the moon affected the number of individuals of any other species which was attracted to the light-trap.

To avoid the confusion of these lunar fluctuations, it is advisable to consider the numbers per four-week period. The data for the seven most common taxa, in order of decreasing abundance, are given in Figure 3, and for the five less common taxa in Figure 4. The other eight taxa occurred too infrequently for meaningful analysis. One period (marked by an asterisk) yielded no good data, and the period preceding that is based on only two weeks of data so that the number presented for that period is twice the actual number caught. The general decrease in abundance which was in evidence in Figure 1 is due to the *Leptohyphes* species (Figs. 3A and 3B), *Dactylobaetis* (Fig. 4A), and *Campsurus* (Fig. 4C), but is not obvious in the other taxa. Most species of mayflies were found throughout the year or, in case of the less common species, appeared to occur throughout the year. Some taxa, however, appeared to be present during only part of the year. *Tricorythodes* (Fig. 3D) was, with the single exception of one individual in September, found only from December through March. *Baetodes* (Fig. 3F) had a maximum from September through November and was absent from February through April. *Haplohyphes* (Fig. 4B) occurred mostly between March and September. The genera which occurred or probably occurred year-round showed variations in abundance apart from the general decrease in some species noted above. Because no rainfall data are available for Miramar, no correlation analysis could be attempted. However, none of the species shows an obvious correlation between the variation in abundance and the general rainfall pattern.

DISCUSSION

Most groups of insects are much more diverse in the tropics than in the temperate zone; however, exceptions may exist, such as the parasitic Hymenoptera (Owen and Chanter 1970, Owen and Owen 1974, Owen and Svensson 1974, Hespenheide 1979, Morrison *et al.* 1979, Janzen 1981) and bees (Michener 1979). Stout and Vandermeer (1975) discussed the controversy about the diversity of tropical aquatic insect samples relative to temperate ones and concluded that tropical aquatic insects are more diverse. Conclusions to the contrary they blamed on inadequate sampling; however, their own conclusions were based on extensive extrapolations from rather small samples. Caddisflies may be slightly more diverse in the tropics (McElravy *et al.* 1981) and stoneflies less diverse (Illies 1969). Table 2 suggests that the Ephemeroptera also may not be more diverse in the tropics. Light-traps and nets tended to collect more diverse samples than emergence traps. This was to be expected if there were different habitats outside of the emergence traps from which adult mayflies could have come to the vegetation and the light. However, if some tropical mayfly adults are shorter lived than temperate ones, and if there were such short-lived species in Miramar, and if these flew at dawn when the light-trap was not operating, then we have underesti-

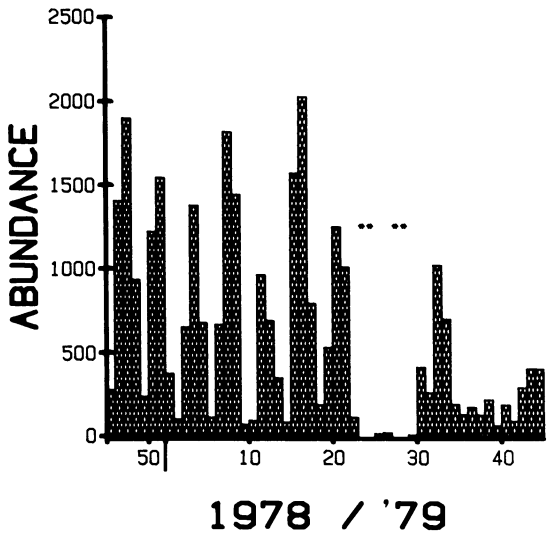

FIGURE 1. The number of mayflies per week in a light-trap at Miramar. Asterisks refer to missing data. Numbers along the abscissa refer to the number of weeks since the beginning of January.

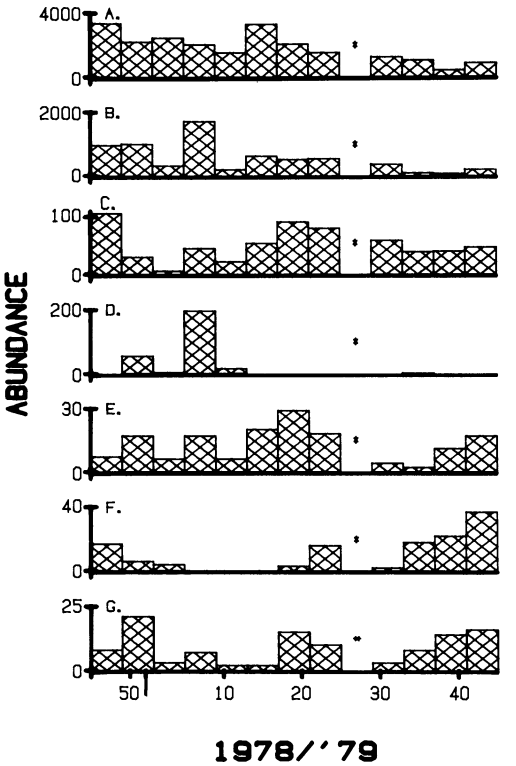

FIGURE 3. Number of individuals per four weeks in the six most common taxa of mayflies (genera or species) caught in the light-trap at Miramar. An asterisk refers to a period with no data. In order of abundance: A. *Leptohyphes* sp. A, B. *Leptohyphes* spp., C. *Farrodes* sp., D. *Tricorythodes* sp., E. *Pseudocloeon* spp., F. *Baetodes* spp., and G. *Euthyplocia hecuba*.

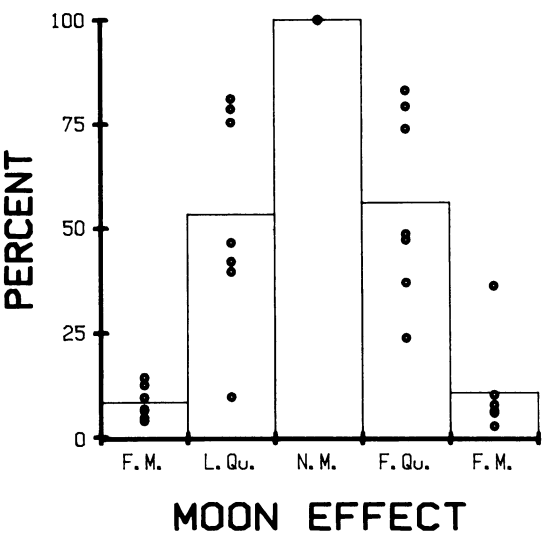

FIGURE 2. Effect of the phases of the moon on the number of mayflies in the genus *Leptohyphes* caught during the first seven mooncycles of the study period. The number caught during the week with the new moon is set at 100 percent. The numbers caught in the two weeks before and after the new moon are expressed as a percentage of the number at the new moon. Mean percentages are given by the histogram.

mated the diversity of the mayflies at that locality. The same applies to Corriente Grande, the other Panamanian locality noted in Table 2. The aquatic fauna in Miramar may have been depauperate because of environmental degradation, but the one at Corriente Grande was not.

In many species of insects the number of individuals caught in light-traps varies with the phases of the moon. Many more individuals are caught during the new moon than during the full moon, although this is not true for all species nor at all times of the year (Brown and Taylor 1971, Goel 1976, Wolda 1977). The same conclusion applies to the mayflies discussed here. It seems likely that this variation was largely due to the moonlight's detracting from the light-trap, but an emergence rhythm related to the mooncycle cannot be ruled out (Hartland-Rowe 1955, Corbet 1964).

Seasonal variation in abundance refers to a fluctuation pattern which repeats itself year after year. No real evidence of seasonality can be extrapolated from only one year of data, but our experience with tropical insects elsewhere in Panama has been that a clearcut variation in

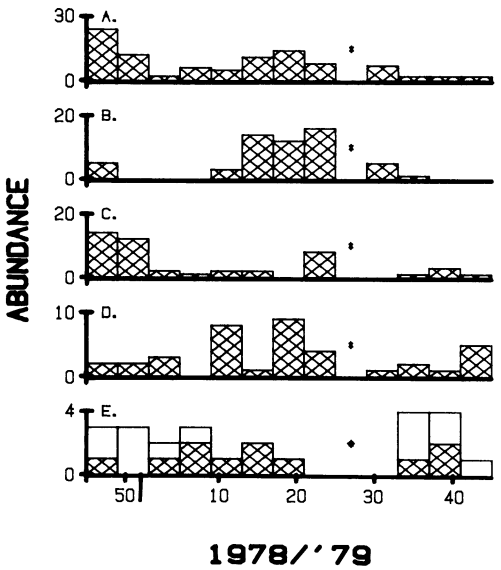

FIGURE 4. Number of individuals per four weeks in five less common genera of mayflies in the light-trap at Miramar. An asterisk refers to a period without data. In order of abundance: A. *Dactylobaetis* sp., B. *Haplohyphes* spp., C. *Campsurus* spp., D. *Baetis* spp., and E. *Terpides* spp. In *Terpides* the crosshatched columns refer to *T.* sp. A and the blank columns to *T.* sp. B.

abundance within a year usually is repeated year after year. We predict that the genera *Tricorythodes, Baetodes, Haplohyphes,* and possibly *Baetis* did have a seasonal variation in abundance (Figs. 3D, 3F, 4B, and 4D). The large variation observed in genera such as *Leptohyphes* was probably not seasonal.

In his study of mayfly emergence in northeast Zaire, an area with a short but clearcut dry season, Kopelke (1981) showed rather large fluctuations in abundance in some species. His species occurred year-round, and he found no obvious correlation with the alternation of wet and dry seasons. However, because his study was also short (16 months), any conclusion about seasonal variation in abundance must remain tentative.

Bishop (1973) studied the seasonal abundance of mayflies and other aquatic insects in a Malayan river and found that fluctuations in numbers were caused at least in part by scouring of the streambed during spates. Similarly Bright (1982) obtained densities of *Baetis* nymphs on Palau that appeared to be correlated to current speed and discharge. Both authors sampled different localities in their study streams, and both found that fluctuations of nymphal abundance differed at different sites in the same stream. Neither author presented data on adult flight periods.

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