10 Yearly fluctuations in the mayfly community of a tropical stream draining lowland pasture in Costa Rica

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Mayfly populations in the Río Sábalo-Esquina, a small pasture stream on the border of the La Selva Biological Station, Costa Rica, were followed for two and one-half years, using weekly Surber samplers. Although the region is considered to have a non-seasonal, stable climate, populations of nymphs of all common species showed large fluctuations, whose timing varied from year to year. Similar fluctuations have been noted in light-trap samples of both adult mayflies and terrestrial insects in Central America. Numbers of individuals taken in the samples were low, although species richness of the Sábalo-Esquina is high and comparable to other streams of the lowland Central American tropics. There is evidence that fish predation has a depressing effect on the mayfly populations of this stream.

Introduction

Recent studies of seasonality and annual variability in tropical insects have provided important insights into some of the basic workings of tropical ecosystems. As a result of recent work on this topic (e.g., Wolda 1977, 1980, 1983a; Wolda and Galindo 1981; McElravy et al. 1982; Wolda and Flowers 1985), the "climatic stability" hypothesis as applied to the tropics (Klopfer 1959) has been disproved. Many tropical areas are moderately to highly seasonal with respect to rainfall. Insects in these areas exhibit seasonal fluctuations comparable to temperate insects. Even in non-seasonal areas, some species still display seasonal patterns (Wolda and Fisk 1981; Wolda and Flowers 1985).

While most of the data from the tropics are for terrestrial insects, there has been some attention paid to aquatic insects. McElravy et al. (1982), Wolda and Flowers (1985), Kopelke (1981), Ferrington et al. (1993), Masteller and Buzby (1993), Pescador et al. (1993) used light and emergence traps to study aquatic

insect population fluctuations in tropical streams. While the emphasis in these studies has been on adult emergence patterns and environmental factors that affect these patterns, seasonality studies on adult aquatic insects tell us little about fluctuations in communities of aquatic insect larvae over time. Only two exceptions, Bishop (1973) and Pearson et al. (1986) consider fluctuations in aquatic insect faunas of tropical Asian streams over time. In contrast, studies of temperate aquatic insects often use both adults and larvae to work out life cycles; such studies have shown that in cold temperate areas the majority of mayfly species are univoltine, but as one moves south into warm temperate regions (eg. the Southeast U.S.), multivoltinism becomes common (Jacobi and Benke 1991). In tropical streams, many mayfly species emerge throughout the year, although some species have a shorter period of peak emergence (Wolda and Flowers 1985).

In this paper, we present data from two-and-one-half-years' sampling of a mayfly community in a small stream in Costa Rica's Atlantic slope drainage. While the time period of this study must be considered "short-term" according to the less than three years criterion established by McElravy et al. (1989), and is far less than the six years recommended by Wolda (1983a) for studying fluctuations in tropical insect populations, these data still give one of the longest-running pictures to date of a community of tropical mayflies.

Materials and Methods

Study Site

The samples are from a single site (Fig. 1) on Río Sábalo-Esquina, a small fifth-order stream that forms the east boundary of the La Selva Biological Station, Sarapiquí region of Costa Rica (Pringle et al. 1990, site 41 in their Fig. 2). The area receives an average annual rainfall of 4000 mm. There is no pronounced dry season, but when 25 years of rainfall data were considered, the driest months occurred on average from February to April. The west bank of the Sábalo-Esquina retains the original tropical wet forest vegetation while the east bank has been cleared for pasture in the lower watershed. The Sábalo is in the Río Guacimo watershed. The sampling site is located on a Pleistocene lava flow with an elevation of 40 m. An area-wide survey of basic stream water chemistry in 1986 recorded a nitrate (NO_2+NO_3-N) concentration of 75 µ/L, ammonia (NH_4-N) of 18 µ/L and soluble reactive phosphorus (SRP) of 21 µ/L (Pringle et al. 1990). Stream width is 4-6 m, and the bottom consists of small stones to large (15 cm) cobbles in riffles and silt and detritus in pools and depositional areas. This site was previously sampled in Stout and Vandermeer's (1975) study on tropical stream diversity (Sábalo).

Figure 1. **View of the study site on the Río Sábala-Esquina: the structures in the stream are cages the junior author used in the fish exclosure/enclosure experiments.**

Sampling

Sampling was done with a Surber sampler between May 1988 and November 1990. During most of this time samples were collected weekly, although there are several gaps in 1988 and at the end of 1989. On each sampling date, five separate Surber samples were taken randomly within a large sunny riffle occurring in a 30-40 m stream segment. Invertebrates were picked from the debris in the laboratory at the La Selva Biological Station, then the samples were sent to the United States and sorted to morphospecies at Cornell University and Florida A&M University. Mayflies were identified to genus and species-level units using available literature, then counted and tabulated. Water level in the Sábalo-Esquina was measured from a permanent stream gauge.

Results

The water levels of the Río Sábalo-Esquina between May 1988 and the end of 1990 are shown in Fig. 2. We use gauge height rather than the more common discharge as a measure of stream flow because there in not a straight-line relationship between discharge and depth, and the required measurements for accurate calculation of discharge were made only once. This was when the gauge height was at 42 cm; at this height a discharge of 0.87 m^3/s was calculated. From Fig. 2 it can be seen that 42 cm is a moderately low depth for this stream, and thus a discharge of 0.87 m^3/s is a reasonable estimate of base flow. There was no obvious seasonal pattern of discharge fluctuations during our sampling period; however, several spikes occurred each year as a result of high rainfall occurring at La Selva or in the highlands of the upper Sábalo-Esquina watershed.

Thirty-seven morphospecies of mayflies were found in the Rio Sábalo-Esquina during the 1988-1990 sampling period. Table 1 illustrates the seasonal range (for the first to last week [counted from the beginning of January] when a given species was present) and total number collected for each mayfly species and morphospecies in each of the three years. Five families were found but two, the Caenidae and Heptageniidae, were represented by single individuals. Thirteen taxa (35 per cent of the total mayfly fauna) were found during only one of the three years and seven taxa (18 per cent of the fauna, including the two cases just mentioned) were represented by single individuals. Tricorythidae was the numerically dominant family, reaching a maximum during 1989, while the Baetidae had the largest number of taxa. As with other studies of Central American Ephemeroptera, the vast majority of taxa are undescribed in the nymphal stage, therefore most species were only identifiable to genus.

Figures 3-5 show the weekly totals for numbers of species and individuals. No year-to-year pattern is apparent, nor is there evidence of seasonal variability within years. Diversity is also shown, calculated as Fisher's alpha of the log series. This diversity index is independent of sample size and does not give excessive weight to the most common species in a sample (Wolda 1981, 1983a, 1983b). Points are omitted for weeks where numbers were very low or when the variance of alpha was larger than its value. In 1989 and 1990, the two years with reasonably complete sets of values, peaks in diversity (alpha) coincide well with peaks in numbers of species, somewhat less so with the peaks of numbers of individuals (Figs. 4-5). The agreement in our data between changes in alpha and fluctuations of numbers of species and individuals is better than that reported by Wolda (1983b) for tropical cockroaches. However, the lack of correlation in the case of the cockroaches was caused by very abrupt seasonal peaks of individuals, a phenomenon that did not occur in the Sábalo mayflies.

Figure 2. **Water levels of the Río Sábalo-Esquina during the 1988-1990 sampling period: numbers along the abcissa refer to the weeks since the beginning of January (for discussion of discharge, see text).**

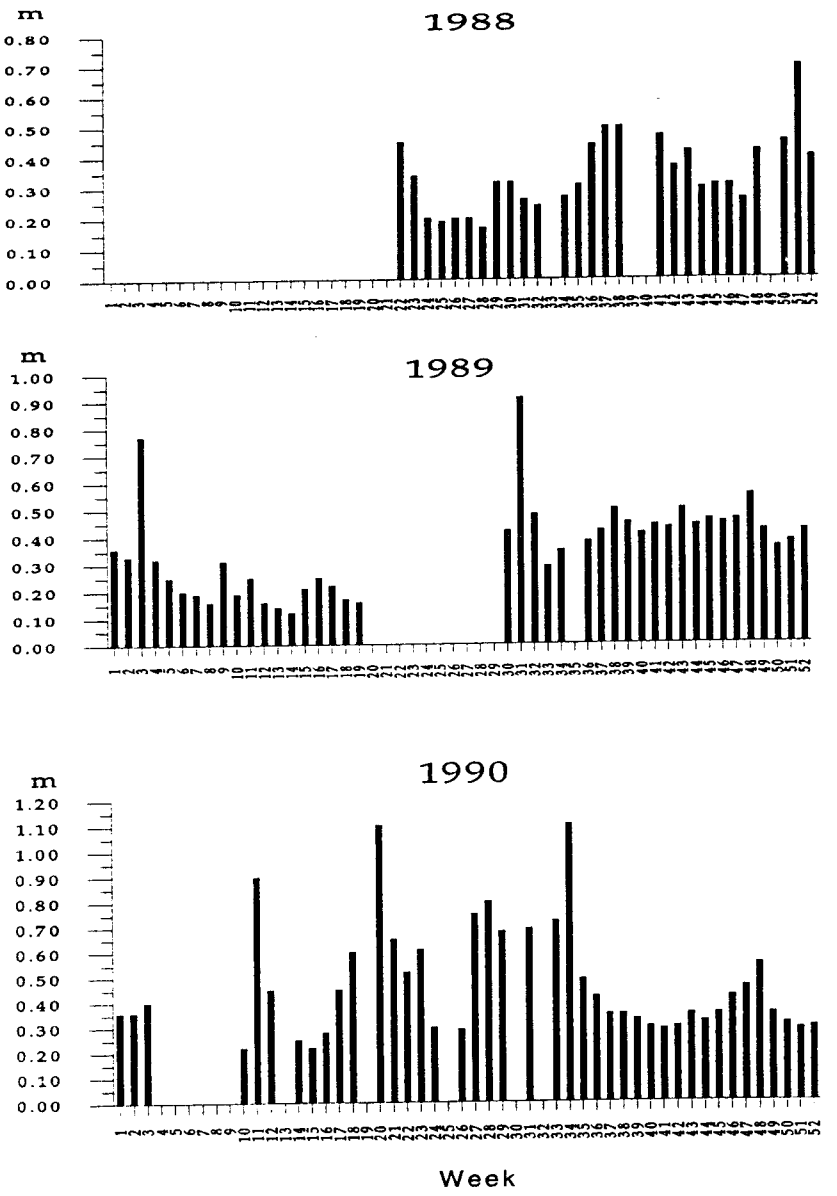


Table 1. Ephemeroptera of the Río Sábalo-Esquina (for details, see text).

Taxon	1988		1989		1990	
	Seasonal Range	Total Number	Seasonal Range	Total Number	Seasonal Range	Total Number
Leptophlebiidae						
Traverella	29	1	27-38	7	10-49	43
Hydrosmilodon			38	1		
Farrodes	14-36	17	6-40	9	10-49	24
Thraulodes sp. 1	14-32	26	6-42	26	10-45	77
Thraulodes sp. 2	24	1	33-40	6	18-45	25
Thraulodes sp. 3	14	2			19	2
Hagenulopsis					18, 45	3
Baetidae						
Moribaetis ellenae	36	1				
Baetodes sp. 1	14-34	9	24-38	4	14-45	20
Baetodes sp. 2			24-37	3		
Camelobaetidius sp. 1	14-34	19	24-42	9	19-45	17
Camelobaetidius sp. 2	32-51	2	24-37	4	37-40	2
Guajirolus			38	1	39-42	2
Cloeodes	14-46	5	27	1	26	1
Baetidae sp. 1	14-51	19	21-36	11	18-44	11
Baetidae sp. 2			14-20	3		
Baetidae sp. 3			21-24	2		
Baetidae sp. 4	29	4	23-24	4		
Baetidae sp. 5			24	1		
Baetidae sp. 6			15-24	2	37-42	6
Baetidae sp. 7			38	1		
Baetidae sp. 8	14-36	2			19-28	2
Baetidae sp.	14-29	6	15-17	2	19-42	7

Table 1. (continued)

Tricorythidae						
Leptohyphes packeri	14-46	32	6	1		
Leptohyphes sp. 2	14-46	55	11-41	30	10-49	82
Leptohyphes sp. 3	14-32	8	21-40	21	10-49	68
Leptohyphes sp. 4	14	1	26	1	22	1
Leptohyphes sp. 5	14-46	6	6-30	11	15	2
Leptohyphes sp.			32	1	18-44	7
Haplohyphes	25-29	3				
Tricorythodes "corpulentus"			1	1		
Tricorythodes 2	14-51	6	11-42	103	10-49	71
Tricorythodes 3	24-51	70	1-40	200	15-49	31
Tricorythodes 4	29-46	6	40	2		
Tricorythodes 5	29-32	12	20-31	3		
Tricorythodes 6	29-32	12				
Tricorythodes 7	24	6			42	1
Tricorythodes sp	46	2				
Caenidae						
Caenis			20	1		
Heptageniidae						
Stenonema mexicanum	25	1				

Figure 6 shows the contributions of the three major families (Baetidae, Leptophlebiidae, Tricorythidae) to the total Ephemeroptera fauna. No regular patterns of annual or seasonal variation are apparent although the composition of the fauna changed towards the latter half of 1988 when the Tricorythidae became the overwhelmingly dominant family. This pattern persisted until mid 1989, when first the Baetidae and then the Leptophlebiidae again began increasing. In 1990 the Leptophlebiidae became relatively more important, and around week 40 of that year the three families reached approximately the same balance they had during the first sampling week of 1988. However, even in 1990 the stream had not regained its

Figure 3. **Fluctuations in numbers of species and individuals, and diversity, as alpha of the log series, of mayflies taken in Surber samples during 1988: black bars, numbers of species; white bars, numbers of individuals; grey bars, diversity.**

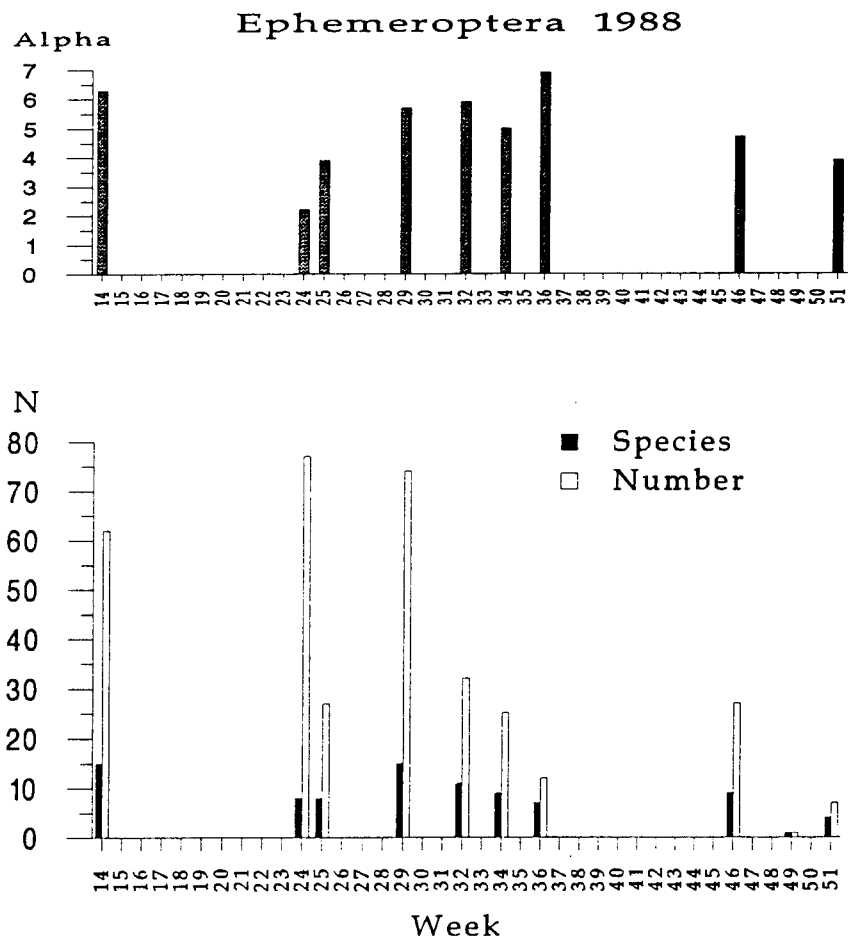


Figure 4. **Fluctuations in species, individuals and diversity of mayflies taken in Surber samples during 1989 (units are the same as in Figure 3).**

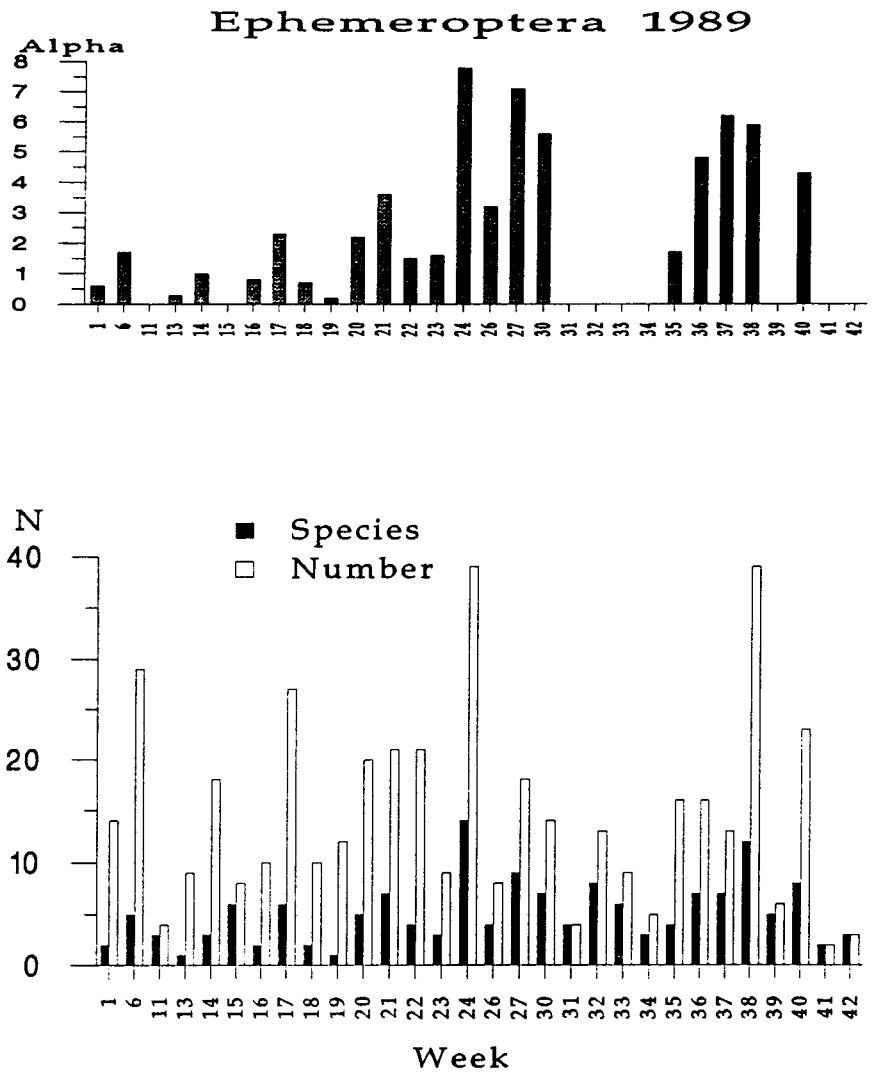
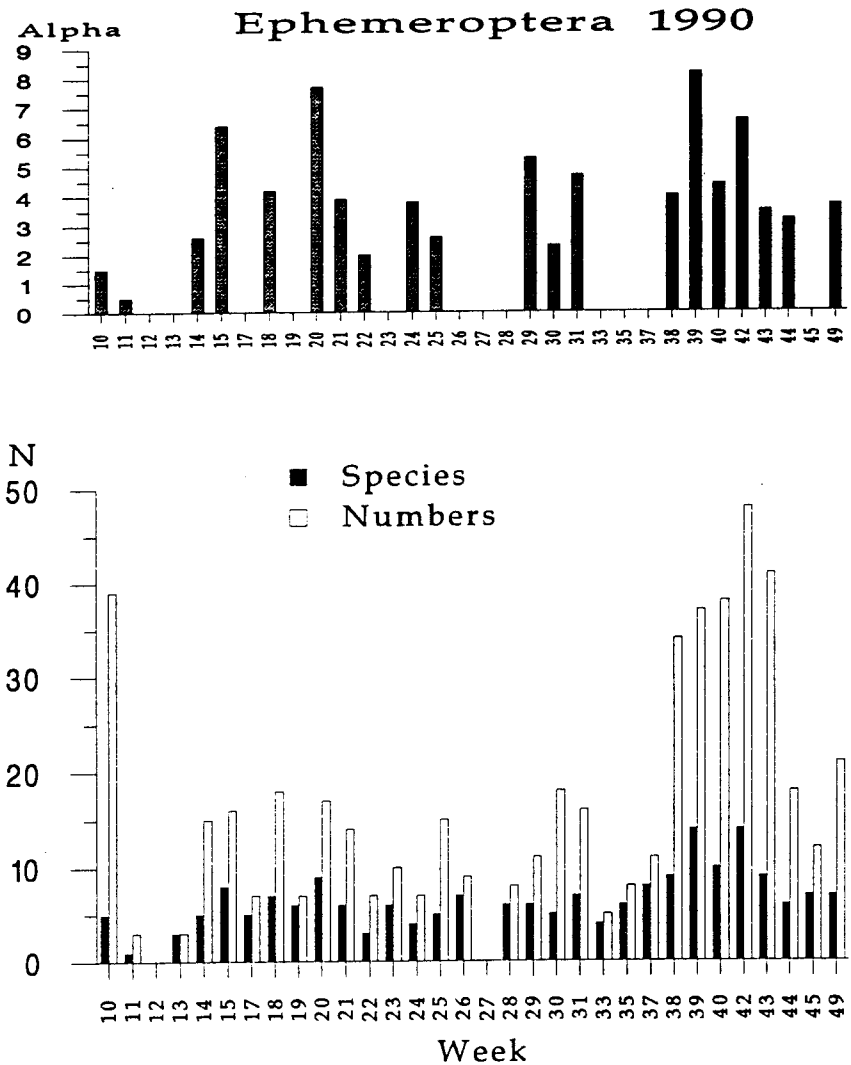


Figure 5. **Fluctuations in species, individuals and diversity of mayflies taken in Surber samples during 1990 (units are the same as in Figure 3).**



earlier fauna. A number of species that were represented in the early 1988 samples — even in the dominant family Tricorythidae — never reappeared in 1990, or were present only as one or two individuals. On the other hand, several species that were absent in early 1988 appeared in 1989 and were present in most of the 1990 samples (Table 1). Figures 7-9 show contributions of the most common genera within the Baetidae, Leptophlebiidae and Tricorythidae for 1988 to 1990. No seasonal fluctuations are apparent, nor is there any indication that the high discharge events had any effects on mayfly nymph populations.

The Tricorythidae was the dominant family in the Sábalo-Esquina. Within the Tricorythidae, three species, *Leptohyphes* sp. 2 and *Tricorythodes* sp. 2 and 3, were dominant (Table 1). In terms of relative abundance, *Leptohyphes* and *Tricorythodes* switched places in 1989 and 1990 (Fig. 9). The Baetidae were present initially but became scarce during much of 1989 and the first two-thirds of 1990 (Fig. 7). The Leptophlebiidae virtually vanished from mid 1988 to mid 1990, after which they reappeared in significant numbers (Fig. 8). Some species (eg., *Traverella* sp., *Thraulodes* sp. 3, *Leptohyphes* sp. 3) were found in increasing numbers from 1988 to 1990; other species (*Leptohyphes packeri* Allen, *Tricorythodes* spp. 5 and 6) were present at the beginning of the study in 1988 and virtually disappeared thereafter (Table 1).

Discussion

Although strongly impacted by human activity, e.g., active pasture in the lower watershed, the Río Sábalo-Esquina retains a mayfly fauna characteristic of clean lowland streams such as those encountered by Flowers (1991) on the Atlantic coast of Panama. Total species richness of Ephemeroptera in the Sábalo-Esquina is high, with 37 morphospecies; Stout and Vandermeer (1975) previously recorded 15 morphospecies from this locality. Our higher figure is a cumulative total over two and one-half years, while Stout and Vandermeer's figure should be compared with species richness of a single week's sample. In fact, our maximum species richness in a single week was also 15 (achieved twice in 1988), a figure that also compares favourably with the more diverse streams in the Panama study. However, there were many weeks of much lower mayfly diversity. In their year-long study of Yuccabine Creek, a diverse Australian rainforest stream, Pearson et al. (1986) found 16 morphospecies of Ephemeroptera. However, some of these species were present in much greater numbers than any Sábalo mayflies. In Yuccabine the most abundant species was a member of the genus *Atalophlebioides*, which achieved a mean of 16 individuals per sampling unit (calculated by dividing the yearly total by the number of kick samples taken during the year); by contrast, our most abundant species (*Tricorythodes* sp. 3, 1989) reached only 1.33 individuals per sampling unit (assuming one of our Surber samples is equivalent to one of Pearson et al.'s kick

Figure 6. **Contributions of the three major families to mayfly samples in the Sábalo-Esquina: white bars, Tricorythidae; grey bars, Leptophlebiidae; black bars, Baetidae.**

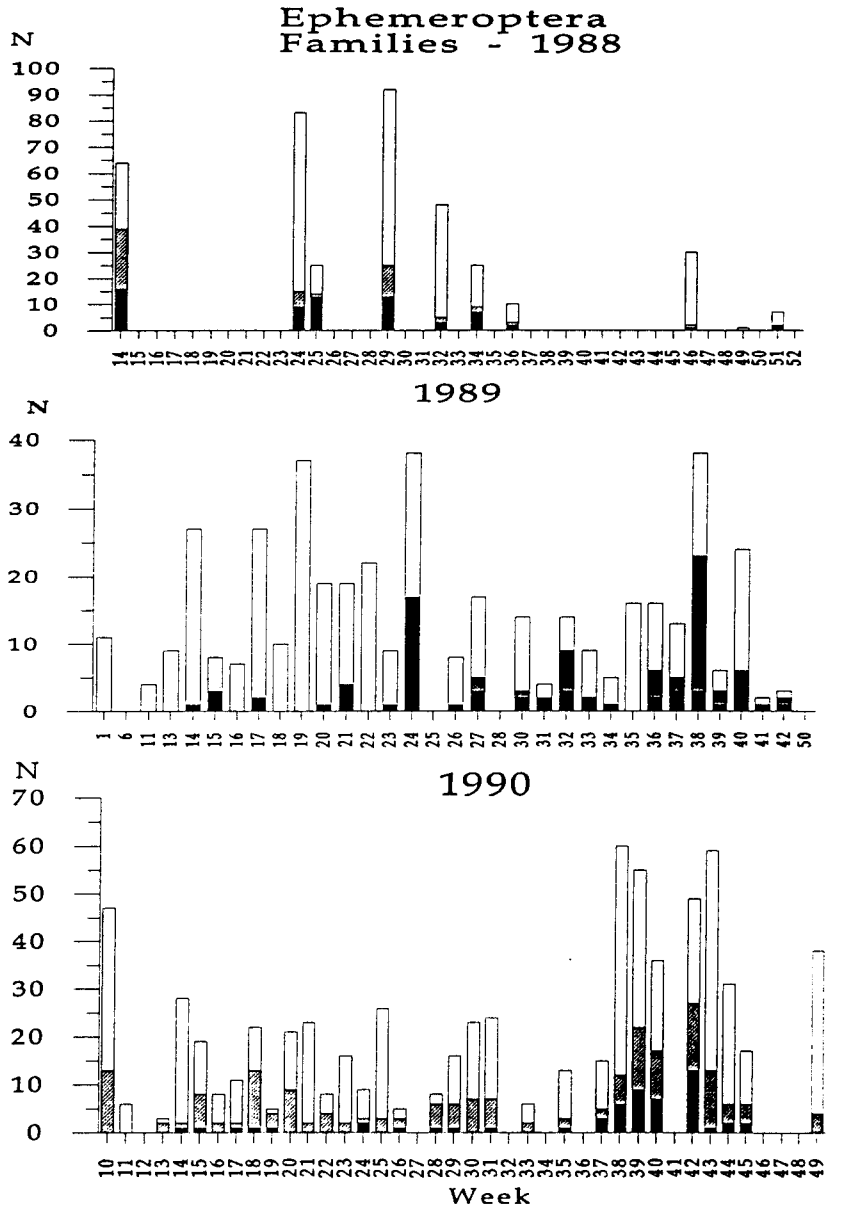


Figure 7. **Baetidae genera in the Sábalo-Esquina: white bars, *Baetodes*; black bars, *Camelobaetidius; grey bars, all other taxa.***

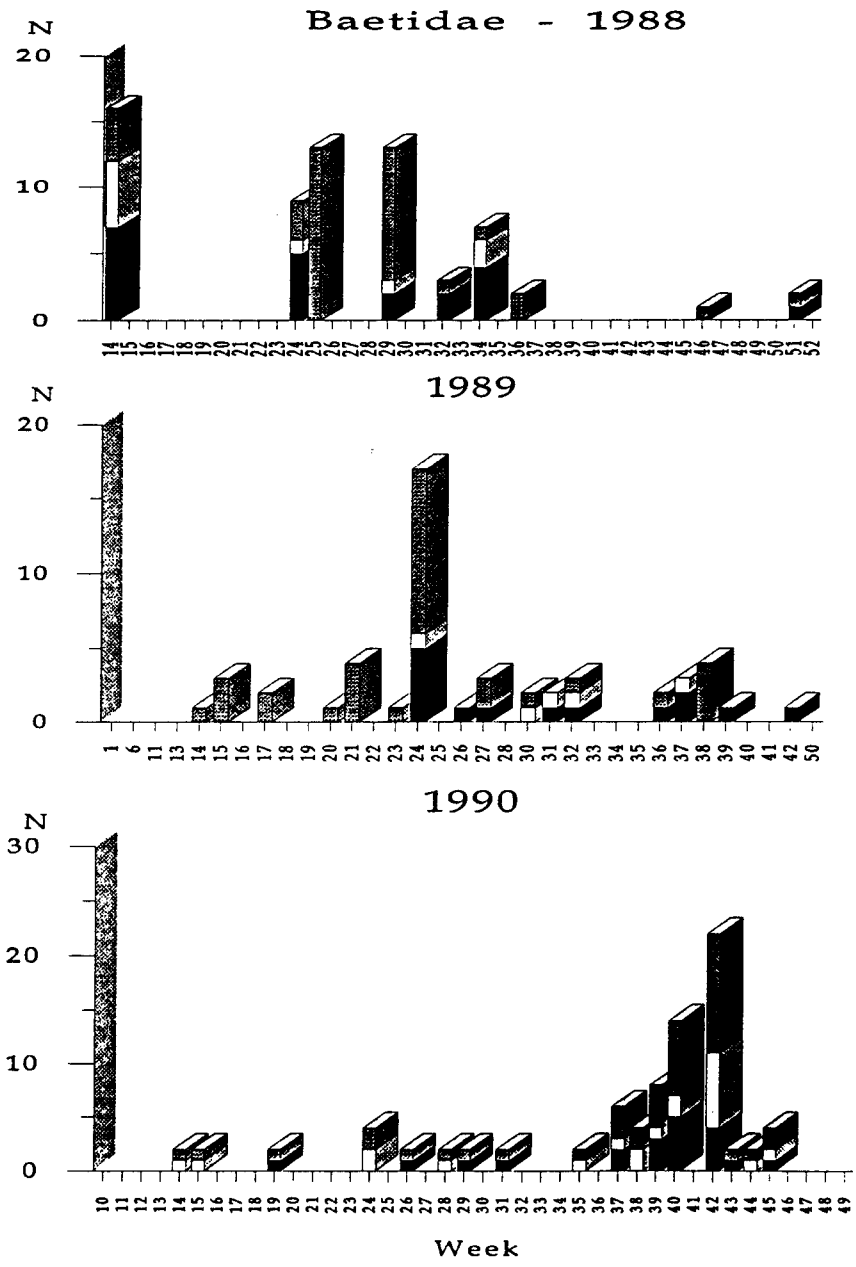


Figure 8. **Major Leptophlebiidae genera in the Sábalo-Esquina: white bars, *Thraulodes*; grey bars, *Traverella; black bars, Farrodes.***

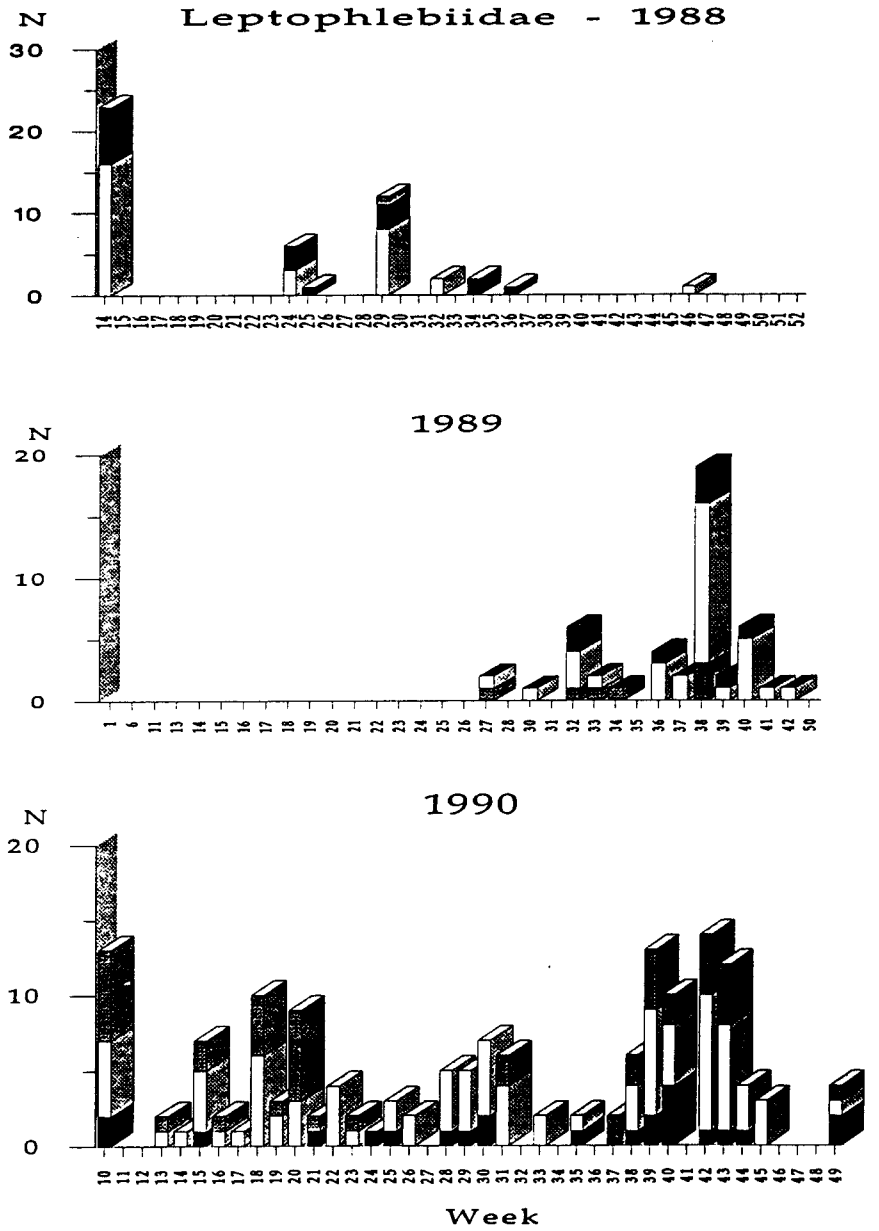
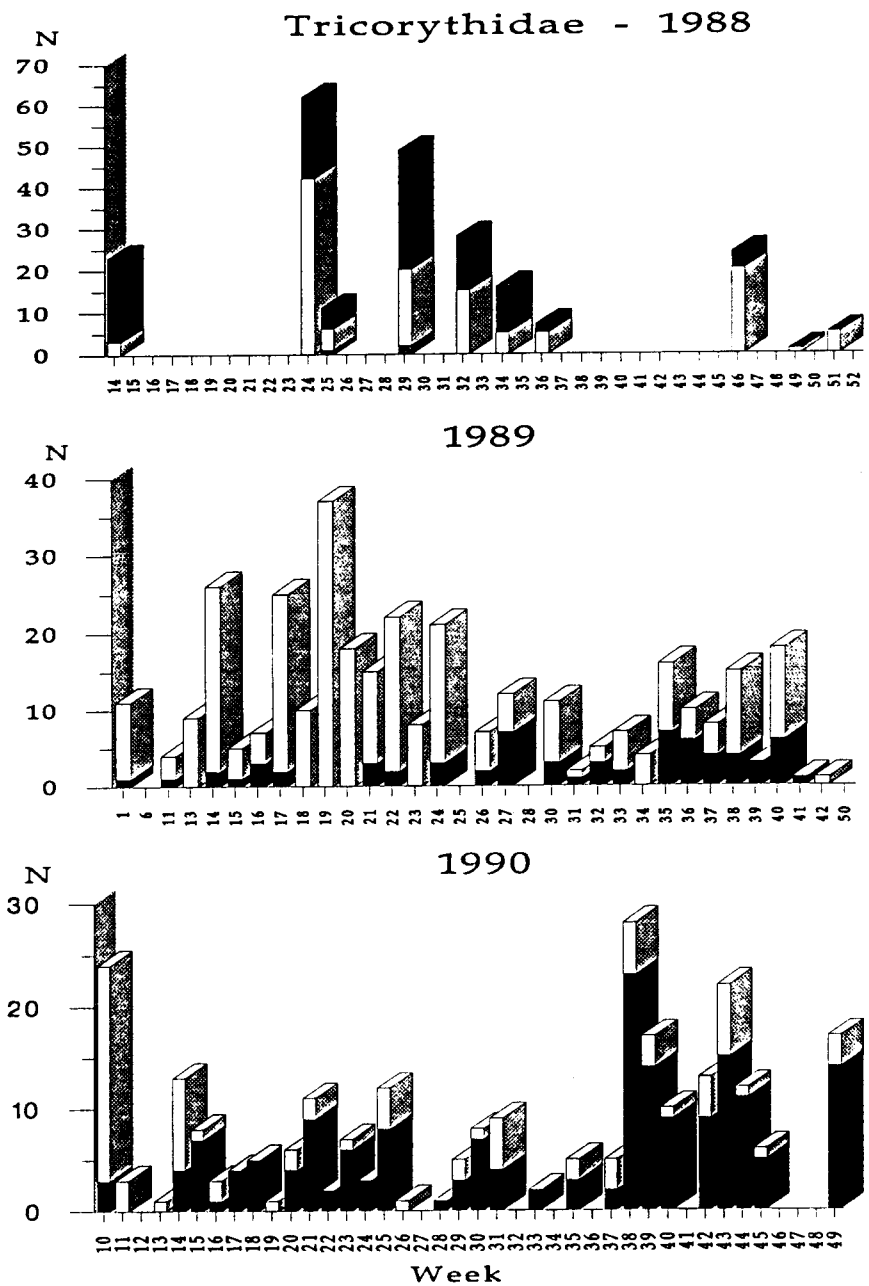


Figure 9. **Tricorythidae genera in the Sábalo-Esquina: white bars, *Tricorythodes*; black bars, *Leptohyphes; grey bars, Haplohyphes.***



samples). Although figures on uniquely occurring taxa in Yuccabine Creek are not available for mayflies only, 21 per cent of the total insect taxa were found as single specimens (as compared with 18 per cent of Sábalo-Esquina mayflies found as single specimens). These results emphasize the importance of long-term studies in evaluating diversity in aquatic ecosystems. Depending on when it was sampled, single samples of the Sábalo mayflies could lead one to conclude that this stream was highly diverse (e.g., weeks 14 and 29, 1988; 24 and 38, 1989; 20 and 39, 1990: Figs. 3-5) or impoverished (e.g., weeks 13, 16, 19, 1989; 11, 22, 1990: Figs. 4 and 5).

The lack of seasonal or annual pattern in the variation in mayfly abundances during the course of this study is consistent with studies on terrestrial insects in non-seasonal tropical environments. Similar lack of pattern has been reported for psocids (Psocoptera; Wolda and Broadhead 1985), sphinx moths (Sphingidae, Lepidoptera; Wolda 1980), Homoptera (Wolda 1983a) and mosquitoes (Culicidae, Diptera; Wolda and Galindo 1981). Even in non-seasonal environments, some mayflies display seasonality in emergence patterns (Wolda and Flowers 1985; Pescador et al. 1993); a few of the Sábalo-Esquina mayflies appeared for short periods in 1989 and 1990. However, the low numbers of these species preclude drawing any firm conclusions from this.

Given the "cumulative" richness of the mayfly fauna in the Río Sábalo-Esquina, why is it so rarely evident in the weekly samples? Natural fluctuations of aquatic insect populations are well documented and can often be explained by discharge, including seasonal fluctuations in discharge and the effect of discharge on substrata (Minshall and Winger 1968; Stout and Vandermeer 1975; Ciborowski and Clifford 1983; Pearson et al. 1986; McElravy et al. 1989; Cobb and Flannagan 1990). However, discharge does not seem to be a satisfactory explanation for the mayfly fluctuations in the Sábalo-Esquina. During 1989 and 1990 there were five high discharge events measured on the gauge (Fig. 2), none of which had a serious effect on the mayflies during subsequent weeks. On the other hand, the most sweeping change in the mayfly fauna, the large drop in species diversity in early 1989 (Fig. 4), is not associated with a change in discharge or, for that matter, with any other event or combination of events known to the authors.

While fluctuations in diversity of the Sábalo-Esquina mayfly populations may have no obvious explanation, the low overall biomass of mayflies may be a result of high predation pressure by fish on mayfly nymphs. In temperate streams there have been few population studies of the effects of predation, but in one Norwegian lake, trout consumed 30-40 per cent of mayfly production (Brittain 1982). Experiments conducted at the Sábalo study site assessed effects of fish on aquatic insects and algae using both cages and elevated tiles that excluded fish from feeding on the artificial substrata (Pringle and Wootton in prep.). In the presence of fish, total invertebrate abundance is much lower than in the absence of fish. Both

Table 2. **Relative proportions of Ephemeroptera in the foreguts of dominant fish insectivores and omnivores in the Sábalo-Esquina (pasture) and Salto (interior forest) rivers, as determined by gut analysis of 2-10 individuals per species per month over a 16-month period: N = number of stomachs examined (data from Perez and Pringle, unpublished)**

Fish taxa	Trophic category	N	River	Ephem. (%)
Alfaro culratus	insectivore	158	Sábalo	14
		138	Salto	0
Astyanax fasciatus	omnivore	170	Sábalo	19
		19	Salto	29
Brycon guatemalensis	insectivore	53	Sábalo	0
		62	Salto	27
Cichlasoma septemfasciatum	omnivore	59	Sábalo	7
		27	Salto	0
Melaniris chagresi	omnivore	164	Sábalo	5
		62	Salto	11

Ephemeroptera and Diptera were significantly greater on caged tiles excluding fish than on tiles that were accessible to fish. In addition, when elevated tiles (suspended 2 cm below the water surface and therefore inaccessible to fish) were exposed to fish by placing them on the stream bottom, 100 per cent of all Ephemeroptera and Simuliidae were eaten within one-minute observation periods.

Analysis of the stomach contents of eight dominant taxa of fish in the Sábalo-Esquina and an interior forest stream, the Salto, indicate that five taxa consistently consume Ephemeroptera (Table 2, from Perez and Pringle, unpublished.): *Alfaro cultratus* (Poeciliidae), *Astyanax fasciatus* (Characidae), *Brycon guatemalensis* (Characidae), *Cichlasoma septemfasciatum* (Cichlidae) and *Melaniris chagresi* (Atherinidae). Given the soft-bodied nature of nymphal Ephemeroptera and their potentially rapid digestion by fish into "unidentifiable material" (Perez and Pringle, unpublished), it is probable that estimates presented in Table 2 are conservatively low. The effect of predators on tropical mayflies is not always readily discernable.

Kopelke (1981) found that neither predator nor seasonal climactic fluctuations adequately explained population fluctuations of mayflies in a tropical African rainforest stream.

In 1960, the forests at La Selva Biological Station were contiguous with undisturbed primary forest stretching north to the Caribbean and south to Braulio Carrillo Park. Today, La Selva is a tiny island of forest in a sea of cleared agricultural land. Losses in biodiversity around La Selva have been catastrophic, and there has been erosion within the reserve as well (Pringle et al. 1984; Pringle 1988; Stiles and Clark 1989). Yet, a final and hopeful point that emerges when comparing our data to the earlier survey of Stout and Vandermeer is that there is no evidence of loss of mayfly biodiversity in the Sábalo-Esquina during the intervening 13 years between the two studies. This period includes the years of some of the most drastic ecosystem alterations. If the Sábalo-Esquina is typical of tropical streams "on the edge", Ephemeroptera — practically synonymous in popular culture with brevity and fragility — are proving tough and tenacious in the face of massive environmental degradation.

Acknowledgements

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