



Invertebrate drift and benthic community dynamics in a lowland neotropical stream, Costa Rica

Alonso Ramírez & Catherine M. Pringle

Institute of Ecology, University of Georgia, Athens, GA 30602, U.S.A.

Received 9 February 1998; in revised form 25 August 1998; accepted 16 September 1998

Key words: drift dynamics, larval shrimp migrations, diel periodicity, benthos, tropical streams

Abstract

In this study we quantified invertebrate drift and related it to the structure of the benthic community, over a 6–8 month period, in a 4th-order tropical stream in Costa Rica. Relative to reports from similar-sized temperate and tropical streams, drift densities were high (2-fold greater: mean 11.2 m^{-3} ; range $2.5\text{--}25 \text{ m}^{-3}$), and benthic insect densities were relatively low (>3-fold lower: mean 890 m^{-2} ; range $228\text{--}1504 \text{ m}^{-2}$). Drift was dominated by larval shrimps that represented more than 70% of total drift on any given date; the remaining 30% was composed of 54 insect taxa. Among insects, Simuliidae and Chironomidae (Diptera) and Baetidae, *Leptohyphes* and *Tricorythodes* (Ephemeroptera) comprised 24% of total drift. Drift periodicity was strongly nocturnal, with peaks at 18:00 h (sunset) and 03:00 h. Our results, and those of previous experiments in the study stream, suggest that nighttime drift is driven by the presence of predatory diurnal drift-feeding fishes and nocturnal adult shrimps. There were no clear seasonal patterns over both 'dry' and wet seasons, suggesting that benthic communities are subject to similar stresses throughout the year, and that populations grow and reproduce continuously.

Introduction

Drift, the downstream movement of organisms in the water current, is a common phenomenon that occurs in stream ecosystems (Allan, 1995). Drifting organisms can result from: (i) accidental dislodgement from the substratum; (ii) changes in the physical environment (e.g., high discharge); and/or (iii) interactions with other invertebrates (Kohler, 1983; 1985). Drift is also an effective way for some aquatic organisms to colonize new areas (Cellot, 1989; Müller, 1982). Normally a combination of these factors causes drift, which can reach high densities and have large impacts on benthic community dynamics (Waters, 1972).

In tropical regions, invertebrate drift has received little attention (Brewin & Ormerod, 1994; Brittain & Eikelands, 1988). Available information suggests that drift dynamics in tropical streams are similar to those described for temperate regions. Strong nocturnal diel periodicity (i.e., peaks in nocturnal drift) is found in streams where diurnal predators are present (Flecker, 1992), and drift is mainly dominated by mayflies and

dipterans (Flecker, 1992; Hynes, 1975; Pringle & Ramírez, 1998; Turcotte & Harper, 1982). In contrast to temperate regions, drift in many aseasonal tropical areas lacks strong fluctuations related to seasonal temperature changes, and drifting organisms can be found throughout the entire year (Hynes, 1975). However, in some cases drift fluctuations in more seasonal tropical streams are associated with dry and wet seasons (Turcotte & Harper, 1982). Lack of seasonality suggests the presence of active and growing benthic invertebrate populations during the entire year, similar to the case of subtropical lowland rivers (Benke et al., 1986, 1991). Other characteristics of drift, such as the relationship between drift and benthic community dynamics, have not been studied in tropical streams. In addition, benthic insect communities in many tropical streams interact with a more diverse community of omnivorous macroconsumers (i.e., fishes and shrimps), which can have strong interactions with insects by preying upon them and reducing food resources (e.g., Pringle & Hamazaki, 1998).

This study is an outgrowth of previous studies (Ramírez, 1997a; Ramírez & Pringle, 1998) that assessed community structure and estimated secondary production in a neotropical lowland stream in Costa Rica. Here we focus on drift, contrasting it with the structure of the benthic community. Our main objective is to quantify drift and relate it to the dynamics of the benthic invertebrate assemblage described by Ramírez & Pringle (1998).

Study Site

The study took place in the Sábalo stream on the eastern boundary of La Selva Biological Station (10° 26' N, 84° 01' W), which is owned and operated by the Organization for Tropical Studies. La Selva is on the Caribbean slope of Costa Rica, near sea level (35 m a.s.l.), in the transition zone between the coastal plain and the foothills of the central mountain range, Cordillera Central. The station and adjacent Braulio Carrillo National Park protect much of the study stream's catchment. Mean annual rainfall at La Selva averages 4 m, with a dryer season from December to March (Sanford et al., 1994).

Sampling took place in a 4th-order reach of the Sábalo, which has a low gradient and water temperatures that vary from 24 to 26°C. Substratum is gravel/cobble in riffles and silt in pools, with leaf accumulations common in both habitats. The macroconsumer community is composed of fishes and shrimps. The fish assemblage is composed of over 30 diurnally active species which are mostly omnivorous, with diets that include algae, detritus, seeds, and both terrestrial and aquatic insects (Burcham, 1988; Busling, 1993, 1994). The shrimp assemblage includes at least eight nocturnally active species which are largely omnivorous (Pringle & Hamazaki, 1998).

Further description of the Sábalo and other streams at La Selva can be found elsewhere (Pringle, 1991; Pringle & Triska, 1991; Ramírez & Pringle, 1998).

Materials and methods

Drift was assessed monthly from November 1993 to May 1994 and then again in August 1994. Thus, our sampling regime spanned an entire 4-month 'dry' season (January–April 1994) and 4 months occurring in the wet season (November–December 1993, May–August 1994). Samples were collected using

Wildco® drift nets (opening 0.1 m², length 1.5 m, mesh 363 μm). On each date, samples were collected every 3 h over 24 h using two nets located within the main stream channel. Nets were left in the water for 10–20 min, usually sampling the entire height of the water column. Current velocity (m s⁻¹) was measured once every sampling time in front of the net with a Marsh McBirney® current meter. Invertebrate drift density was calculated by dividing the number of invertebrates in a sample by the volume of water sampled. Water volume was calculated by multiplying submerged net area, current velocity at the net mouth, and sampling time.

From January to May 1994 and again in August 1994, benthic samples were also collected monthly at a site 10 m downstream from the drift sampling site, during the day. On each sampling date, three samples were collected from riffles and three from pools, using a Surber sampler (mesh 363 μm). Riffle samples were collected from turbulent areas with fast flow (>0.5 m s⁻¹) and shallow depth (<35 cm), while pool samples were collected from areas of still water or low flow (<0.3 m s⁻¹) and with a water depth >40 cm.

All samples were preserved using 5–10% formalin. Invertebrates were later sorted from debris and placed in 70% ethanol. Aquatic insects were identified to genus whenever possible. Keys to genera were available for Ephemeroptera (Flowers, 1992), Odonata (Ramírez, 1996, 1997b, unpublished data), and Trichoptera (M. Springer, unpublished data). Diptera, Lepidoptera, Hemiptera, and Coleoptera were identified to family using keys by Roldán (1988) and Merritt & Cummins (1996), and later separated into morphotypes. Keys to identify larval shrimp are not available.

Results

Drift was composed of both insect and non-insect taxa. A total of 55 taxa were collected during the study and drift was dominated by larval shrimps, Diptera, Ephemeroptera, Trichoptera and Coleoptera. At least 70% of the mean drift density during the study period was the result of larval shrimps migrating downstream to the estuary (Table 1). Among insects, Simuliidae, Chironomidae, Baetidae, and two genera of Lepto-hyphidae (*Leptohyphes* and *Tricorythodes*) comprised more than 80% of the mean total insect drift (Table 1). These dominant taxa were found drifting during the entire study and fluctuations in their drift patterns re-

Table 1. Mean densities and percentage of the total for drift and benthos in the Sábalo stream

	Drift			Benthos		
	No. m ⁻³	S.E.	%	No. m ⁻²	S.E.	%
Decapoda						
Larval shrimp	7.65	1.54	70.70	—	—	—
Diptera						
Simuliidae	0.77	0.41	7.14	28.39	13.87	3.19
Chironomidae	0.75	0.50	6.90	253.16	74.94	28.46
Ephemeroptera						
Baetidae	0.54	0.12	4.96	63.96	16.31	7.19
<i>Leptohyphes</i>	0.38	0.14	3.51	159.91	86.40	17.98
<i>Tricorythodes</i>	0.13	0.11	1.22	105.81	21.67	11.90
<i>Thraulodes</i>	0.01	0.01	0.08	13.75	6.74	1.55
Trichoptera						
Hydropsychidae	0.23	0.16	2.12	17.63	3.75	1.98
Hydroptilidae	0.09	0.05	0.87	30.49	11.70	3.43
<i>Wormaldia</i>	0.01	0.01	0.05	9.27	6.80	1.04
Coleoptera						
Elmidae larvae	0.05	0.04	0.42	89.67	32.35	10.08
Elmidae adult	0.08	0.03	0.73	58.58	25.85	6.59
Psephenidae	0.03	0.03	0.25	8.07	3.65	0.91
Odonata						
<i>Argia</i>	0.01	0.01	0.11	23.61	7.10	2.65
Total	10.80	3.22		889.49	318.76	

Only those taxa with a proportion >1% are included (S.E., one standard error; %, percent composition).

flected patterns observed for total drift (Figures 1a and 2).

Drift and benthos were composed of similar groups of species, however, they occurred in different proportions. The most abundant insect taxa in drift were Simuliidae, Chironomidae, and Baetidae, while Chironomidae, *Leptohyphes* and *Tricorythodes* were the most abundant in benthos (Table 1). Larval shrimps were a major component of drift that were never found in benthic samples and, when we excluded this taxon from our analyses, the percentage contribution of insect taxa to drift and to benthos were significantly correlated ($r^2=0.50$; $P<0.01$). However, larval Elmidae (Coleoptera) and *Argia* (Odonata: Coenagrionidae) were collected in the benthos more often than in drift, whereas Simuliidae and Hemiptera were more commonly found in drift (Table 1).

Mean drift density for all organisms combined was 11.2 m⁻³ (range, 2.5–25 m⁻³). Drift of aquatic insects had a mean of 3.2 m⁻³ (range, 0.7–11.8 m⁻³), while benthic densities during the same period showed a mean of 890 m⁻² (range, 228–1504 m⁻²). Although taxonomic composition was similar between drift and benthos, drift magnitude and fluctuations were not significantly correlated with benthic densities ($r^2=0.53$; $P=0.08$). Insect drift densities peaked in March and May (Figure 1a). Benthic communities were relatively constant until August, when densities were lowest (Figure 1b). Drift densities of all major insect taxa showed fluctuations similar to that shown by total drift densities, with peaks in March and May (Figure 2).

Drift was strongly nocturnal, with densities several times higher during the night than during the day (Figure 3). Day to night drift ratios showed that all major

Table 2. Monthly day to night drift ratios for all major invertebrate taxa in the Sábalo stream

	Month								Mean
	Nov	Dec	Jan	Feb	Mar	Apr	May	Aug	
Decapoda									
Larval shrimp	>0.01	0.27	>0.01	>0.01	>0.01	>0.01	0.2	>0.01	0.06
Diptera									
Simuliidae	0.10	0.69	0.11	0.23	17.27	0.20	0.11	0.23	2.37
Chironomidae	1.10	0.55	0.65	0.56	4.18	0.41	0.20	0.30	0.99
Ephemeroptera									
Baetidae	0.08	0.23	0.06	0.03	1.82	0.06	0.04	0.36	0.33
<i>Leptohyphes</i>	0.07	0.27	0.14	0.48	1.24	0.26	0.06	0.28	0.35
<i>Tricorythodes</i>	0.13	>0.01	0.20	0.72	8.31	0.02	—	—	1.17
<i>Thraulodes</i>	>0.01	>0.01	>0.01	—	—	0.20	>0.01	—	0.03
Trichoptera									
Hydropsychidae	0.03	—	>0.01	0.46	7.20	0.33	0.06	0.42	1.06
Hydroptilidae	2.80	—	0.09	>0.01	2.74	>0.01	0.06	0.10	0.72
<i>Wormaldia</i>	—	—	>0.01	—	>0.01	>0.01	>0.01	>0.01	>0.01
Coleoptera									
Elmidae larvae	0.62	—	—	—	12.31	0.06	0.10	>0.01	1.64
Elmidae adult	0.04	>0.01	0.14	0.29	0.70	—	>0.01	>0.01	0.15
Psephenidae	—	—	—	—	17.05	0.44	—	—	2.19
Odonata									
<i>Argia</i>	—	—	—	—	—	0.85	0.26	—	0.14
Total	0.06	0.28	0.01	0.13	1.69	0.07	0.15	0.03	0.03

insect taxa, as well as total drift, were consistently higher during the night than day (Table 2). Generally, diel drift periodicity showed a peak at 18:00 h (sunset) and sometimes at 03:00 h (Figure 3). The only exception to this pattern was found in March, when a dark cloudy morning was probably responsible for unusually high drift densities collected at 09:00 h (Figure 3).

Discussion

Information on drift and benthic community dynamics in tropical streams is limited to few geographic areas. The only published drift studies in Central America that we are aware of are Füreder (1994) and Pringle & Ramírez (1998) in Costa Rica. These studies were short-term (one diel sampling per site), whereas the

present study is the first to relate invertebrate drift and benthic community dynamics in a lowland neotropical stream over a 6–8 month period.

Drift densities in the Sábalo were higher than in similar-sized streams in other regions, indicating that drift might play an important role in benthic community dynamics in this tropical stream. Most drift studies report densities within the range of 0.5–5.0 m⁻³ (e.g., Armitage, 1977; Cellot, 1989; O'Hop & Wallace, 1983), and streams with similar discharge as the Sábalo (range, 0.3–0.5 m³s⁻¹) have drift densities ranging from 0.91 to 3.4 m⁻³. Mean drift density in the Sábalo (11.2 m⁻³, Table 1) is more similar to reports from large (>5th order) rivers (range, 2–20 m⁻³, Benke et al., 1986, 1991). In contrast to drift, benthic densities were lower than in similar-sized systems in temperate or tropical regions, coinciding with previous findings for the same stream (Pringle & Ramírez,

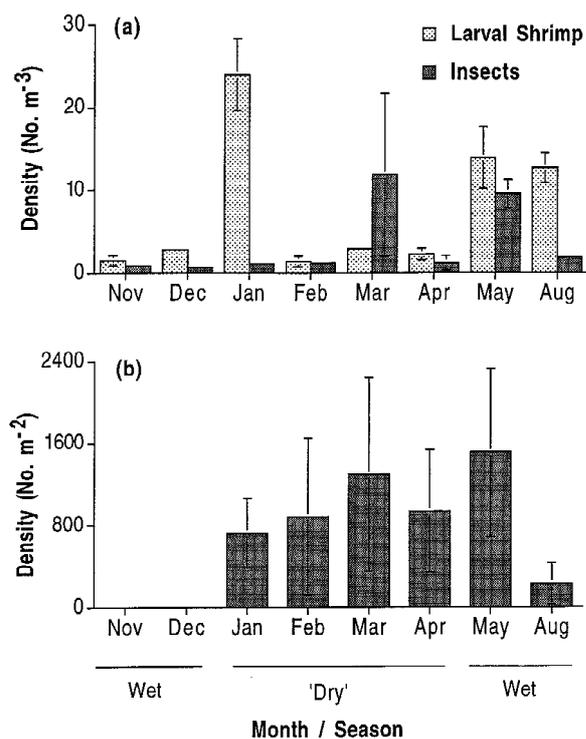


Figure 1. Monthly fluctuations in invertebrate densities in the Sábalo. (a) Insect and larval shrimp drift fluctuations (No. m⁻³); and (b) benthic invertebrate fluctuations (No. m⁻²). All values are monthly means \pm 1 SE (drift, $n=16$, benthos $n=6$).

1998; Ramírez & Pringle, 1998) and others in the Caribbean of Costa Rica (Ramírez et al., 1998). Given the low densities of insects that we observed in benthic samples of the Sábalo, relative to data from similar-sized streams in temperate and tropical areas, it was surprising to find such high drift densities.

One potential explanation for nocturnal drift periodicity and high insect drift densities relative to benthic densities might be interactions between insects and macroconsumers (i.e., fishes and shrimps). The 'risk of predation' hypothesis states that in the presence of diurnal, drift-feeding, predators (e.g., fishes), benthic invertebrates are more active during the night (Allan, 1995). Evidence supporting this hypothesis in tropical systems is that invertebrate drift is nocturnal only in those systems where diurnal fish predators are present (Flecker, 1992; Pringle & Ramírez, 1998). In addition to diurnal fish predators, the presence of nocturnal shrimps which are benthic omnivores/predators may result in increased drift because insects tend to release themselves into the water current to escape predation during the night (Hildrew & Townsend,

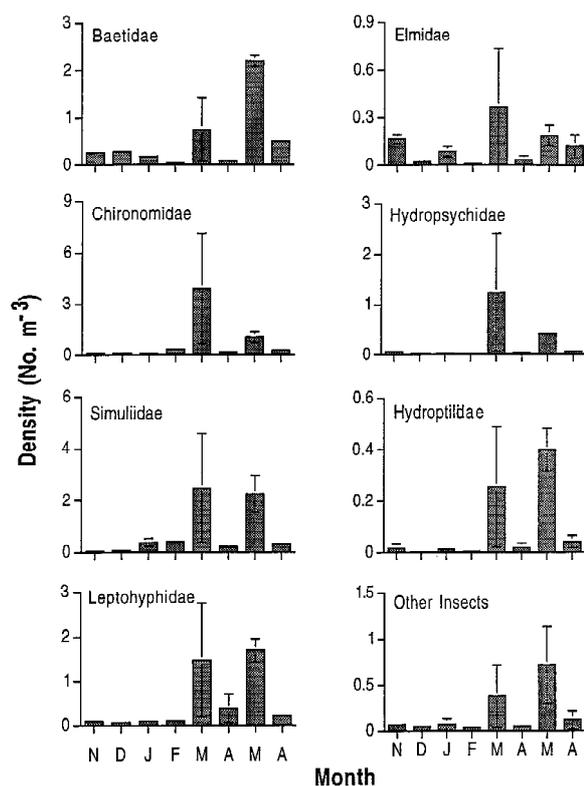


Figure 2. Monthly drift patterns (No. m⁻³) for major insect taxa in the Sábalo. All values are monthly means \pm 1 SE ($n=16$).

1980; Peckarsky, 1980; Walton, 1980). Other factors that might play a role in determining drift periodicity are changes in temperature and circadian rhythms of invertebrates (Brewin & Ormerod, 1994). Although we did not account for these factors in this study, variations in temperature between day and night were very small ($<2^{\circ}\text{C}$). While few insect predators were found, the benthic community was dominated by nocturnally active adult shrimps which have been observed to decrease insect abundance (Pringle & Hamazaki, 1998; Rosemond et al., 1998). In addition, omnivorous fishes in the Sábalo exert strong effects on benthic communities by reducing potential food resources for insects, such as standing crop of algae, other fine particulate organic material, and by altering community composition (Pringle & Hamazaki, 1997, 1998; Rosemond et al., 1998). Lower food resources can also enhance drift as benthic invertebrates become dislodged or drift in their search for food (Kohler, 1983, 1985).

Another factor that may explain the high drift densities that we observed is drift distance. If drift

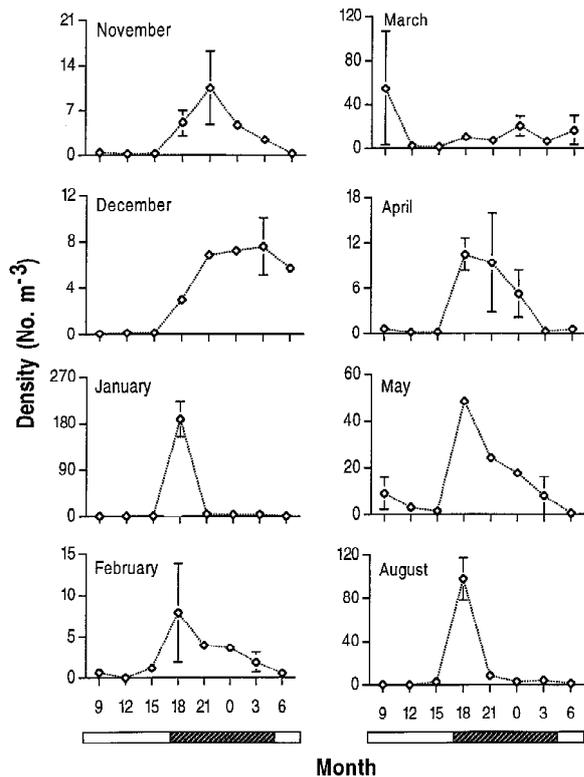


Figure 3. Insect diel drift periodicity in the Sábalo by month. All values are means \pm 1 SE ($n=2$). Dark part of the bar indicates night time.

distances are long, densities will become high as more invertebrates enter drift. However, studies of streams similar in size to the Sábalo suggest that drift distances are short, ranging 1–10 m (Elliott, 1971; Lancaster et al., 1996), and long drift distances are more likely to occur in extremely large (>5th order) rivers (Koetsier & Bryan, 1996).

Larval shrimps were an important component of drift throughout the study and, to our knowledge, no previous studies have provided data on migratory shrimp drift over such a long time period (8 months). The magnitude of larval shrimp migrations potentially represents a large amount of food available for filter-feeding invertebrates and drift-feeding fishes throughout the year. In addition, shrimps link headwater streams with estuaries and have the potential to be an important tool in monitoring watershed integrity. Larval shrimp migrations to estuarine areas have been reported for other streams in the Caribbean of Costa Rica (Pringle & Ramírez, 1998) and for Caribbean islands, such as Puerto Rico (Benstead et al., 1999;

March et al., 1998). In the Sábalo, shrimps were a major taxon collected in drift and never found in benthos (Table 1). Although densities of migratory shrimps were higher than total insect drift densities, they were lower than values reported for streams in Puerto Rico (range, 1–700 m^{-3} ; March et al., 1998).

Although, long-term studies are recommended to assess seasonality in tropical regions (e.g., Wolda & Flowers, 1985), our results suggest that there are no seasonal fluctuations in drift. All major taxa were found during the entire study, generally in similar densities. The lack of seasonality in larval shrimp migrations is consistent with the observed trend that populations of tropical freshwater shrimps have continuous reproduction (e.g., Bauer & Vega, 1992; Hancock & Bunn, 1997; Walker, 1992). Other studies conducted in aseasonal tropical environments have reported similar lack of seasonality in insect drift (Hynes, 1975; Turcotte & Harper, 1982) and benthic assemblages (Flowers & Pringle 1995).

In conclusion, drift composition in our study differs greatly from other studies in both temperate and tropical streams where drift has been reported to be dominated by insects. Results of this study suggest that larval shrimps are an important and often ignored component of drift in tropical streams. Although the consequences of larval shrimp migrations on benthic community dynamics remain to be investigated, larval shrimps represent a major resource that is available to the stream community. Finally, while longer studies are necessary, the lack of seasonality we observed over both wet and dry seasons suggests that benthic communities are subject to similar stresses throughout the year, and that populations grow and reproduce continuously.

Acknowledgments

We thank Luis Vargas, Minor Hidalgo and Brian Frizelle for collecting and processing samples. We are also grateful to the Organization for Tropical Studies and the staff at La Selva Biological Station for their help in facilitating our research. Special thanks to S. Davis, J. Hutchens, J. March, S. Pohlman, A. Rosemond, K. Schofield, B. Toth and S. Wenger for their comments and suggestions on the manuscript. This research was supported by grants awarded to C. M. Pringle and F. J. Triska by the National Science Foundation (grant # BSR-91-07772 and DEB-95-284340).

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