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TEMPORAL PARTITIONING OF CHIRONOMIDAE EMERGENCE IN AN INSULAR, TROPICAL RAINFOREST STREAM

R. William Bouchard, Jr.[1,2*] & Leonard C. Ferrington Jr.[2†]

[1]*Minnesota Pollution Control Agency, Saint Paul, Minnesota, USA.*
E-mail: bouc0048@umn.edu
[2]*Department of Entomology, University of Minnesota, Saint Paul, Minnesota, USA.*
[†] *deceased*
[*]*Corresponding author*

Abstract

Annual water temperature variation strongly influences larval growth of aquatic insects in streams located in temperate regions or at high elevations, which produces cohorts with highly synchronized emergence periods and short average annual durations of emergence. Studies of Chironomidae in tropical streams indicate that species in these habitats have longer average durations of emergence due to reduced annual variation in water temperature. We used emergence trap data collected over one year from Quebrada Prieta (El Verde Field Station, Puerto Rico) to test the prediction that chironomids of an insular rainforest stream should have longer average annual durations of emergence than chironomids in both temperate streams and mainland streams in continental tropical regions. Taxa richness was relatively low with twenty-eight Chironomidae taxa collected from Quebrada Prieta. Emergence patterns of the most common taxa demonstrated some seasonally with the highest emergence generally occurring during the dry season (January through April). The estimated average emergence duration of Chironomidae in Quebrada Prieta was 205 days/species/year, which was greater than estimates of average durations for chironomids of three streams in Pennsylvania, USA (70 days/species/year), 6 streams in Minnesota, USA (89 days/species/year), and four streams in Guanacaste National Park in northwestern Costa Rica (116 days/species/year). The emergence duration for the chironomid community in Quebrada Prieta was most similar to another tropical, mountain stream in the Democratic Republic of the Congo (255 days/species/year). Although many taxa emerged throughout the one-year sampling period, some taxa in Quebrada Prieta had distinct emergence peaks. This demonstrates that although environmental conditions are stable enough to allow for emergence throughout the year for many species, there is some seasonality in the development of chironomid taxa in this tropical stream. These results are consistent with predictions that invertebrates in tropical streams will have longer, less synchronous emergence periods than species in temperate regions with high annual fluctuations in temperature. However, this research is also similar to several other studies that have identified seasonal emergence peaks in tropical chironomids which demonstrates a need to better understand the exogenous cues that affect these patterns.

Introduction

Temporal partitioning of emergence is commonly documented in Chironomidae from aquatic habitats located in temperate regions or at high elevations where this group has been more thoroughly studied (Armitage 1995). Coffman and de la Rosa (1998) quantified patterns of emergence in three temperate streams and four tropical streams, and developed testable hypotheses and predictions related to the patterns of temporal duration of emergence that may operate over large geographic scales. Their results documented longer average durations of emergence and greater degrees of overlap in emergence among species in tropical streams when compared with streams at higher latitudes. Wolda (1988) also observed reduced seasonality in temporal patterns in duration of emergence for several terrestrial insect species in the tropics but concluded that studies of seasonal patterns of insects in tropical areas were relatively rare and generally focused only on one or a few taxa in a restricted geographic area. Consequently, he recommended that studies of longer duration and dealing more broadly with local faunas would provide a better understanding of factors related to the timing of life history features and their seasonality in insects. Although reduced seasonality appears to be typical for tropical midge communities, several studies on Chironomidae have identified seasonal changes in emergence or abundance of midges in tropical habitats (e.g., Lehmann 1979, Ramírez and Pringle 1998, Sonoda and Trivinho-Strixino 2000, da Silva et al. 2009, Kranzfelder and Ferrington 2016). However, most of these studies only report on seasonal changes in richness or abundance of the total chironomid community and not individual species. Regardless, there is evidence that seasonal exogenous cues do influence chironomid emergence patterns in tropical habitats, but there is a need for additional research to document and determine the factors that affect these patterns.

The aquatic insect fauna of Quebrada Prieta in the Caribbean National Forest in Puerto Rico was the focus of a comprehensive emergence and phenological study in 1990 and 1991 (Masteller and Buzby 1993). The climatic seasonality of weather conditions of the Caribbean National Forest is low, with air temperatures often varying as much on a daily basis as on an annual basis. There is a weak dry season from January through April (Masteller and Buzby 1993) and leaf fall is weakly seasonal although it occurs continuously through the year (Weigart 1970). Ferrington et al. (1993) determined the taxonomic composition and annual patterns of species richness and abundance of the chironomid community but did not make quantitative comparisons of the durations of emergence and temporal overlap of the fauna. Based on the model provided by Coffman and de la Rosa (1998), we developed predictions regarding temporal durations and overlap of emergence of chironomids and re-analyzed the data from Ferrington et al. (1993) to determine if the patterns conformed to our predictions. In addition, we compare our results for Quebrada Prieta with the values presented by Coffman and de la Rosa (1998) for three temperate streams in western Pennsylvania (USA) and four mainland tropical streams in Guanacaste National Park (Costa Rica) and by Bouchard (2007) for six temperate streams in Minnesota (USA). We also re-analyzed emergence data published by Lehmann (1979) for the Kalengo River in the Democratic Republic of the Congo to extend our comparisons to another mainland tropical stream.

Quebrada Prieta experiences very minimal seasonality in terms of temperature, photoperiod, incident solar radiation, rainfall, and changes in the input of allochthonous organic matter. Consequently, we predicted that chironomid species in Quebrada Prieta would emerge continuously throughout the year with no or only minimal peaks in emergence. In addition, we predicted the durations of emergence would be broader on average than species of Chironomidae for streams in western Pennsylvania and Minnesota, which experience greater seasonality for all of these parameters. We also predicted that durations of emergence for chironomids in Quebrada Prieta would be greater compared to species emerging from the four streams in Guanacaste National Park and the Kalengo River where species richness is higher. Finally, we predicted that there would not be a strong relationship between community dissimilarity as the interval between samples increased. As a result, average annual change in emergence should be less than that measured for streams in the two areas investigated by Coffman and de la Rosa (1998) and the Kalengo River in the Democratic Republic of the Congo (Lehmann 1979).

Materials and Methods

Site description

The main study site, Quebrada Prieta, is located in the Luquillo Mountains of northeastern Puerto Rico within the Luquillo Experimental Forest (El Yunque National Forest). It is a second-order, steep-gradient stream with an average slope of approximately 20% in the vicinity of the sample site. The stream originates at approximately 600 meters above sea level and flows into Quebrada Sonadora at approximately 310 meters elevation. The emergence trap was located at 390 meters elevation at the approximate coordinates of 18.32°, -65.81°. The stream is roughly 1.5 kilometers long and it is fully contained within the El Yunque National Forest. The predominant substrates at the study site were bedrock, large boulders, and cobbles, with finer substrates of sand and silts in pools. Quebrada Prieta flows through tabonuco forest at the sample site, which is the predominant forest type at this level of elevation, gradient, and slope stability (Snyder et al. 1987). Compared to temperate habitats, Quebrada Prieta is exposed to limited seasonality, although there is some seasonality in water temperature, rainfall, and input of allochthonous organic matter. Mean monthly water temperatures from a nearby stream (Quebrada Sonadora) ranged from approximately 20-23 ºC with higher temperatures from June through October (Fig. 1a). However, this range is much lower than is typically observed in surface-water fed streams in temperate regions. Rainfall is more variable in the Luquillo Mountains, but there is a weak dry season from January through April (Masteller and Buzby 1993; Fig. 1b). Although most trees drop their leaves throughout the year, there is some seasonality with increased leaf fall from April through July and decreased leaf fall from December through March (Masteller and Buzby 1993). Maps and more information about the stream, including water chemistry and the surrounding riparian setting, are available in Masteller and Buzby (1993).

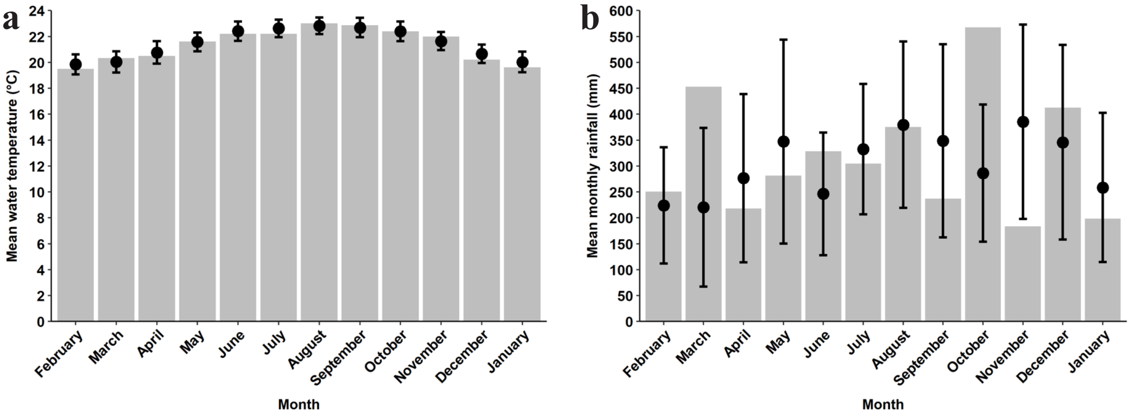

Figure 1. Average monthly water temperature (a) and rainfall (b) from stations near the sample site on Quebrada Prieta. Circles are average values of water temperature (1983-2018) and rainfall (1975-2021) with error bars representing standard deviation. Grey bars are data for February 1990 through January 1991. Water temperature data are from a downstream station in Quebrada Sonadora (McDowell 2021) and rainfall data are from the El Verde Field Station (Ramirez 2021).

Sampling Methodology and Specimen Processing

Samples of emerging aquatic insects were collected for one year with an aspirator from a walk-in emergence trap ($4m^2$) suspended over Quebrada Prieta (Fig. 2). Additional details on the trap design are in Masteller and Buzby (1993). Emerging insects were collected 2-3 times weekly from February 1990 through the end of January 1991. Insects were preserved in 70% ethanol, identified to genus or species, and enumerated. Selected specimens of each taxon were cleared and slide mounted in Euparal using the method described by Schlee (1966).

Analyses

Counts of each taxon were aggregated by month due to the relatively small number of specimens collected in each sample. This also allowed comparison with other studies of chironomid emergence. Community level emergence patterns (abundance and taxa richness) and taxon specific patterns were assessed against seasonal patterns to identify emergence patterns that may be related to exogenous cues. Emergence patterns were categorized based on the number of emergence peaks, the timing of these peaks in relation to seasonal rainfall patterns, and the synchronicity of emergence peaks. Durations of emergence for each species were calculated by dividing the number of months each taxon was collected by 12 and multiplying this value by 365 days. This approach was similar to the method used by Coffman and de la Rosa (1998) to estimate durations of emergence. Bray-Curtis dissimilarity coefficients were calculated between all 66 pairs of monthly samples. The individual and average dissimilarity values were graphed as a function of the number of days between the two months being compared. Monthly emergence totals published by Lehmann (1979) were analyzed in a similar manner for comparison with another tropical habitat. All statistical analyses and plots were generated using R 4.0.4 (R Core Team, 2021). Bray-Curtis dissimilarity coefficients were calculated using “vegdist” function in the “vegan” package (Oksanen et al., 2020).

Figure 2. Emergence trap on Quebrada Prieta.

Table 1. Chironomidae collected from Quebrada Prieta (Puerto Rico) with estimated emergence durations and emergence categories. Emergence categories: Wet = taxa with an emergence peak during the wet period; Dry = taxa with an emergence peak during the dry period; Aseasonal = taxa with multiple emergence peaks which did not correspond to a seasonal rainfall period; and Rare = taxa sampled in low numbers which did not permit emergence pattern categorization.

Taxon	**Total Count**	**Number of months collected**	**Estimated emergence duration**	**Emergence Pattern**
Chironomidae				
Tanypodinae				
Ablabesmyia	38	10	304	Wet
Djalmabatista	2	2	61	Rare
Labrundinia	111	11	335	Aseasonal
Larsia	273	12	365	Dry
Pentaneura	183	12	365	Aseasonal
Procladius	1	1	30	Rare
Orthocladiinae				
Corynoneura	8	6	183	Rare
Cricotopus	103	12	365	Aseasonal
Diplosmittia	40	3	91	Dry
Limnophyes	65	11	335	Dry
Parametriocnemus	83	12	365	Dry
Thienemanniella	4	3	91	Rare
Unknown orthoclad genus # 1	2	2	61	Rare
Unknown orthoclad genus # 2	7	3	91	Rare
Chironominae				
Chironomini				
Fissimentum	5	4	122	Rare
Paratendipes reidi Freeman, 1957	26	9	274	Aseasonal
Polypedilum sp. 1	4	3	91	Rare
Polypedilum sp. 2	21	7	213	Rare
Polypedilum sp. 3	6	3	91	Rare
Polypedilum sp. 4	8	5	152	Rare
Polypedilum sp. 5	3	2	61	Rare
Stenochironomus cf. *innocuus* (Williston, 1896)	12	4	122	Rare
Stenochironomus sp. 1	463	12	365	Wet
Xestochironomus furcatus (Johannsen, 1938)	6	5	152	Rare
Xestochironomus cf. *nebulosus* Sublette & Wirth, 1972	623	12	365	Dry
Tanytarsini				
Rheotanytarsus	1	1	30	Rare
Tanytarsus sp. 1	211	12	365	Wet
Tanytarsus sp. 2	43	10	304	Dry

Results

Total taxa richness in Quebrada Prieta was low with twenty-eight species of Chironomidae from three subfamilies identified from 137 sample events over the one-year period the stream was monitored (Table 1). As noted in Ferrington et al. (1993), the most common trophic category was xylophages (47% of individuals). The 28 species of Chironomidae from Quebrada Prieta had an estimated average duration of 205 days based on the aggregated monthly data. Chironominae species had the shortest average estimated emergence duration at 193 days/species/year (d/sp/yr). Tanypodinae had the longest average emergence duration (243 d/sp/yr) and Orthocladiinae were intermediate at 198 d/sp/yr. Fifteen taxa in the study each had cumulative abundances that were less than 1% of total annual emergence and were considered rare taxa (Table 1). Rare taxa were present in seven or fewer months and their monthly abundance was low with fewer than 10 individuals collected in any month. Accordingly, the estimated annual durations of emergence for rare taxa were short. When rare taxa were deleted from the analyses, the estimated emergence durations were 323 d/sp/yr for all common taxa and 342, 289, and 355 d/sp/yr, respectively, for Tanypodinae, Orthocladiinae, and Chironominae.

The seven most abundant taxa occurred in all months and accordingly, had the longest estimated durations of emergence (Table 1). These taxa included *Larsia*, *Pentaneura*, *Cricotopus*, *Parametriocnemus*, *Stenochironomus* sp. 1, *Xestochironomus* cf. *nebulosus*, and *Tanytarsus* sp. 1, and all of these taxa had estimated emergence durations of 365 d/yr when samples were composited at monthly intervals. Some seasonal patterns in abundance and richness of the overall chironomid community were observed with declining abundance and taxa richness from January or February and an increase from July through December or January (Fig. 3). These patterns were not as evident as those typically observed in temperate streams and were largely the result of changes in a small number of abundant taxa. Many of the rare taxa were sporadically collected and did not substantially contribute to the community-level emergence patterns (Table 2). Examination of monthly emergence patterns for taxa comprising at least 1% of total abundance did indicate that some had seasonal emergence patterns (Figs. 4-6). Some taxa had emergence peaks that suggested these taxa were univoltine, bivoltine, or multivoltine. Species were divided into the following emergence patterns: (1) peak emergence during the wet period (*Ablabesmyia*, *Larsia*, *Stenochironomus* sp. 1, and *Tanytarsus* sp. 1), (2) peak emergence during the dry period (*Diplosmittia*, *Limnophyes*, *Parametriocnemus*, *Xenochironomus* cf. *nebulosus*, and *Tanytarsus* sp. 2), and (3) aseasonal emergence with one or more emergence peaks (e.g., *Labrundinia*, *Pentaneura*, *Cricotopus*, *Paratendipes reidi*). Taxa categorized as emerging during either the wet or dry periods had a single, broad emergence peak that corresponded to seasonal rainfall patterns. Aseasonal taxa were those that had multiple emergence peaks which did not correspond to seasonal rainfall patterns. Despite seasonal timing and the observation of emergence peaks, most taxa had moderate emergence throughout the year with one or more peaks in emergence. However, some taxa had highly synchronized emergence with a single, distinct peak in emergence and low emergence throughout the rest of the year (e.g., *Diplosmittia*, *Xenochironomus* cf. *nebulosus*, and *Tanytarsus* sp. 2). All three of these taxa had an emergence peak in January at the beginning of the dry season.

Forty-five species of Chironomidae were collected

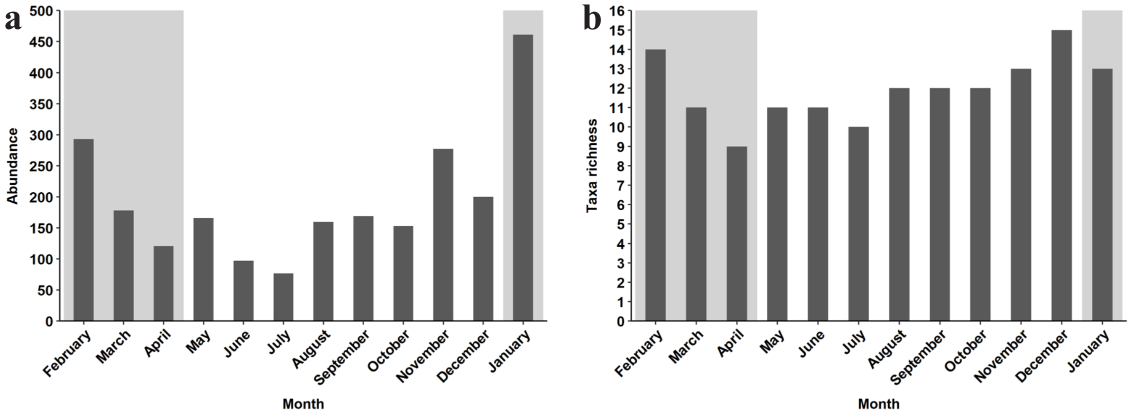

Figure 3. Monthly total abundance (a) and taxa richness (b) of emerging Chironomidae from Quebrada Prieta. Shaded area indicates dry season.

over a one-year period from the Kalengo River by Lehmann (1979) (Table 3). On average, the chironomid community from this stream had an estimated average duration of 255 d/sp/yr. Tanypodinae species had the shortest average estimated emergence duration of 225 d/sp/yr. Orthocladiinae averaged 243 d/sp/yr and Chironominae averaged 281 d/sp/yr. Thirteen taxa each had abundances of at least 1% of the total abundance and all of these abundant taxa emerged during every month. In total, twenty-one taxa (47% of total richness) were collected every month.

Dissimilarities between samples from Quebrada Prieta and the Kalengo River were low although dissimilarity was higher in Quebrada Prieta (Fig. 7). For all 66 pairs of samples, the average dissimilarity among any two months was 0.462 (Quebrada Prieta) and 0.277 (Kalengo River). When considered as a function of the number of months between composited monthly samples, there was

Table 2. Monthly emergence of individual Chironomidae taxa (abundance coding: white = 1, light gray = 2-4, medium gray = 5-9, dark gray = 10-24, black = >25).

Taxon	Month											
	F	M	A	M	J	J	A	S	O	N	D	J
Tanypodinae												
Ablabesmyia	5		2	3	2		4	3	7	2	4	6
Djalmabatista	1				1							
Labrundinia	11	2	7	35	6	5	15	7	4	8	11	
Larsia	15	11	1	11	14	11	28	31	44	36	30	41
Pentaneura	15	21	7	13	17	11	16	38	9	19	10	7
Procladius									1			
Orthocladiinae												
Corynoneura	1				1		1			1	1	3
Cricotopus	9	6	9	13	6	3	17	8	5	10	1	16
Diplosmittia	1			1								38
Limnophyes	5	9	15	3	1		3	6	3	4	9	7
Parametriocnemus	12	14	19	5	3	1	6	1	3	2	3	14
Thienemanniella			1		2			1				
Unknown Orthoclad Genus 1	1		1									
Unknown Orthoclad Genus 2									3		3	1
Chironominae												
Chironomini												
Fissimentum	2	1				1			1			
Paratendipes reidi	1	1	1	1		1	4	10			2	5
Polypedilum sp. 1				1					1	2		
Polypedilum sp. 2		2		1	2	2			8	2	4	
Polypedilum sp. 3	4	1								1		
Polypedilum sp. 4	1					2	1	3	1			
Polypedilum sp. 5										1	2	
Stenochironomus cf. *innocuus*	5	4	1					2				
Stenochironomus sp. 1	171	64	24	22	11	11	6	15	10	68	40	21
Xestochironomus furcatus			1	1			1				2	1
Xestochironomus cf. *nebulosus*	20	38	25	47	27	22	32	25	23	67	45	252
Tanytarsini												
Rheotanytarsus						1						
Tanytarsus sp. 1	9	1	6	5	1	3	21	19	30	52	30	34
Tanytarsus sp. 2	4	3	1	4	3	3	5			2	3	15

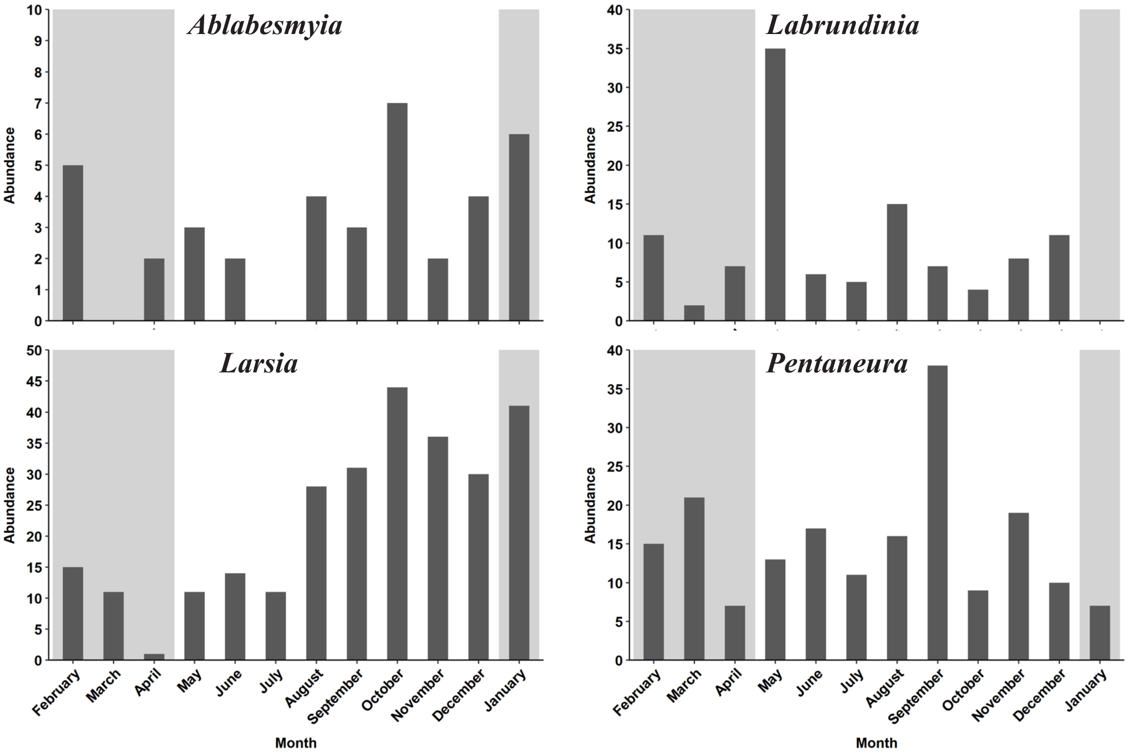

Figure 4. Monthly emergence of abundant Tanypodinae taxa (>1% of total abundance). Shaded area indicates dry season.

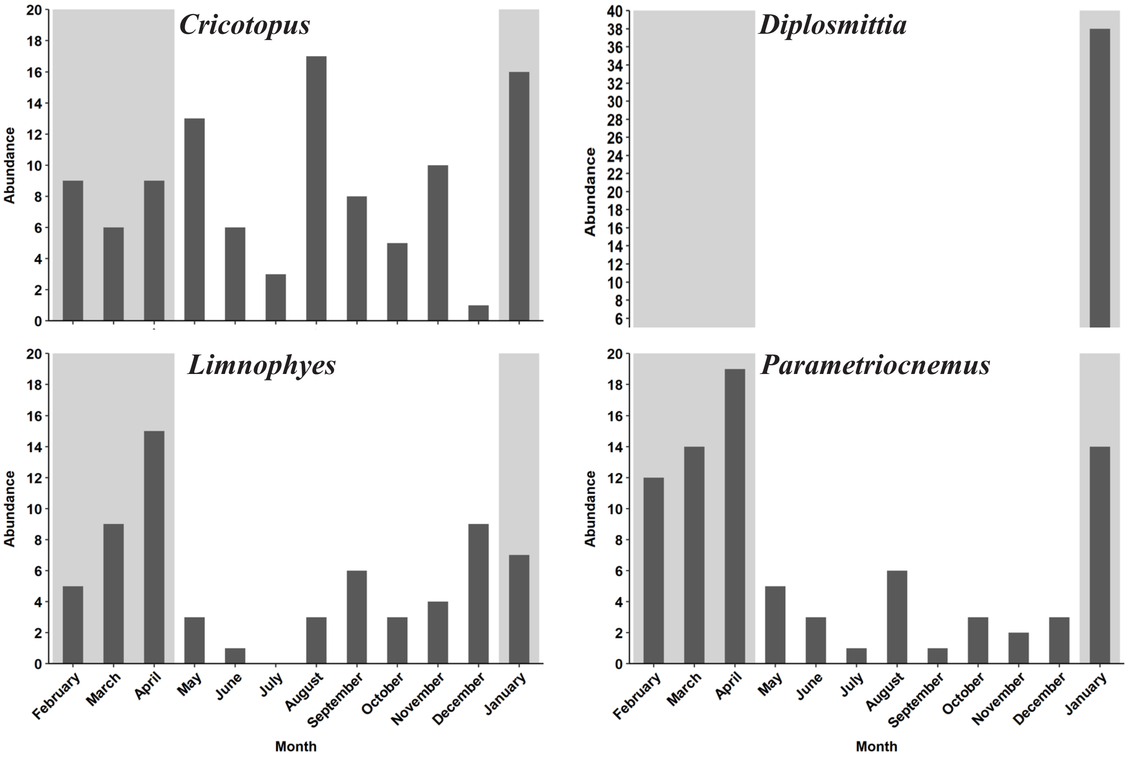

Figure 5. Monthly emergence of abundant Orthocladiinae taxa (>1% of total abundance). Shaded area indicates dry season.

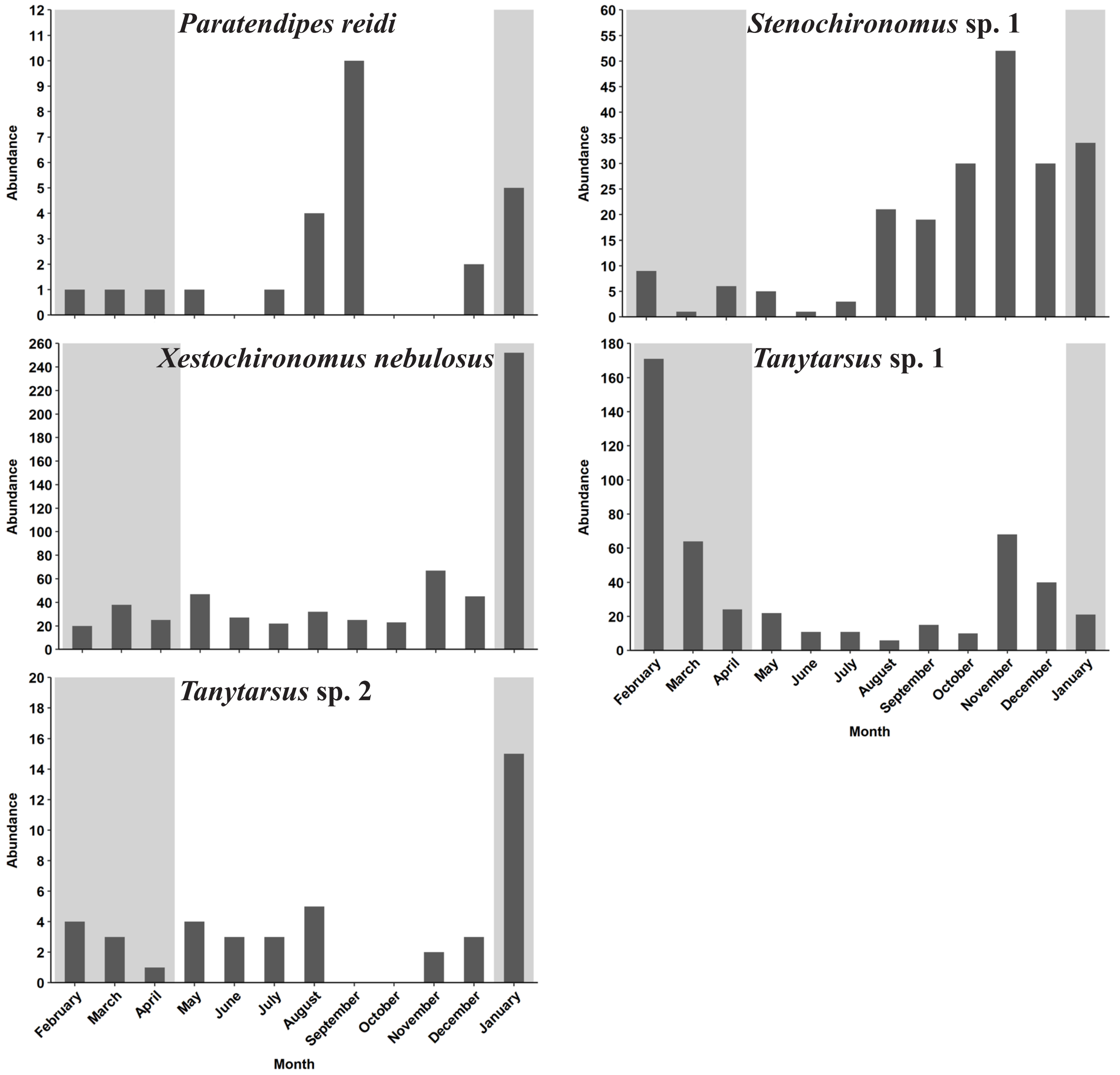

Figure 6. Monthly emergence of abundant Chironominae taxa (>1% of total abundance). Shaded area indicates dry season.

a gradual increase in dissimilarity as the time between samples became greater. However, this increasing trend was only observed when the gap between samples was 1 to 4 (Kalengo) and 1 to 7 (Quebrada Prieta) months. Overall, dissimilarity in both streams was lower than that observed for temperate streams in Coffman and de la Rosa (1998) and Bouchard (2007).

Discussion

Quebrada Prieta is an insular, topical stream and as a result ecological theories predict that this habitat will have a Chironomidae community with low taxa richness (MacArthur and Wilson 1967) and taxa which emerge continuously throughout the year (Coffman and de la Rosa 1998). Based on the model by Coffman and de la Rosa (1998), we predicted that the strongly reduced climatic seasonality in the Caribbean National Forest, would result in longer emergence durations of chironomids in Quebrada Prieta than in temperate habitats. The low taxa richness was expected to reduce temporal niche partitioning which would further lengthen emergence durations such that they exceeded those in other tropical habitats with greater species richness. Finally, emergence patterns of midges in Quebrada Prieta were predicted to be largely aseasonal in contrast to the emergence patterns of many temperate taxa. Some of these predictions were supported by adult emergence data collected over one year from Quebrada Prieta. As expected, midge emergence occurred year-round and many of the most common taxa were present throughout the year. However, when examined in more detail, seasonal emergence patterns in abundance were apparent for the total chironomid community and for some taxa. Overall, chironomid taxa richness and abundance of emerging chironomids increased

Table 3. Chironomidae collected from the Kalengo River (Democratic Republic of the Congo; see Lehmann (1979)).

Taxon	Total count	Number of Months collected	Estimated Emergence duration
Tanypodinae			
Cantopelopia robacki Lehmann, 1979	1	1	30
Conchapelopia zairensis Lehmann, 1979	86	12	365
Larsia africana Lehmann, 1979	31	10	304
Nilotanypus comatus (Freeman, 1953)	179	12	365
Paramerina sp. 1	3	2	61
Orthocladiinae			
Bryophaenocladius brincki (Freeman, 1955)	1	1	30
Bryophaenocladius kalengoensis Lehmann, 1979	1	1	30
Cardiocladius hessi Freeman, 1956	82	9	274
Corynoneura dewulfi Goetghebuer, 1935	394	12	365
Cricotopus (*C.*) *albitibia* (Walker, 1848)	567	12	365
Cricotopus (*C.*) *flavozonatus* (Freeman, 1953)	168	7	213
Cricotopus (*C.*) *harrisoni* Freeman, 1956	39	7	213
Cricotopus (*M.*) *kisantuensis* Goetghebuer, 1934	2	2	61
Eukiefferiella kivuensis Lehmann, 1979	118	9	274
Limnophyes natalensis (Kieffer, 1914)	125	12	365
Nanocladius (*N.*) *jannae* Lehmann, 1979	3554	12	365
Nanocladius (*N.*) *ortsi* Lehmann, 1979	227	12	365
Parakiefferiella ephippium (Freeman, 1956)	1342	12	365
Parametriocnemus scotti (Freeman, 1953)	363	12	365
Paratrichocladius micans (Kieffer, 1918)	1670	12	365
Paratrichocladius pierretti Lehmann, 1979	1	1	30
Pseudorthocladius bernadetti Lehmann, 1979	41	8	243
Pseudosmittia subtrilobata (Freeman, 1956)	2	2	61
Pseudosmittia topei Lehmann, 1979	5	4	122
Rheocricotopus capensis (Freeman, 1953)	18	10	304
Smittia subnigra Freeman, 1956	2	2	61
Thienemanniella fuga Lehmann, 1979	185	12	365
Thienemanniella safi Lehmann, 1979	138	9	274
Tvetenia calvescens (Edwards, 1929)	56	12	365
Chironominae **Chironomini**			
Cryptochironomus incertus Lehmann, 1979	3	2	61
Demicryptochironomus zairensis Lehmann, 1979	55	12	365
Microtendipes kahuziensis Lehmann, 1979	118	11	335
Microtendipes numerous Lehmann, 1979	17191	12	365
Polypedilum aethiops Lehmann, 1979	27	4	122
Polypedilum brunneicornis Kieffer, 1911	855	12	365
Polypedilum majiis Lehmann, 1979	1071	12	365
Polypedilum melanophilus Kieffer, 1911	211	12	365
Stenochironomus spatuliger Kieffer, 1922	14	6	182

Tanytarsini			
Cladotanytarsus/*Tanytarsus* (3 spp.)	1848	12	365
Rheotanytarsus montanus Lehmann, 1979	530	12	365
Rheotanytarsus ororus Lehmann, 1979	5	3	91
Rheotanytarsus Samaki Lehmann, 1979	91	11	335
Tanytarsus luctuosus Freeman, 1958	8	3	91

through the wet season and declined through the dry season. Patterns of individual taxa were more variable than the overall community with some taxa increasing emergence during the dry or wet seasons while others indicated possible patterns of bi- or multi-voltinism. This contradicts predictions that tropical communities would largely be aseasonal due to the lack of strong seasonal cues (Coffman 1989, Coffman and de la Rosa 1998). The apparent seasonality of emergence peaks of some tropical midge species raises questions regarding which exogenous cues or environmental drivers are important for these patterns.

One of the strongest seasonal patterns in tropical systems is precipitation and this has been suggested as a possible important factor for the phenology of many tropical insects (Wolda 1988). In Quebrada Prieta, the overall midge community increased in abundance and richness through the wet season and declined during the dry season. However, it should be noted that even though long-term rainfall averages indicate a regular, weak wet-dry season pattern in the Caribbean National Forest, actual rainfall patterns vary year-to-year. This variability was apparent during the study sampling period (1990-1991) when March (dry period) had the second highest monthly rainfall total. Regardless, there appears to be a direct or indirect effect of precipitation on midge emergence in Quebrada Prieta which is supported by other research. Several other studies have noted changes in tropical midge richness or abundance patterns with most of these studies determining that chironomid abundance was greatest during the dry period (Ferrington et al. 1993, Coffman and de la Rosa 1998, Ramírez and Pringle 1998, Sonoda and Trivinho-Strixino 2000, da Silva et al. 2009, Kranzfelder and Ferrington 2016). Lower abundances of aquatic insects during the wet season have been proposed to be the result of high precipitation events causing spates that disturb habitats and dislodge invertebrates (Ramírez and Pringle 1998, da Silva et al. 2009). In Quebrada Prieta, abundance on average was higher during the dry season (January through April; 263 individuals/month) compared to the wet season (May through December; 162 individuals/month). However, there was an overall decline in emergence abundance through the dry season followed by increasing abundance through the wet season in Quebrada Prieta. In contrast, Lehmann (1979) identified seasonal patterns in chironomid emergence from a continental, tropical stream with increasing emergence through the dry season and declining emergence in the wet season. Regardless, the available research indicates that there is a general pattern of higher emergence in tropical habitats during the dry season and this is at least anecdotally related to the impact of spates on aquatic invertebrates.

Although, most studies of tropical chironomids report emergence patterns at the community level, more interesting patterns may emerge at the spe-

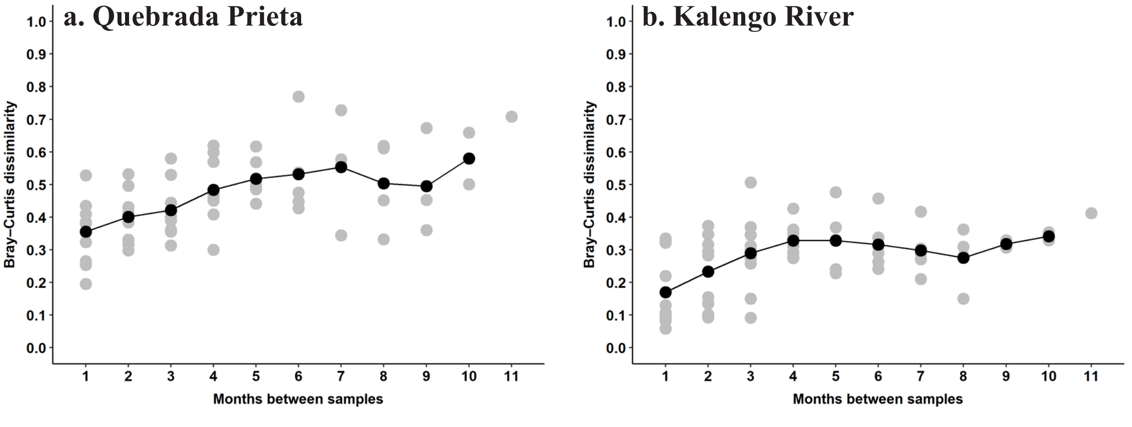

Figure 7. Dissimilarities (Bray-Curtis) between monthly samples of emerging Chironomidae for (a) Quebrada Prieta (USA; Puerto Rico) and (b) Kalengo River (Democratic Republic of the Congo). Grey circles are individual paired months and black circles are the average dissimilarities of all pairs of samples separated by the same number of months.

cies level. In contrast to the general pattern of increasing chironomid emergence during the dry season, Strixino and Sonoda (2006) determined that a species of *Tanytarsus* had higher emergence during the wet period when rainfall and temperatures were higher. Lehmann (1979) determined that several species had seasonal emergence patterns and these patterns differed between species with some increasing emergence in the dry period whereas other increased during the wet period. The presence of different voltinism types have been identified among emerging tropical chironomid species (Arpellino et al. 2022). Rare taxa (<1% of total individuals) in Quebrada Prieta showed limited seasonality which may be the result of a failure to detect these taxa. Therefore, is it possible that rare taxa also have seasonal emergence patterns, but the sampling effort was not sufficient to measure these patterns. However, seasonal emergence patterns were apparent for many common taxa (>1% of total individuals) in Quebrada Prieta with these taxa showing different seasonal patterns of emergence. It should be noted that although possible seasonality was identified for many taxa, emergence peaks were not as strong as those observed for many temperate midge species. This is likely due weaker seasonal patterns in Quebrada Prieta compared to temperate regions. Low temperatures and freezing of aquatic habitats greatly reduce or halt emergence of chironomids in temperate habitats in the winter. In contrast, the specific factors influencing the phenology of individual chironomid species are often difficult to determine due to weaker exogenous cues in tropical habitats.

Taxa emerging from Quebrada Prieta were divided into three emergence pattern types including: (1) emergence during the wet period, (2) emergence during the dry period, and (3) aseasonal emergence with one or more emergence peaks. Most surprising was the highly synchronous emergence peaks of three taxa, but apparent emergence patterns were also observed for other common taxa and suggest that the phenologies of many species were structured by exogenous cues. For example, there is indirect evidence that stream discharge was important as there was an increase in *Limnophyes*, a genus generally considered to be semiaquatic, during the dry season. In general, the taxa that had their highest emergence during the dry period may be responding to the reduced disturbance caused by spates during this period. However, there were also taxa that had emergence peaks during the wet period. Possible factors that may be influencing this emergence pattern could be higher temperatures or increased leaf fall. Average monthly water temperatures in this region only vary 3 °C over the course of the year so the input of allochthonous matter may be more probable. Increased leaf fall generally begins at the end of the dry season and extends into the wet period. The increased emergence of these taxa through the wet season could reflect patterns of allochthonous matter inputs and the utilization of this resource as it conditions in the stream during the wet season. However, the variable timing of emergence peaks for other taxa in Quebrada Prieta suggest that different exogenous cues may be important for these taxa. However, for the taxa with aseasonal emergences patterns, no obvious exogenous cues could be assigned to these patterns.

The study of midge emergence in Quebrada Prieta supports the work of other studies (e.g., Sonoda and Trivinho-Strixino 2000) which indicate that in tropical midge communities, emergence of the most common taxa are continuous throughout the year with apparent pulses in emergence that may correspond to exogenous cues. However, other than noting the correspondence of some chironomid emergence peaks to seasonal precipitation or leaf fall patterns, we were unable to explicitly link these emergence patterns to specific exogenous factors. This was complicated by the fact that temperature and leaf fall patterns in the Caribbean National Forest largely covaried with precipitation patterns. Other studies of tropical aquatic communities have indicated that seasonal patterns of temperature, rainfall, photoperiod, and lunar period can result in synchronized emergence patterns (e.g., Fryer 1959, Arpellino et al. 2022). Although Siqueira et al. (2008) identified some peaks in emergence of tropical chironomids, these pulses could not be linked to specific exogenous factors and the authors hypothesized that this could be the result of “chaotic” emergence patterns or to a failure to measure important exogenous factors. Further study of the phenology of aquatic communities are needed, particularly research to better determine the factors that influence these patterns. Specifically, it would be interesting to determine if seasonal emergence patterns are linked to measurable abiotic factors or if emergence pulses are more stochastic. This would require multiple years of sampling coupled with detailed measurement of possible emergence cues.

Although the apparent seasonal emergence patterns of some chironomid taxa contradicted our expectation that the emergence patterns of midges in Quebrada Prieta would be aseasonal, our results do support the predictions for estimated durations of emergence based on the hypothesis by Coffman and de la Rosa (1998). An average emergence duration of 205 d/sp/yr in Quebrada Prieta was higher than those estimated for temperate communities (Table 4; 61-120 d/sp/yr). In comparison to tropical chironomid communities, the estimated emergence duration in Quebrada Prieta was greater than that for Costa Rican chironomid communities (110-126 d/sp/yr) and less than chironomids from a river in the Democratic Republic of the Congo (255 d/sp/yr; Table 4). Similarity between monthly samples also followed predicted patterns with overall low dissimilarity between samples which slightly increased as the interval between samples became greater. A similar pattern was observed in a headwater stream in Brazil by Siqueira et al. (2008). These results further demonstrated that although seasonal patterns measured as peaks in emergence are present in tropical stream habitats, they are weaker than those observed in temperate habitats. This pattern is likely due to the strong thermal ranges in temperate habitats compared to tropical habitats, but other seasonal cues may also be important.

The long emergence durations for Chironomidae in Quebrada Prieta and the Kalengo River were considerably higher than other tropical habitats in Costa Rica. If we can accept that methodical differences were not the cause of this difference, it raises the question as to why emergence duration is approximately double in in Quebrada Prieta and the Kalengo River. Our expectation was that monthly dissimilarity in the Kalengo River would exceed the values for Quebrada Prieta due to the continental habitat of the Kalengo River and the associated greater taxa richness. However, the dissimilarities between monthly samples for the Kalengo River were consistently low, both in terms of the annual average dissimilarity and among all combinations of months regardless of the time interval between the monthly pairs. Although the Kalengo River had nearly double the taxa richness of Quebrada Prieta, both habitats are unremarkable for tropical habitats with only 46 and 28 taxa, respectively. In comparison, taxa richness in the Costa Rican streams ranged from 142-151 species (Coffman and de la Rosa 1998). Although the seasonality of all habitats is reduced relative to temperate regions, it can be hypothesized that in communities that are lower in species richness, the degree of temporal spacing of lifecycle dynamics, including larval growth, emergence duration,

Table 4. Average emergence durations for tropical and temperate Chironomidae communities. The average sampling interval is based on either the average number of days between samples (Coffman and de la Rosa (1998)) or the aggregation unit (i.e., months) for multiple samples (this study, Lehmann (1979), and Bouchard (2007)). *These studies are based on adult emergence traps whereas the remaining studies are based on pupal exuviae sampling. #Biweekly sampling intervals were used in Bouchard (2007) and these samples were aggregated into monthly samples for the present study.

Locality	**Emergence duration**	**Average sampling interval***	**Source**
			Tropical streams
Quebrada Prieta, Puerto Rico, USA	205	30	This study*
Kalengo River, Democratic Republic of the Congo	255	30	Lehmann (1979)*
Quebrada Las Yegüitas (Maritza), Costa Rica	110	23	Coffman and de la Rosa (1998)
Quebrada Las Yegüitas (Orosí), Costa Rica	126	28	Coffman and de la Rosa (1998)
Rio Tempisquito Sur, Costa Rica	118	28	Coffman and de la Rosa (1998)
Rio Tempisquito, Costa Rica	111	16	Coffman and de la Rosa (1998)
			Temperate streams
Powdermill Run (Moul), USA	71	17	Coffman and de la Rosa (1998)
Powdermill Run (Headquarters), USA	61	18	Coffman and de la Rosa (1998)
Linesville Creek, USA	77	9	Coffman and de la Rosa (1998)
Chub Creek, USA	91	30#	Bouchard (2007)
Credit River, USA	120	30#	Bouchard (2007)
Sunrise River, USA	84	30#	Bouchard (2007)
Cedar Creek, USA	71	30#	Bouchard (2007)
Rock Creek, USA	85	30#	Bouchard (2007)
Rush Creek, USA	84	30#	Bouchard (2007)

and overlap, is less than it is in more diverse chironomid communities that experience similar degrees of seasonality. Perhaps the higher biological diversity can only be achieved by greater degrees of temporal isolation among growing larvae, thus reducing competition for limiting food resources, rather than finer degrees of food resource sharing among larvae of species with overlapping periods of growth. In general, studies of niche partitioning among tropical aquatic insect communities are needed to understand how these communities are structured by biotic and abiotic factors.

Although predicted differences in emergence duration were apparent between tropical and temperate studies of chironomid emergence, differences in sampling methodology can complicate these patterns and these effects should be considered. Our data and those of Lehmann (1979) were derived from single emergence traps at one stream site. In contrast, Coffman and de la Rosa (1998) and Bouchard (2007) collected surface-floating pupal exuviae to determine the phenology of emerging species. There are two main issues that may impact the comparability between emergence trap and pupal exuviae data: 1) habitat types sampled and 2) the relative sampling effort. Use of an adult emergence trap is more restrictive in that only adults from the area covered by the trap are collected. The method of collecting surface-floating pupal exuviae, by comparison, provides samples of exuviae that are left behind by adults emerging from a larger stream area, perhaps as much as several meters to several decimeters or more upstream. Although our emergence trap effectively captured adults of species that live in microhabitats covered by the trap, the trap did not extend over the entire adjoining pool habitats. However, it is possible that some individuals came from upstream habitats when pupae in the process of emerging were carried downstream as the adults were eclosing. The effect of sampling methodology may also be impacted by changes in the habitat when stream discharge changes during trap deployment. This possibly impacted emergence patterns in Quebrada Prieta as some taxa associated with the stream margins became more common during the dry period (e.g., Limnophyes). Alternatively, the increase in these taxa may have been the result of stream-wide changes caused by seasonal patterns. In contrast, sampling surface-floating pupal exuviae result in collections of specimens of exuviae for species that occur in a wide variety of microhabitats, including species living at different depths, substrates, and habitat types (Kranzfelder et al. 2015). Consequently, the use of an emergence trap could have resulted in several species that are common in pools showing up as rare in our collections, and only being collected on a few sample dates. This would cause our estimates of the average emergence duration for all chironomids to be lower than if taxa from pools were more efficiently collected. Lehmann (1979) also used an emergence trap, but the trap area was more than double that of the trap used in Quebrada Prieta which may explain the longer emergence durations. As a result, we cannot rule out the effects of sampling method differences on estimates of emergence durations and community dissimilarity between months.

Coffman and de la Rosa (1998) discussed another important aspect associated with estimating emergence duration and drew attention to the importance of how one interprets the significance of intervals when individual species are not present in samples. Gaps in detecting a species over one or more sample dates could either reflect sampling error or could indicate a period between emergence of successive generations, and these gaps require that a judgment be made regarding two alternatives. If a gap reflects a sampling error, counting the sample as a period when the species is not emerging results in a shorter estimated annual duration of emergence. Alternatively, counting a gap as a sampling error when it actually represents a period of no emergence between successive generations will result in an over-estimate of the annual emergence duration. In our study, the estimate derived from analysis of monthly data may miss small gaps in emergence of species and means that species with short, synchronous generation times may appear to have continuous, asynchronous emergence. Consequently, the estimates based on monthly data may miss seasonal patterns or over-estimate emergence durations. By compositing our data according to monthly intervals, we minimize the significance of shorter gaps in appearance of a species in the samples, and only accept larger gaps as indications of breaks in emergence between successive generations.

The research in Quebrada Prieta and from several other studies demonstrate that taxa in tropical chironomid communities largely emerge throughout the year. Rare taxa in tropical habitats are an exception as they often appear to have sporadic emergence patterns, but this may be due to a failure to detect these species when they are in fact present. Although adults of common species are present year-round, there are apparent pulses of emergence which may correspond to seasonal, exogenous cues. Based on this study and several others, there is evidence that some degree of seasonality occurs and may in fact be common in tropical midge communities. Most commonly, increased emergence is associated with the dry season indicating that spates increase stream disturbance and lower larval midge densities. However, some tropical midge taxa had higher emergence during the wet season (*Ablabesmyia*, *Larsia*, *Stenochironomus* sp. 1, and *Tanytarsus* sp. 1 (this study); *Tanytarsus obiriciae* Strixino and Sonoda (Strixino and Sonoda 2006)). Variable timing of emergence peaks may correspond to differences in emergence cues between species (e.g., discharge, temperature, photoperiod, lunar period, food resources) or this may reflect stochastic emergence patterns among these species. Most studies of tropical insect emergence are limited to a single year and to understand if regular, seasonal cues are important or if emergence peaks are stochastic, long-term studies of emergence is needed. Seasonality of insect activity in tropical habitats are likely to be widespread (Wolda 1988), but there continues to be limited detailed studies of the ecology and phenology of tropical chironomids. The ability to describe and model these patterns is of interest for the conservation of these species as they face threats including climate change, habitat loss, and water quality degradation.

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