J. N. Am. Benthol. Soc., 2006, 25(1):108–125

Temporal and spatial patterns in stream physicochemistry and insect assemblages in tropical lowland streams

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Abstract. Stream physicochemistry and insect assemblages were studied in lowland tropical streams in Costa Rica to determine physicochemical variables explaining temporal and spatial variations in insect density and biomass. Streams drained a tropical wet forest landscape and had similar geomorphology, but differed in their water chemistry because of differential inputs of solute-rich (i.e., P, Cl^-, and Mg) geothermally modified groundwater. We hypothesized that, within a stream, physical factors, such as discharge, would result in temporal variation in insect assemblages, whereas interstream differences in solute composition would result in differences in insect assemblages among streams. Insect density, biomass, richness, and stream physicochemistry were measured monthly for 1 y in 6 streams. Insect samples were collected with a core sampler in runs where leaf litter overlying fine sediments was the main substrate. Streams with high inputs of geothermally modified groundwater had high conductivity and high concentrations of soluble reactive P (SRP). Annual temporal patterns in stream physicochemistry were related either to rainfall, with subsequent changes in discharge, or to the % geothermally modified groundwater entering streams. Streamwater pH decreased throughout the year, and unbuffered, nongeothermally modified streams changed from near neutral (pH >6) to near acidic (pH <4.5). In all streams, insect density and biomass were highest during the dry season and lowest during the wet season. Insect density and biomass were related positively to pH and to the number of days since the last storm. Insect taxonomic composition was similar among streams. Moreover, interstream variation in insect assemblages was small, and insect density and biomass were not related to any of the measured physicochemical variables, including SRP, which ranged from <5 to 267 μg/L. Overall, the physicochemical characteristics of the study streams were related mainly to geothermally modified groundwater inputs and seasonal patterns in rainfall. Streams with geothermally modified groundwater inputs were better buffered against pH changes than the other streams. Insect assemblages reflected fluctuations in stream physicochemistry during the year and were associated with 2 main factors: floods and pH. Physicochemical characteristics were very different among streams, but insect assemblages were not related to them. We hypothesize that the heterogeneous nature of benthic substrata in the streams resulted in high variation in density and biomass of insects, potentially obscuring differences in insect assemblages among streams.

Key words: physicochemistry, invertebrates, benthos, phosphorus, geothermally modified groundwater, disturbance, discharge, pH, tropical streams, Costa Rica.

The importance of physicochemical variables in controlling animal communities has received much attention from stream ecologists. Streams are characterized by large physicochemical variability in time and space, and a small group of physicochemical variables is responsible for most of the variation in insect assemblages (see reviews in Hynes 1970, Allan 1995). Among these variables, temperature influences growth and distribution of benthic insects in many temperate streams (Hynes 1970, Sweeney 1984). In contrast, temperature remains constant during the year in tropical streams, and it is not considered important in controlling tropical benthic communities (Hynes 1970). Discharge is another important factor

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structuring stream ecosystems (e.g., Resh et al. 1988, Yount and Niemi 1990). Insect assemblages increase in density with the amount of time since the last storm in both temperate (e.g., Grimm and Fisher 1989, Grimm 1994) and tropical streams (Flecker and Feifarek 1994, Ramírez and Pringle 1998). Low pH also can be important in some streams (e.g., streams impacted by acid deposition or mining), as variation in pH results in changes in insect assemblages (e.g., Townsend et al. 1983, 1987, Winterbourn and Collier 1987, Gower et al. 1994). We can expect similar effects in tropical streams, but the importance of pH changes in structuring insect assemblages has received little attention in tropical streams (Cranston et al. 1997). In addition, evidence indicates that differences in landscape characteristics among regions can result in large variability in streamwater chemistry (Allan 1995). For example, lowland streams draining volcanic landscapes can vary in their water chemistry depending on whether or not they receive inputs of geothermally modified groundwater, which can be rich in solutes (Pringle et al. 1993, Pringle and Triska 2000). The consequences of these inputs on stream insect assemblages have received little attention (Rosemond et al. 2002).

We examined relationships between physicochemical characteristics and benthic insect assemblages in lowland streams in Costa Rica's Caribbean slope. The volcanic origin of the landscape drained by the study streams results in differential inputs of geothermally modified groundwater to the streams. Our specific objectives were to: 1) quantify temporal variation (i.e., during a year) in physicochemical variables within 6 streams, 2) determine which physicochemical variables were significantly related to temporal variation (i.e., within a stream) in insect assemblages, 3) quantify spatial variation (i.e., among streams) in physicochemical variables, and 4) examine the relation between interstream differences in physicochemistry and insect assemblages.

Study System

La Selva Biological Station (lat 10°26′N, long 84°01′W) is adjacent to Braulio Carrillo National Park (area ~45,000 ha), which protects the entire watershed of the study streams. La Selva receives almost 4000 mm of rainfall a year, with a wet season (>400 mm/mo) occurring from June to December (Sanford et al. 1994). The dry season is the period from January to June. Based on vegetation and climatic characteristics, La Selva is classified as tropical wet forest (Holdridge et al. 1971).

Geomorphological features of the La Selva landscape result in differential inputs of geothermally modified groundwater to some of the streams, changing their chemical characteristics (Pringle 1991). Groundwater is modified by volcanic activity at high elevations, cools as it moves downhill, and finally enters lowland streams as geothermally modified groundwater. One of the main signatures of geothermally modified groundwater is high solute concentration (e.g., P, Na, and Cl^-; Pringle et al. 1993). The dense riparian vegetation along streams at La Selva results in light-limited algal communities (Pringle et al. 1986) and detritus-based food webs. Previous studies have shown that P-rich inputs of geothermally modified groundwater can enhance fungal biomass (Rosemond et al. 2002) and microbial activity (e.g., respiration rates; Ramírez et al. 2003) on leaf detritus.

Methods

Sampling sites

We chose 6 streams that differed in their inputs of geothermally modified groundwater and, therefore, had different solute concentrations (Table 1). All streams were of low order (~2nd–3rd), in close proximity to each other, and surrounded by primary forest. Riparian vegetation was dense, provided large amounts of leaf litter to streams, and reduced light availability for algal communities (Pringle et al. 1986).

TABLE 1. Annual means (and ranges) of physicochemical variables in the study streams. Streams are ordered by decreasing proportion of geothermally modified groundwater (%GMG). SRP = soluble reactive P.

Variable	Arboleda	Sura-30	Saltito	Salto	Sura-60	Piper
Discharge (m^3/s)	0.17 (0.09–0.21)	0.61 (0.43–0.86)	0.11 (0.04–0.20)	0.45 (0.07–0.93)	0.19 (0.05–0.55)	0.03 (0.01–0.10)
pH	6.0 (5.8–6.4)	6.2 (5.5–6.8)	6.2 (5.5–6.9)	5.8 (5.0–6.6)	5.4 (4.3–6.9)	5.1 (4.0–6.0)
Temperature (°C)	26 (25–26)	26 (25–27)	25 (25–26)	26 (25–27)	26 (25–26)	26 (25–26)
SRP (μg/L)	267.3 (190–450)	194.8 (127–288)	99.4 (36–225)	22.6 (15–42)	4.8 (1–20)	4.8 (1–15)
NO_3-N (μg/L)	199.2 (150–247)	219.0 (193–242)	164.4 (125–218)	272.8 (195–470)	212.8 (181–267)	204.6 (183–256)
N:P ratio	1.8 (1–3)	2.7 (1–4)	4.9 (2–13)	30.5 (14–48)	166.0 (24–386)	267.0 (40–715)
Conductivity (μS/cm @ 25°C)	342 (297–368)	203 (145–268)	146 (73–263)	43 (23–95)	21 (17–26)	23 (21–24)
%GMG	45 (32–53)	22 (14–33)	18 (6–38)	2 (1–6)	1 (0–1)	<1 (0–8)

Channel widths varied from 2 to 3 m, and the dominant substrata were detritus and sediments (e.g., silt and clay), with boulders present at some sites. Stream banks and margins were covered with leaf litter and were partially inundated during high-flow periods, mainly during the wet season.

Large streams (order $>4^{\text{th}}$) at La Selva support diverse assemblages of fishes and shrimps, but small streams like those studied here (order $<3^{\text{rd}}$) contain only a subset of those assemblages. For example, of the >40 fish species recorded at La Selva (Bussing 1994), only ~10 species are found in the study streams (e.g., Burcham 1988). In addition, fishes and shrimps do not appear to control insect assemblage structure in these streams (Ramírez and Pringle 2004).

Physicochemical variables

All physicochemical variables were measured monthly in each stream from January to December 1998. Flow was measured with a Marsh–McBirney current meter, and discharge was estimated using the velocity–area method (Gordon et al. 1992). We avoided measuring discharge during peak storm flow, so the values obtained represent changes in nonstorm conditions throughout the year. Water pH, temperature, and conductivity were determined in the field using Hanna meters. Nutrient concentrations were measured by collecting 2 filtered (0.45-μm Millipore filters) water samples in each stream using new 125-mL bottles. Samples were kept frozen until analyzed at the University of Georgia. NO_3-N, NH_4-N, and P (as soluble reactive P [SRP]) concentrations were measured using continuous-flow colorimetry and an Alpkem RFA 300 colorimetric analyzer. The Cd reduction, phenate, and ascorbic acid methods were used for NO_3-N, NH_4-N, and SRP, respectively (APHA 1992). Atomic N:P ratios were calculated using $NO_3\text{-N} + NH_4\text{-N}$ and SRP.

The monthly proportion of geothermally modified groundwater (%GMG) present in each stream was determined using a chemical mixing model (Genereux and Pringle 1997, Wood 1999). The model determines the %GMG entering the streams based on differences in Cl^- levels in stream water and known sources of geothermal water (Wood 1999). Monthly Cl^- levels for each stream were determined by ion chromatography (APHA 1992) using one of the water samples collected for nutrient analyses. Seasonal and annual values were calculated as monthly means over the period of interest.

Insect sampling

Aquatic insects were sampled monthly from January to December 1998. On each sampling date, 3 core samples (0.006 m^2 each) were collected from runs where leaves were the dominant substrate. The core was forced into the substrate, cutting through debris, to a depth of 10 cm. Samples were preserved in formalin (~5%), and insects were removed from organic material later under a dissecting microscope at 10×. Organic matter was dried at 70°C for 24 h to determine dry mass and then ashed at 500°C for 1 h to determine ash-free dry mass (AFDM).

Insects were identified to the lowest taxonomic level possible (genus for most orders, except Diptera and Coleoptera, which were identified to family or subfamily). Chironomidae (Diptera) were divided into 3 groups, the shredder genus *Xestochironomus*, which was abundant and tended to be larger in size than other midges, the mostly predatory subfamily Tanypodinae, and remaining larvae, which were mainly collector-gatherers in the subfamily Chironominae. Functional feeding groups were assigned using Jackson and Sweeney (1995) and Merritt and Cummins (1996). Biomass was estimated by measuring the length of each individual to the nearest 0.5 mm and applying length–mass relationships (Benke et al. 1999) derived from insects of similar morphology and typically from the same family. Insect density and biomass were expressed as no./m^2 and mg/m^2, respectively.

Statistical analysis

Relationships between physicochemical and environmental parameters were assessed using regression analyses. Effects of particular physicochemical parameters on insect density and biomass, functional feeding groups, and major taxa were assessed using stepwise multiple regression. Repeated measures (RM) ANOVAs were used to assess monthly changes in variables, and 2-way ANOVAs were used to compare seasonal changes among streams. Regressions and ANOVAs were run using JMP (version 4.04, SAS Institute, Cary, North Carolina). For stepwise multiple regression, the forward model was used, with a probability to enter the model of 0.25 and to leave the model of 0.10 (i.e., default setting in JMP). All variables were tested for normality and log-transformed ($\log_{10}[x+1]$) if required. Statistical results are reported with significance values grouped as $p < 0.10$ (significant) and $p < 0.05$ (highly significant).

Similarities among streams in physicochemical characteristics and insect composition were assessed using semistrong hybrid multidimensional scaling (SSH; Belbin 1991). SSH is a modification of the hybrid technique of multidimensional scaling (Faith et al. 1987, Belbin 1991).

Ordinations were run using monthly data for each stream and 2 and 3 dimensions, each with 50 random starting configurations. Stress values were examined

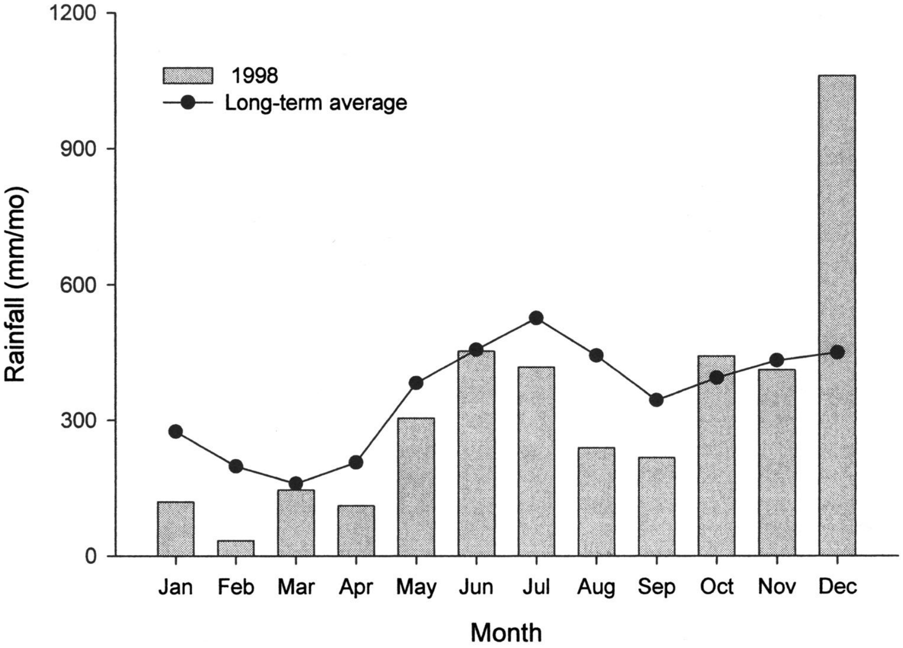

FIG. 1. Monthly rainfall at La Selva Biological Station in 1998. The line is the long-term average (1957–2004) calculated from the La Selva long-term records.

for each solution. Stress values indicate how well the between-sample relationships of the dissimilarity matrix are represented in ordination space (Kruskal and Wish 1978). The 2-dimensional solution was retained if stress values were >0.2 (Clarke 1993). Principle Axis Correlation (PAC) was used to determine which variables were important in structuring each data set (Belbin 1993). PAC calculates a vector of maximum linear correlation for each taxon or physicochemical variable in ordination space. The direction of each vector was plotted to compare it with the ordination plot. The significance levels of correlation coefficients were then tested using Monte Carlo procedures (Belbin 1993). Ordinations were done on an association matrix calculated using the Bray–Curtis dissimilarity measure as recommended by Faith et al. (1987). The physicochemical variables were range-standardized prior to analysis because they were expressed in a variety of different units and scales. Analyses were done using PATN (Belbin 1993)

Results

Physicochemical parameters

Annual rainfall during the study was 3953 mm, slightly below the long-term mean annual rainfall of 4200 mm (Sanford et al. 1994). Distribution of rainfall showed monthly values below 200 mm/mo from January to April, and monthly values ranging from 250 to 1060 mm/mo from May to December (Fig. 1). December was unusually wet during the study year (Fig. 1). Most other physicochemical parameters measured also varied during the year and among streams (Table 1).

Mean annual discharge ranged from 0.03 m^3/s in Piper to 0.61 m^3/s in Sura-30 (Table 1). Maximum nonstorm discharge values recorded in all streams were almost an order of magnitude greater than their respective minimum discharge values (Table 1). Measurements of monthly discharge were positively related to total rainfall during the previous 30 d in all streams. Rainfall explained 46% of the variation in discharge in Arboleda, 35% in Sura-30, 37% in Saltito, 28% in Salto, 67% in Sura-60, and 50% in Piper.

Water-column pH decreased considerably over time, ranging from near neutral at the beginning of the year

TABLE 2. Regression coefficients (r^2) and significance (p) for the relationships between pH and gauge height in all streams. ns = not statistically significant.

	Gauge height		Rainfall	
Stream	r^2	p	r^2	p
Arboleda	0.76	0.00	0.41	0.02
Sura-30	0.76	0.00	0.17	ns
Saltito	0.74	0.00	0.42	0.02
Salto	0.67	0.00	0.25	0.09
Sura-60	0.47	0.01	0.26	0.08
Piper	0.07	ns	0.47	0.02

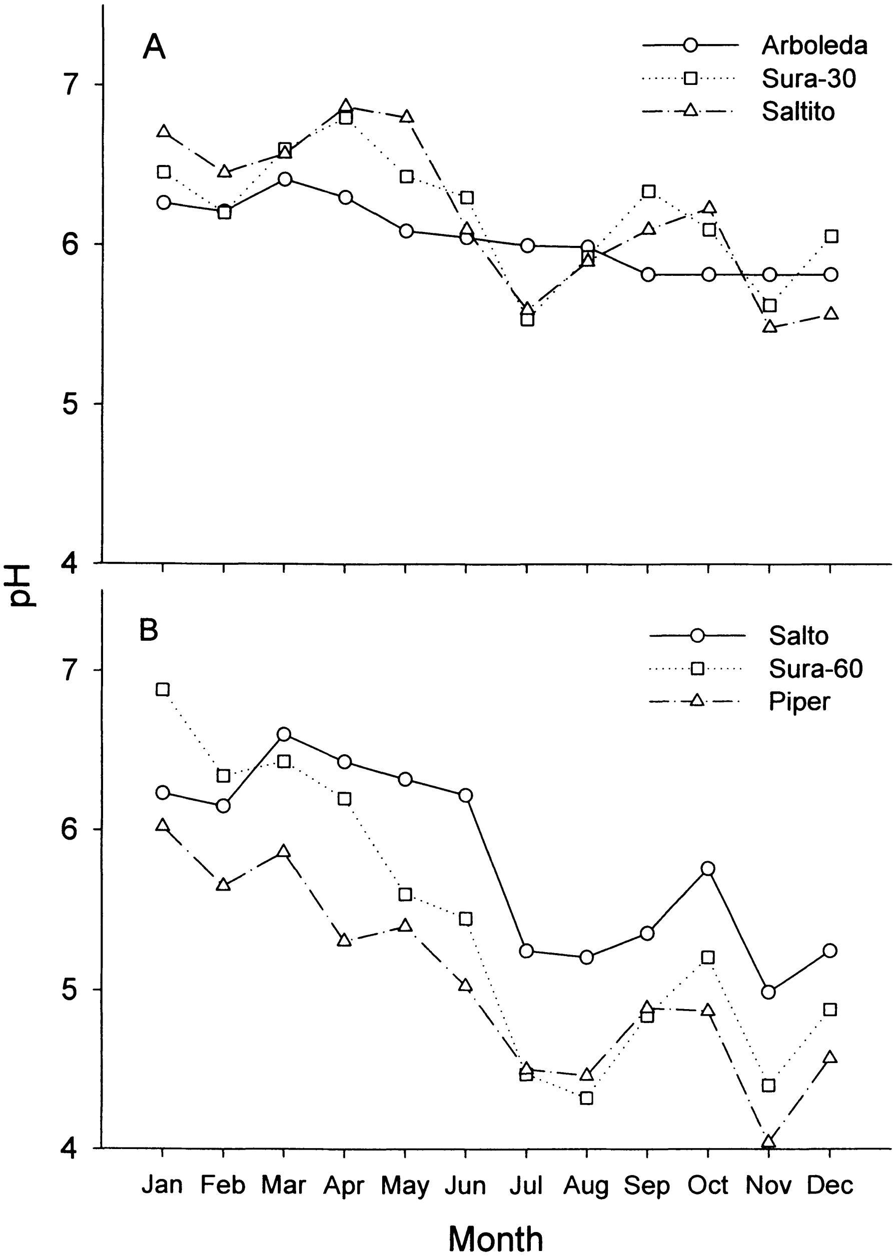

FIG. 2. Mean monthly pH for all study streams during 1998. A.—Streams receiving geothermally modified groundwater inputs. B.—Streams without those inputs.

in all streams to acidic (pH <4.5) during the last months of the year in some streams (Fig. 2). Streams with and without geothermal inputs of groundwater had similar pH values during the first part of the year, at least until July (Fig. 2). During the latter part of the year, however, streams without geothermal inputs had the lowest values (RM ANOVA, stream type: df = 2, $F = 3.9$, $p = 0.04$; month: df = 11, $F = 26.1$, $p < 0.01$; interaction: df = 11, $F = 3.9$, $p = 0.04$). Sura-60 and Piper showed the largest within-year changes, both decreasing by >2 pH units by the end of the year (Table 1). Changes in pH were related to both streamwater level and monthly rainfall. Thus, a significant negative relationship was found between pH and gauge height in all streams except Piper, and between pH and rainfall in all streams except Sura-30 (Table 2). The

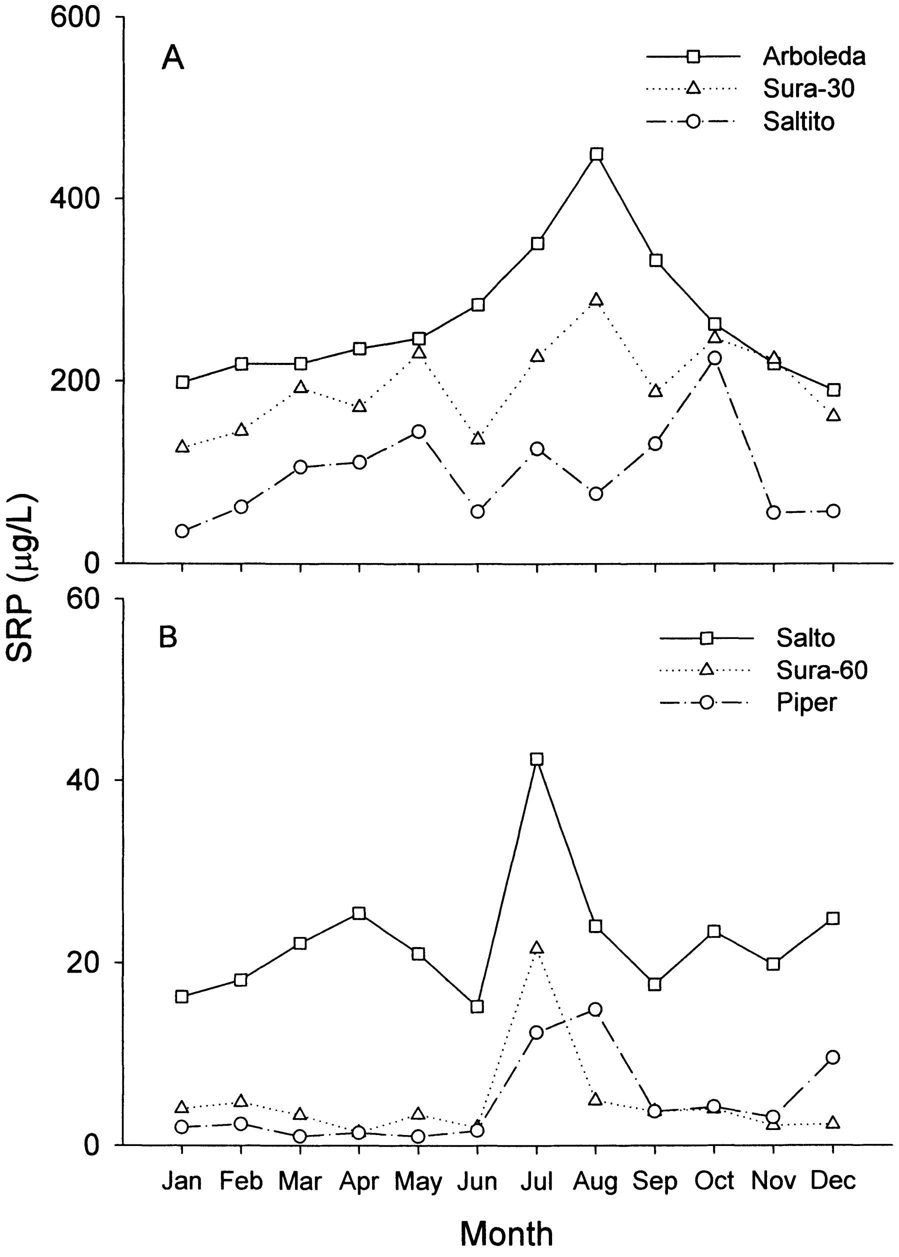

FIG. 3. Mean ($n = 2$) soluble reactive P concentration (SRP) for all study streams. A.—Streams receiving geothermally modified groundwater inputs. B.—Streams without those inputs. Note the large difference in y-axis scales.

amount of variation in pH values explained by the relationship with gauge height was larger (range 47–76%, excluding Piper) than that explained by the relationship with total rainfall during the previous 30 d (range 25–47%, excluding Sura-30). These relationships indicate that pH during the study period decreased as the streams inundated their floodplains and as overland flow increased during rainy months. pH values returned to near neutral in all streams by February of the next year (CMP, unpublished data).

A general increase in SRP concentrations was found during July and August (Fig. 3); however, SRP concentrations were related to discharge only in Arboleda and Saltito (Table 3). Interstream variations in SRP concentrations were large, with mean annual concentrations ranging from <5 μg/L in Piper to ~267μg/L in Arboleda (Table 1). Interstream differ-

Table 3. Regression coefficient (r^2) and significance (p) for the relationships between soluble reactive P (SRP), NO_3-N, and conductivity vs discharge and proportion of geothermally modified groundwater (%GMG) monthly in each stream and seasonally (wet and dry) and annually among streams. ns = not significant.

	SRP (µg/L)		NO_3-N (µg/L)		Conductivity (µS/cm)	
	r^2	p	r^2	p	r^2	p
Discharge						
Arboleda	–0.82	<0.001	0.00	ns	–0.21	ns
Sura-30	0.16	ns	–0.40	ns	–0.98	<0.001
Saltito	–0.36	0.03	–0.20	ns	–0.89	<0.001
Salto	0.00	ns	0.00	ns	–0.75	<0.001
Sura-60	0.00	ns	0.00	ns	–0.50	0.01
Piper	–0.12	ns	0.00	ns	–0.41	0.02
Dry season	0.37	ns	0.26	ns	0.23	ns
Wet season	0.04	ns	0.35	ns	0.00	ns
Annual	0.07	ns	0.37	ns	0.02	ns
%GMG						
Arboleda	0.22	ns	0.00	ns	0.63	0.00
Sura-30	0.00	ns	0.00	ns	0.97	<0.001
Saltito	0.00	ns	0.30	ns	0.97	<0.001
Salto	0.00	ns	0.30	ns	0.00	ns
Sura-60	0.00	ns	0.33	ns	0.00	ns
Piper	0.00	ns	0.00	ns	0.00	ns
Dry season	0.93	0.00	0.00	ns	0.99	<0.001
Wet season	0.91	0.00	–0.16	ns	0.99	<0.001
Annual	0.94	0.00	–0.14	ns	0.99	<0.001

ences in SRP concentrations were independent of stream size (i.e., mean discharge) and strongly related to the %GMG entering each stream (Table 3). Highest SRP concentrations were found in streams receiving the greatest %GMG.

NO_3-N concentrations were high throughout the year, similar among streams (Table 1), and independent of discharge and the %GMG (Table 3). N:P ratios were very different among streams, as a consequence of the large range in SRP concentrations, and ranged from 1.8 in Arboleda to 267 in Piper (Table 1).

Temporal variation in conductivity within a stream was small (Table 1), but monthly fluctuations were related negatively to discharge and positively to the %GMG at the 3 sites receiving those inputs (Table 3). Interstream differences in conductivity followed a pattern similar to that observed for SRP, with P-rich streams having higher conductivity than P-poor streams (Table 1). Differences in conductivity among streams were independent of stream size (i.e., mean discharge) and positively related to the %GMG in the stream (Table 3).

Overall, clear differences in physicochemical parameters were found among streams (Fig. 4A). In ordination space, SRP, conductivity, and the %GMG separated streams along Axis 1, whereas discharge and NO_3-N separated them along Axis 2 (Fig. 4B). In addition, streams with inputs of geothermally modified groundwater had negative values on Axis 1, indicating they had higher pH than the other streams (Fig. 4A). Streams with the highest %GMG showed the least amount of variation in physicochemical parameters.

Temporal variation in insect assemblages

Overall, insect density and biomass were significantly highest during the dry part of the year, from January to May. Highest density and biomass occurred early in the dry season (January or February) or late (April or May) (Figs 5A–E, 6A–E), except in Salto where both density and biomass were both variable throughout the year (Figs 5F, 6F). Total insect density and biomass decreased by >50% during the wet season (Fig. 7A, B), except in Saltito and Salto where biomass showed a small increase in the wet season (Fig. 7B).

Of the measured variables, discharge and pH changed most during the year (Table 1) and were considered to have the greatest potential to influence temporal variation in insect density and biomass. However, these 2 variables were correlated, and pH decreased throughout the year as stream discharge increased. Therefore, to avoid autocorrelation problems, number of days elapsed since the last rainfall event was used instead of discharge as a variable that represented past disturbance. Rainfall events >15 mm in 24 h were designated *storms*, and the number of days elapsed since the last storm (DSLS) was

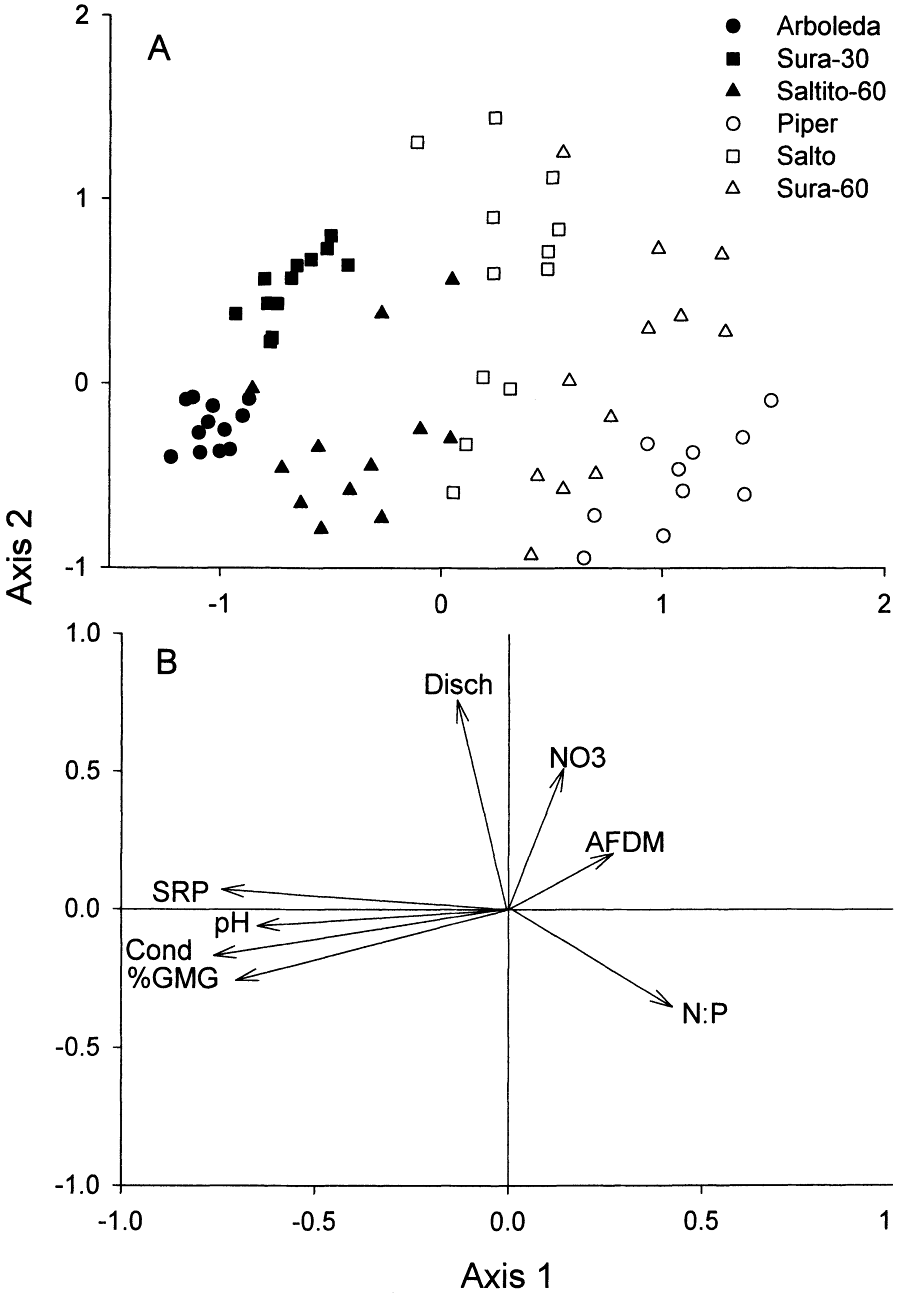

FIG. 4. Ordination plot (A) and vector analysis (B) of all streams based on their physicochemical characteristics. Analysis was based on monthly means. Disch = Discharge, Cond = conductivity, SRP = soluble reactive P, %GMG = proportion of geothermally modified groundwater, AFDM = ash-free dry mass.

correlated negatively with stream depth (i.e., gauge height) for all streams (r^2 for water level vs DSLS ranged from 0.32–0.48, all $p < 0.10$).

Total insect density or biomass were positively related to pH in Arboleda, Sura-30, Salto, and Sura-60 (Table 4). However, both total insect density and biomass in Piper and total insect density in Saltito were positively related to DSLS (Table 4). Taxa richness was positively related to pH in all streams except Sura-30 and Piper (Table 4). The dominant functional feeding groups found were collector-gatherers, shredders, and predators. Density and biomass of collector-

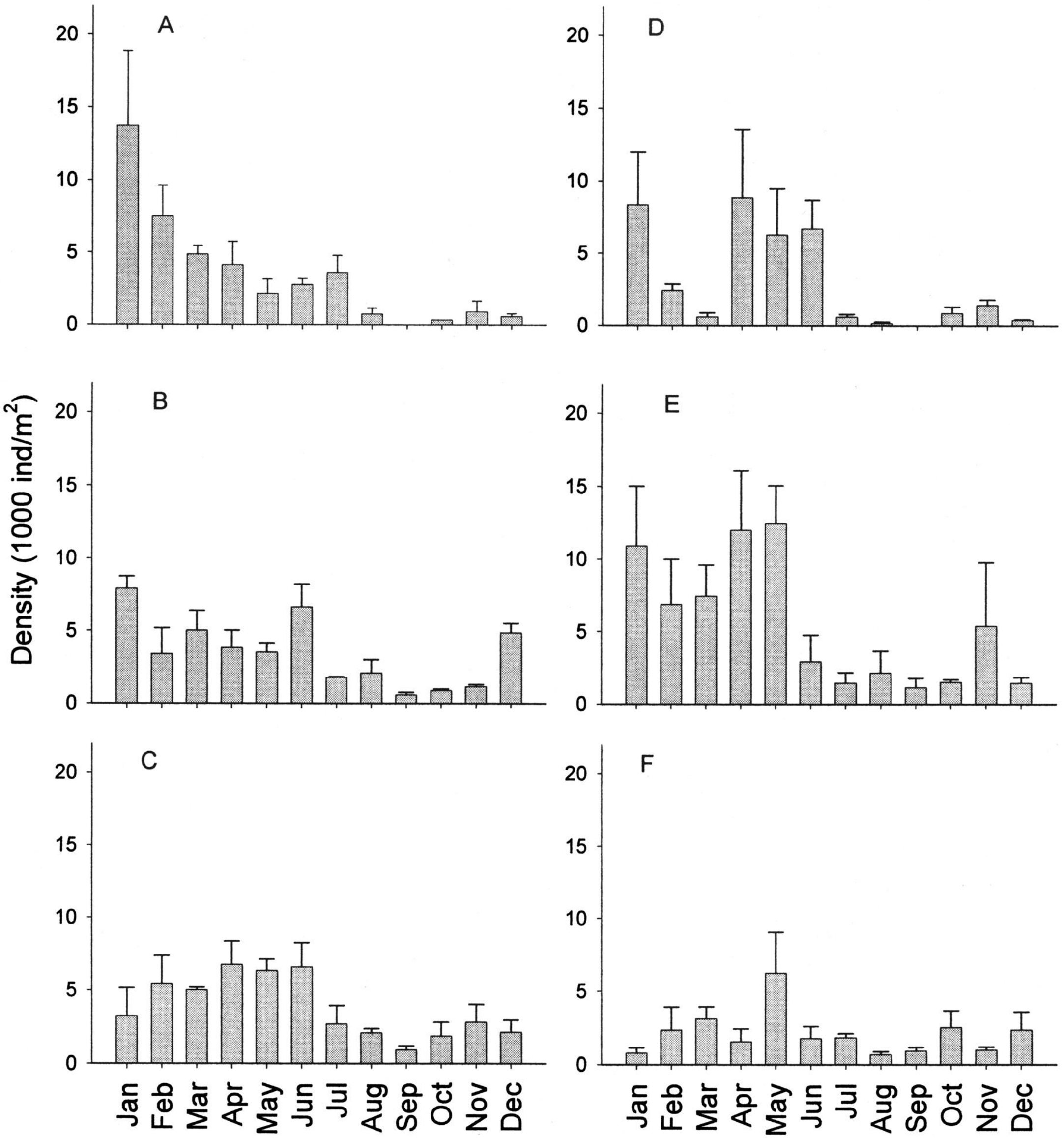

Fig. 5. Mean (+1 SE) monthly insect densities for Arboleda (A), Sura-30 (B), Saltito (C), Piper (D), Sura-30 (E), and Salto (F). Streams in panels A–C receive geothermally modified groundwater inputs. $n = 3$ for each stream.

gatherers were related to pH in all streams except Saltito and Piper (Table 4). The relationships between shredder and predator density and biomass and pH and DSLS had no consistent pattern (Table 4).

Only a small group of insects showed patterns of density and biomass that were significantly related to stream physicochemistry. These patterns were not evident for all taxa in all streams, but the overall trend was a positive relationship between insect density and biomass and pH and DSLS (Table 5).

Interstream variation in insect assemblages

Annual density and biomass of all taxa collected in the study are presented in Appendices 1 and 2. Density was highest in Sura-60 and lowest in Salto, and significantly higher during the dry season than the wet season (2-way ANOVA, stream: df $= 5$, $F = 2.9$, $p = 0.02$; season: df $= 1$, $F = 58.1$, $p < 0.0001$; interaction: df $= 5$, $F = 2.1$, $p = 0.07$; Fig. 7A). Biomass was similar among streams and significantly higher during the dry season than the wet season (2-way ANOVA, stream: df

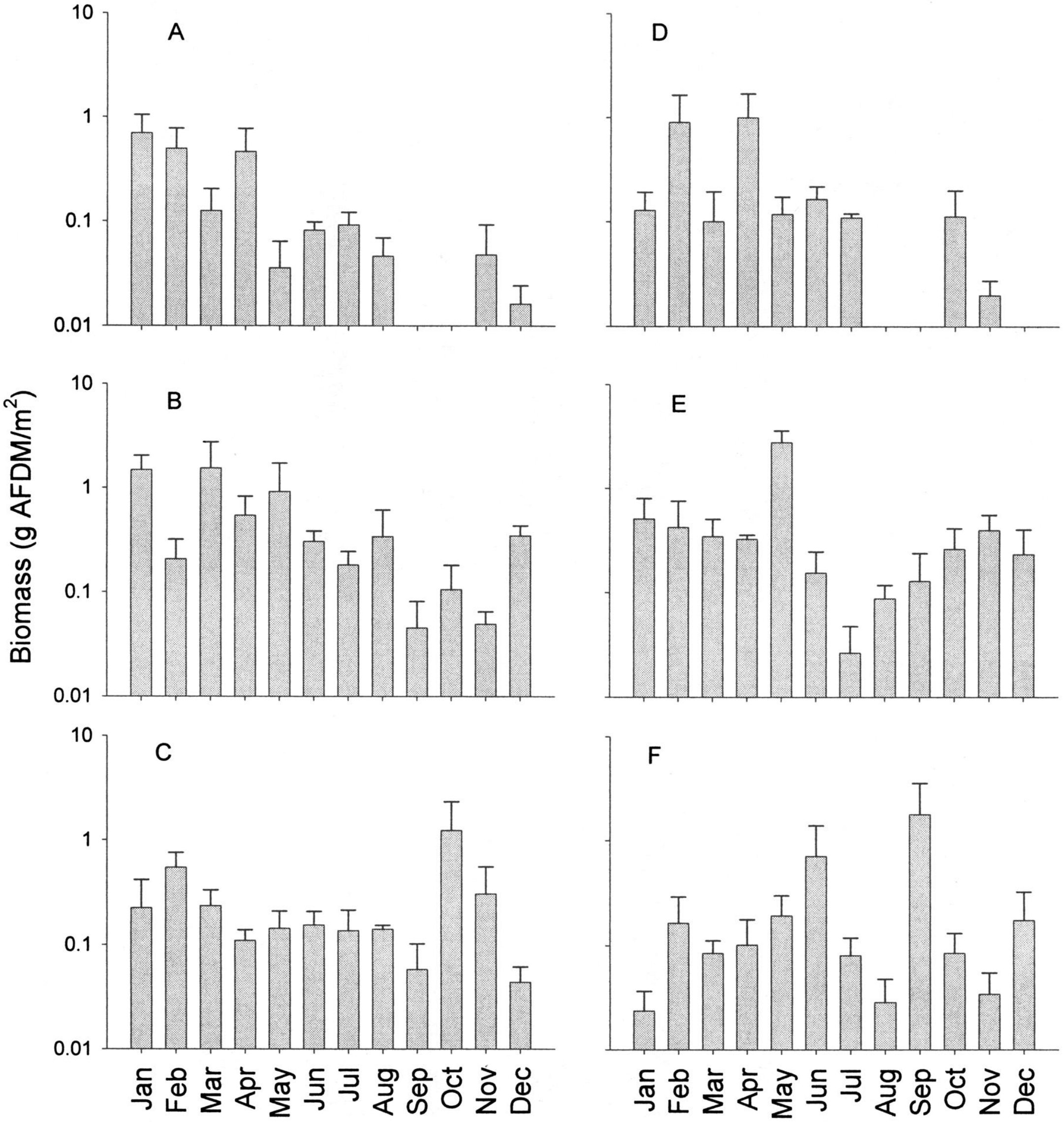

FIG. 6. Mean (+1 SE) monthly insect biomass for Arboleda (A), Sura-30 (B), Saltito (C), Piper (D), Sura-30 (E), and Salto (F). Streams in panels A–C receive geothermally modified groundwater inputs. $n = 3$ for each stream.

= 5, $F = 1.1$, $p = 0.4$; season: df = 1, $F = 6.6$, $p = 0.01$; interaction: df = 5, $F = 1.6$, $p = 0.1$; Fig. 7B).

The main physicochemical differences among streams were for SRP concentration and pH (Table 1). Therefore, these 2 variables were included in multiple regression models to assess their influence on insect assemblages among streams. In addition, mean discharge (i.e., annual or seasonal) for each stream was included in the analyses because the streams differed in size (Table 1).

Insect density and biomass (annual means and means for the dry and wet seasons) were not related to any of the independent variables measured (i.e., SRP, pH, stream size). Among the functional feeding groups, only mean biomass of collector-gatherers during the dry season was significantly related to stream size ($r^2 = 0.75$, $p < 0.05$).

Analyses of taxa that contributed >5% of the total density or biomass showed that *Caenis* density and biomass were mainly related to stream size, with pH explaining some of the variation in density during the wet season (Table 6). *Leptohyphes* density was related to SRP concentration during the dry season and for the year (Table 6). Density and biomass of Elmidae larvae

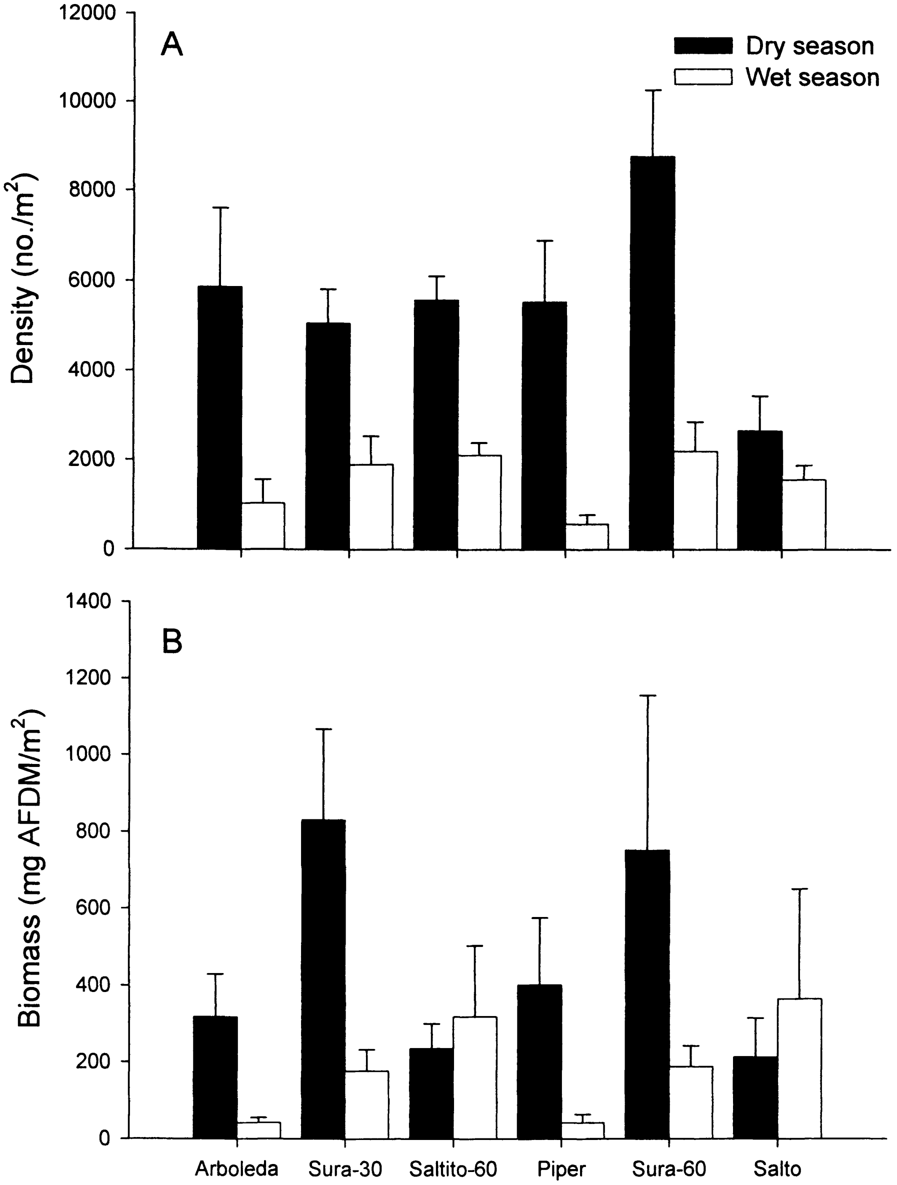

Fig. 7. Mean insect density (A) and biomass (B) during dry (January to June) and wet (July to December) seasons in all study streams. Each column represents the mean of 6 mo. AFDM = ash-free dry mass.

were related to stream size during the dry season and for the year (Table 6).

Ordinations used to assess potential groupings of streams based on insect density, biomass and presence/absence of taxa showed no interpretable groupings in ordination space. Ordinations plots (not shown) indicated that all streams had broadly the same insect fauna and that the composition of the fauna was not related to stream physicochemistry.

Discussion

Temporal changes in physicochemical variables within streams appeared to affect insect assemblages strongly. Insect density and biomass decreased during the year and were related to disturbances by flooding and pH. Physicochemical characteristics differed dramatically among study streams, but they were not reflected by differences in insect assemblages among

TABLE 4. Stepwise multiple regression partial coefficients (r^2) and significance of the relationships between total density and biomass, taxa richness, and density and biomass of functional groups vs the number of days since the last storm (DSLS) and pH. * = $p < 0.10$, ** = $p < 0.05$. – = variable did not enter model.

Variable	Arboleda	Sura-30	Saltito	Salto	Sura-60	Piper
Total density						
DSLS	–	–	0.32**	–	–	0.26**
pH	0.52**	0.18	–	0.56**	0.52**	–
Total biomass						
DSLS	–	–	–	–	–	0.43**
pH	0.48**	0.47**	–	–	0.39**	–
Taxa richness						
DSLS	–	–	–	–	–	–
pH	0.50**	–	0.48**	0.20	0.38**	–
Collector-gatherer density						
DSLS	–	–	0.30*	–	–	0.30*
pH	0.50**	0.25	–	0.29*	0.46**	–
Shredder density						
DSLS	–	0.18	–	0.34**	–	0.17
pH	0.53**	–	0.18	–	0.25*	–
Predator density						
DSLS	–	–	–	–	–	0.23
pH	0.55**	0.16	–	0.44**	0.54**	–
Collector-gatherer biomass						
DSLS	0.56*	–	–	–	–	–
pH	0.38**	0.38**	0.22	0.45**	0.46**	–
Shredder biomass						
DSLS	–	–	–	0.42**	0.29**	0.16
pH	0.39**	–	–	–	–	–
Predator biomass						
DSLS	–	–	–	–	0.19	0.50**
pH	0.20	0.24	–	–	–	–

streams. Insect density, biomass, and taxonomic composition were similar among streams.

Temporal patterns

Variation in physicochemical parameters within each study stream was related to seasonal changes in rainfall and subsequent changes in stream discharge. The only exception was NO_3-N, which was not related to any of the variables measured. In addition, streams receiving inputs of geothermally modified groundwater were more stable over time than streams without those inputs (Fig. 4). Of all physicochemical variables, pH and discharge changed most during the year.

pH was an important factor explaining variation in insect density and biomass through time within a stream. The steady decrease in pH during the year was observed in all streams and was large enough to make some streams acidic (pH <4.5) for part of the year. For example, Piper was circumneutral at the beginning of the year and acidic by the end of the year (Fig. 2). pH values measured early in the year were similar to those reported for many circumneutral streams (Allan 1995). In contrast, low values at the end of the year were close to thresholds below which streams are considered acidic (Townsend et al. 1983, Allan 1995). Anthropogenic effects of pH on stream communities have been studied extensively and in relation to global trends of acidification of freshwater ecosystems (Cresser and Edwards 1987, Charles 1991). Studies comparing streams with different degrees of acidification have shown that insect density and taxon richness usually decrease as stream pH decreases (e.g., Townsend et al. 1983, 1987, Winterbourn and Collier 1987). It is possible that the observed decrease in insect density and biomass in our study was the result of other factors (e.g., increased insect emergence before the beginning of the wet season), but our results suggest that decreases in pH negatively affected insect density and biomass. To our knowledge, ours is the first study to assess impacts of natural changes in pH on insect assemblages in tropical streams.

The changes in acidity occurred seasonally within a particular stream. However, we have observed large interannual variability in the magnitude of pH changes in subsequent years at La Selva (CMP, unpublished data). The underlying mechanism behind the pH drop in unbuffered streams is unclear, but the rainy season of 1998 followed a severe El Niño-related drought.

TABLE 5. Stepwise multiple regression partial coefficients (r^2) and significance of the relationships between density and biomass of the main taxa and the number of days since the last storm (DSLS), and pH. E = Ephemeroptera, C = Coleoptera, D = Diptera. * = $p < 0.10$, ** = $p < 0.05$. – = variable did not enter model.

Variable	Arboleda	Sura-30	Saltito	Salto	Sura-60	Piper
Density						
Caenis (E)						
DSLS	0.13	–	–	–	–	–
pH	–	0.21	0.15	–	–	0.31*
Leptohyphes (E)						
DSLS	0.47	–	–	–	0.31*	–
pH	0.36**	–	0.29*	0.13	–	–
Elmidae (C)						
DSLS	0.51	–	–	0.61	–	–
pH	0.34**	–	0.44**	0.48*	0.18	–
Ceratopogonidae (D)						
DSLS	–	–	–	–	–	0.17
pH	0.43**	0.19	–	–	–	–
Tanypodinae (D)						
DSLS	–	–	–	–	–	0.22
pH	0.54**	–	–	0.46**	0.56**	–
Xestochironomus (D)						
DSLS	–	–	–	0.21	–	0.16
pH	0.50**	0.62**	0.17	–	0.17	–
Other Chironomidae (D)						
DSLS	–	–	0.27*	–	–	0.35**
pH	0.50**	0.33**	–	0.18	0.44**	0.44
Biomass						
Caenis (E)						
DSLS	–	–	–	0.13	–	–
pH	–	–	0.16	–	–	0.31*
Leptohyphes (E)						
DSLS	–	–	–	0.14	0.31*	–
pH	0.26*	–	0.22**	–	–	–
Elmidae (C)						
DSLS	0.57**	–	0.20	–	–	–
pH	0.30	0.43**	–	0.44**	0.24	–
Ceratopogonidae (D)						
DSLS	–	–	–	–	–	0.28*
pH	0.23	–	–	0.24	–	–
Tanypodinae (D)						
DSLS	–	–	–	–	–	0.28*
pH	0.23	–	–	0.24	–	–
Xestochironomus (D)						
DSLS	–	0.16	–	0.42**	–	0.16
pH	0.54**	–	–	–	0.21	–
Other Chironomidae (D)						
DSLS	–	–	–	0.16	–	0.33**
pH	0.37**	0.18	–	–	0.40**	–

Climatic data from La Selva indicates that 1998 was warmer and drier than usual during the first part of the year, and wetter and cooler than usual during the latter part of the year (Loescher et al. 2003). During 1998, other researchers at La Selva reported decreases in annual tree growth, increased tree mortality, and increased litter fall (Clark et al. 2003, D. B. Clark, University of Missouri-St. Louis, personal communication). The negative relationship between pH, rainfall, and water level indicates that pH decreased as streams inundated their floodplains and overland runoff increased. Our study streams are not affected by acid rain (Eklund et al. 1997), but most stream-valley soils at La Selva are acidic, with pH values <4.5 (Sancho and Mata 1987, Sollins et al. 1994). Therefore, we hypothesize that changes in pH were the result of increases in the concentration of humic acids suspended in the water column during the wet season as a result of the increased leaf-litter inputs from riparian vegetation during the abnormally dry season of 1998 (Clark et al.

TABLE 6. Stepwise multiple regression partial coefficients (r^2) and significance of the relationships between density and biomass of the main taxa and discharge, pH, soluble reactive P (SRP), and NO_3-N during the wet and dry seasons and annually. Only significant relationships are shown. * = $p < 0.10$, ** = $p < 0.05$. – = variable did not enter model.

	Density			Biomass		
Taxon	Dry	Wet	Annual	Dry	Wet	Annual
Caenis						
Discharge	0.91**	−0.78**	0.53*	0.91**	−0.82*	0.79
pH	–	0.99**	–	–	–	–
SRP	–	0.41	–	–	0.51**	0.55
Leptohyphes						
Discharge	–	0.44	–	–	–	–
pH	–	–	–	–	0.46	–
SRP	0.77*	–	0.61*	0.49	–	0.93**
Elmidae						
Discharge	0.80**	–	0.52*	0.89**	–	0.55*
pH	–	–	–	–	–	–
SRP	–	–	–	–	–	–

2003). Humic acids can result in much larger decreases in stream pH than observed here. For example, Winterbourn and Collier (1987) found New Zealand streams ranged in pH as low as 4.1 because of inputs of humic acids from surrounding watersheds. Note that changes in pH in streams receiving inputs of geothermally modified groundwater were less than those observed in other streams. Geothermally modified groundwater, rich in carbonates (Pringle 1991), has high buffering capacity that is almost certainly responsible for the more stable pH values.

Tropical wet forests, such as La Selva, are regarded as aseasonal environments and large amounts of rainfall can be expected at any time during the year (Sanford et al. 1994). However, rainfall is clearly lower during the first part of the year, and a dry season can be defined. This seasonality appeared to be reflected by the insect assemblages in all study streams. Insect assemblages increased in density during the dry season (Fig. 7A) when disturbance (i.e., flooding) was low and pH was high. This result supports results from a previous study in a larger order (4th–5th) stream at La Selva in which insect density and biomass decreased during the wet season because of high flood frequency (Ramírez and Pringle 1998). However, relationships between insect assemblage structure and rainfall patterns have not been found in other tropical studies (e.g., Wolda and Broadhead 1985, Wolda and Flowers 1985). Discharge effects on insects in streams at La Selva appear to be more important in riffles than in pools (Ramírez and Pringle 1998), but insect assemblages in pool habitats in large streams appear to be controlled by predators (e.g., fishes). We studied areas of runs and pools with leaf-litter accumulations, but predation by macroconsumers (i.e., fishes and shrimps) appears to play a minor role in our study streams (Ramírez and Pringle 2004).

Spatial patterns

Each study stream was characterized by a distinct chemical composition, and together the streams represented a gradient in solute concentration (Fig. 4). The differences among streams were mainly the result of differential inputs of geothermally modified groundwater, which resulted in more variability among streams than within a particular stream. SRP appears to be the major limiting nutrient in these stream ecosystems (Rosemond et al. 2002). NO_3-N concentrations were similarly high among streams, and there is little evidence for N and P co-limitation (Stallcup 2004).

Insect assemblages were relatively similar among streams, despite large differences in physicochemical variables. Many studies have demonstrated that insects are affected by the physicochemical characteristics of their habitats (see review in Allan 1995). However, differences among our study streams apparently were not large enough to be reflected by the insect assemblage. A lack of differences in insect assemblages among streams contrasts with previous studies at La Selva that have found positive relationships between insect density and biomass and stream P concentrations in the same streams we studied (Rosemond et al. 2002, Ramírez and Pringle 2004). In our study, the only insect with density positively related to SRP concentration was the mayfly *Leptohyphes*. One of the main differences between previous studies and our study was the use of single-species leaf packs in the former and natural benthic substrata in the latter. Natural substrata are heterogeneous, composed of detritus from different riparian plant species that are at different stages of decomposition, and both microbial respiration rate and insect density were more variable in natural substrata than in leaf packs (Ramírez et al. 2003, Ramírez and Pringle 2004). Therefore, insects may have been patchily distributed among the natural benthic substrata sampled in our study, and this patchiness may have introduced large sample variation, reducing the probability of observing any effect of P on insect assemblages.

In conclusion, we found that the physicochemical characteristics of the study streams were mainly related to geothermally modified groundwater inputs and seasonal patterns in rainfall. Our results indicated that the streams with geothermally modified groundwater inputs were better buffered against pH changes than the other streams. Insect assemblages reflected fluctuations in stream physicochemistry during the year and were influenced by 2 main factors: discharge and pH. Physicochemical characteristics were very different among streams, but insect assemblages were not related to those differences. We hypothesize that the study habitat (i.e., runs with leaf litter as substratum) was highly heterogeneous and that insects were patchily distributed, thus reducing our ability to detect differences in insect density and biomass among streams.

Acknowledgements

We are grateful to M. Hidalgo for his invaluable assistance in obtaining field measurements and for his help processing insect samples. The manuscript was greatly improved by comments from R. Carroll, S. Eggert, M. D. Hunter, J. L. Meyer, A. D. Rosemond, J. B. Wallace, and 2 anonymous referees. We thank D. Genereux for analyzing water samples for Cl^- and the Organization for Tropical Studies and the staff of La Selva Biological Station for their help in facilitating this research. Support was obtained from grants awarded to CMP and FJT by the National Science Foundation (DEB-9528434 and DEB-0075339). AR was partially funded by the Luquillo LTER program while writing this manuscript (NSF grant DEB-0218039).

Literature Cited

Allan, J. D. 1995. Stream ecology. Chapman and Hall, London, UK.

APHA (American Public Health Association). 1992. Standard methods for the examination of water and wastewater. 16th edition. American Public Health Association, American Water Works Association, and Water Environment Federation, Washington, DC.

Belbin, L. 1991. Semi-strong hybrid scaling, a new ordination algorithm. Journal of Vegetation Science 2:491–496.

Belbin, L. 1993. PATN, pattern analysis package. Division of Wildlife and Rangelands Research, CSIRO, Canberra, Australia.

Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society 18:308–343.

Burcham, J. 1988. Fish communities and environmental characteristics of two lowland streams in Costa Rica. Revista de Biología Tropical 36:273–285.

Bussing, W. A. 1994. Ecological aspects of the fish community. Pages 195–198 *in* L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (editors). La Selva: ecology and natural history of a neotropical rain forest. University of Chicago Press, Chicago, Illinois.

Charles, D. F.(editor). 1991. Acidic deposition and aquatic ecosystems. Springer–Verlag, New York.

Clark, D. A., S. C. Piper, C. D. Keeling, and D. B. Clark. 2003. Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. Proceedings of the National Academy of Sciences of the United States of America 100:5852–5857.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117–143.

Cranston, P. S., P. D. Cooper, R. A. Hardwick, C. L. Humphrey, and P. L. Dostine. 1997. Tropical acid streams - the chironomid (Diptera) response in northern Australia. Freshwater Biology 37:473–483.

Cresser, M., and A. Edwards. 1987. Acidification of freshwaters. Cambridge University Press, New York.

Eklund, T. J., W. H. McDowell, and C. M. Pringle. 1997. Seasonal variation of tropical precipitation chemistry: La Selva, Costa Rica. Atmospheric Environment 31:3903–3910.

Faith, D. P., P. R. Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69:57–68.

Flecker, A. S., and B. Feifarek. 1994. Disturbance and the temporal variability of invertebrate assemblages in two Andean streams. Freshwater Biology 31:131–142.

Genereux, D., and C. M. Pringle. 1997. Chemical mixing model of streamflow generation at La Selva Biological Station, Costa Rica. Biogeochemistry 199:319–330.

Gordon, N. D., T. A. McMahon, and B. L. Finlayson. 1992. Stream hydrology. John Wiley and Sons, London, UK.

Gower, A. M., G. Myers, M. Kent, and M. E. Foulkes. 1994. Relationships between macroinvertebrate communities and environmental variables in metal-contaminated streams in south-west England. Freshwater Biology 32: 199–221.

Grimm, N. B. 1994. Disturbance, succession and ecosystem processes in streams: a case study from the desert. Pages 93–112 *in* P. S. Giller, A. G. Hildrew, and D. G. Raffaelli (editors). Aquatic ecology: scale, pattern and process. Blackwell Scientific Publications, Oxford, UK.

Grimm, N. B., and S. G. Fisher. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. Journal of the North American Benthological Society 8:293–307.

HOLDRIDGE, L. R., W. C. GRENKE, W. H. HATHEWAY, T. LIANG, AND J. A. TOSI. 1971. Forest environments in tropical life zones: a pilot study. Pergamon Press, Oxford, UK.

HYNES, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto, Canada.

JACKSON, J. K., AND B. W. SWEENEY. 1995. Egg and larval development times for 35 species of tropical stream insects from Costa Rica. Journal of the North American Benthological Society 14:115–130.

KRUSKAL, J. B., AND M. WISH. 1978. Multidimensional scaling. Sage Publications, Beverley Hills, California.

LOESCHER, H. W., S. F. OBERBAUER, H. L. GHOLZ, AND D. B. CLARK. 2003. Environmental controls on net ecosystem-level carbon exchange and productivity in a Central American tropical wet forest. Global Change Biology 9: 396–412.

MERRITT, R. W., AND K. W. CUMMINS (EDITORS). 1996. An introduction to the aquatic insects of North America. 3rd edition. Kendall/Hunt, Dubuque, Iowa.

PRINGLE, C. M. 1991. Geothermally modified waters surface at La Selva Biological Station, Costa Rica: volcanic processes introduce chemical discontinuities into lowland tropical streams. Biotropica 23:523–529.

PRINGLE, C. M., P. PAABY-HANSEN, P. D. VAUX, AND C. R. GOLDMAN. 1986. In situ nutrient assays of periphyton growth in a lowland Costa Rican stream. Hydrobiologia 134:207–213.

PRINGLE, C. M., G. L. ROWE, F. J. TRISKA, J. F. FERNANDEZ, AND J. WEST. 1993. Landscape linkages between geothermal activity and solute composition and ecological response in surface waters draining the Atlantic slope of Costa Rica. Limnology and Oceanography 38:753–774.

PRINGLE, C. M., AND F. J. TRISKA. 2000. Emergent biological patterns and surface-subsurface interactions at landscape scales. Pages 167–193 *in* J. B. Jones and P. J. Mulholland (editors). Streams and ground waters. Academic Press, New York.

RAMÍREZ, A., AND C. M. PRINGLE. 1998. Structure and production of a benthic insect assemblage in a neotropical stream. Journal of the North American Benthological Society 17:443–463.

RAMÍREZ, A., AND C. M. PRINGLE. 2004. Do macroconsumers affect insect responses to a natural stream phosphorus gradient? Hydrobiologia 515:235–246.

RAMÍREZ, A., C. M. PRINGLE, AND L. MOLINA. 2003. Effects of stream phosphorus levels on microbial respiration. Freshwater Biology 48:88–97.

RESH, V. H., A. V. BROWN, A. P. COVICH, M. E. GURTZ, H. W. LI, G. W. MINSHALL, S. R. REICE, A. L. SHELDON, J. B. WALLACE, AND R. C. WISSMAR. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7:433–455.

ROSEMOND, A. D., C. M. PRINGLE, A. RAMÍREZ, M. J. PAUL, AND J. L. MEYER. 2002. Landscape variation in phosphorus concentration and effects on detritus-based tropical streams. Limnology and Oceanography 47:278–289.

SANCHO, F. M., AND R. MATA. 1987. Estudio detallado de suelos: Estación Biológica La Selva. Organization for Tropical Studies, San José, Costa Rica.

SANFORD, R. L., P. PAABY, J. C. LUVALL, AND E. PHILLIPS. 1994. Climate, geomorphology, and aquatic systems. Pages 19–33 *in* L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (editors). La Selva: ecology and natural history of a neotropical rainforest. University of Chicago Press, Chicago, Illinois.

SOLLINS, P., F. SANCHO, R. MATA, AND R. L. SANFORD. 1994. Soils and soil process research. Pages 34–53 *in* L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (editors). La Selva: ecology and natural history of a neotropical rainforest. University of Chicago Press, Chicago, Illinois.

STALLCUP, L. A. 2004. Effects of water chemistry and leaf species on leaf breakdown in neotropical headwater streams. MS Thesis, University of Georgia, Athens, Georgia.

SWEENEY, B. W. 1984. Factors influencing life-history patterns of aquatic insects. Pages 56–100 *in* V. H. Resh and D. M. Rosenberg (editors). The ecology of aquatic insects. Praeger, New York.

TOWNSEND, C. R., A. G. HILDREW, AND J. FRANCIS. 1983. Community structure in some southern English streams: the influence of physicochemical factors. Freshwater Biology 13:521–544.

TOWNSEND, C. R., A. G. HILDREW, AND K. SCHOFIELD. 1987. Persistence of stream invertebrate communities in relation to environmental variability. Journal of Animal Ecology 56:597–613.

WINTERBOURN, M. J., AND K. J. COLLIER. 1987. Distribution of benthic invertebrates in acid, brown water streams in the South Island of New Zealand. Hydrobiologia 153:277–286.

WOLDA, H., AND E. BROADHEAD. 1985. Seasonality of Psocoptera in two tropical forests in Panama. Journal of Animal Ecology 54:519–560.

WOLDA, H., AND R. W. FLOWERS. 1985. Seasonality and diversity of mayfly adults (Ephemeroptera) in a 'non-seasonal' environment. Biotropica 17:330–335.

WOOD, S. J. 1999. Chemical tracing of geothermally modified interbasin transfer at La Selva Biological Station, Costa Rica. MS Thesis, Florida International University. Miami, Florida.

YOUNT, J. D., AND G. J. NIEMI (EDITORS). 1990. Recovery of lotic communities and ecosystems following disturbance: theory and application. Environmental Management 14:515–762.

Received: 15 October 2004
Accepted: 11 July 2005

APPENDIX 1. Annual density (no./m^2) for all taxa found in all study streams.

Taxon	Arboleda	Sura-30	Saltito	Salto	Sura-60	Piper
Ephemeroptera						
Baetidae	39.30	39.30	13.10	4.37	21.83	4.37
Stenonema	0.00	4.37	13.10	0.00	4.37	0.00
Caenis	74.23	323.13	82.97	8.73	0.00	4.37
Farrodes	21.83	34.93	8.73	0.00	39.30	0.00
Thraulodes	266.37	21.83	0.00	0.00	56.77	0.00
Leptohyphes	100.43	144.10	61.13	39.3	48.03	21.83
Tricorythodes	0.00	17.47	56.77	8.73	8.73	0.00
Plecoptera						
Anacroneuria	4.37	4.37	0.00	0.00	4.37	0.00
Odonata						
Hetaerina	8.73	13.10	8.73	8.73	13.10	0.00
Heteragrion	0.00	0.00	4.37	0.00	17.47	0.00
Libellulidae	4.37	0.00	0.00	0.00	13.10	4.37
Coenagrionidae	30.57	26.20	30.57	8.73	30.57	4.37
Epigomphus	0.00	0.00	4.37	4.37	17.47	4.37
Phyllogomphoides	0.00	21.83	30.57	17.47	39.30	13.10
Agriogomphus	4.37	0.00	4.37	4.37	4.37	0.00
Coleoptera						
Elmidae larvae	61.13	323.13	122.27	78.60	148.47	39.30
Elmidae adults	4.37	0.00	0.00	4.37	0.00	4.37
Ptilodactylidae	0.00	13.10	0.00	0.00	0.00	0.00
Megaloptera						
Corydalidae	8.73	4.37	0.00	0.00	0.00	4.37
Trichoptera						
Calamoceratidae	0.00	0.00	0.00	0.00	4.37	0.00
Hydropsychidae	0.00	26.20	4.37	0.00	48.03	0.00
Leptoceridae	56.77	109.17	13.10	4.37	52.40	4.37
Philopotamidae	0.00	0.00	0.00	0.00	0.00	4.37
Polycentropodidae	4.37	17.47	4.37	0.00	8.73	0.00
Diptera						
Tipulidae	21.83	0.00	0.00	4.37	21.83	13.10
Simuliidae	0.00	0.00	0.00	4.37	0.00	0.00
Ceratopogonidae	152.83	209.60	113.53	122.27	275.10	113.53
Stratyomidae	0.00	0.00	0.00	4.37	4.37	4.37
Xestochironomus	218.33	218.33	152.83	305.67	510.90	104.80
Tanypodinae	659.37	510.90	772.90	541.47	2117.83	794.74
Other Chironomidae	1698.63	1392.97	2323.07	925.73	1969.37	1903.87

APPENDIX 2. Annual biomass (mg AFDM/m^2) for all taxa in all study streams.

Taxon	Arboleda	Sura-30	Saltito	Salto	Sura-60	Piper
Ephemeroptera						
Baetidae	2.30	0.93	1.07	0.29	1.27	0.07
Stenonema	0.00	8.18	5.47	0.00	0.22	0.00
Caenis	7.68	17.34	5.95	0.47	0.00	0.02
Farrodes	1.62	1.91	0.21	0.00	1.46	0.00
Thraulodes	11.71	0.59	0.00	0.00	2.65	0.00
Leptohyphes	5.94	4.25	0.83	0.81	1.64	0.36
Tricorythodes	0.00	0.94	2.33	1.83	0.02	0.00
Plecoptera						
Anacroneuria	0.13	10.55	0.00	0.00	4.00	0.00
Odonata						
Hetaerina	0.30	0.06	0.53	0.08	0.06	0.00
Heteragrion	0.00	0.00	6.56	0.00	18.53	0.00
Libellulidae	0.03	0.00	0.00	0.00	0.89	7.06
Coenagrionidae	14.49	5.96	5.54	4.59	15.25	6.56
Epigomphus	0.00	0.00	0.74	0.24	36.89	7.84
Phyllogomphoides	0.00	140.94	138.12	200.47	143.78	138.96
Agriogomphus	21.18	0.00	0.44	11.37	3.07	0.00
Coleoptera						
Elmidae larvae	20.76	146.44	34.81	18.67	31.35	12.99
Elmidae adults	0.21	0.00	0.00	0.21	0.00	0.03
Ptilodactylidae	0.00	57.63	0.00	0.00	0.00	0.00
Megaloptera						
Corydalidae	1.53	0.11	0.00	0.00	0.00	0.01
Trichoptera						
Calamoceratidae	0.00	0.00	0.00	0.00	25.99	0.00
Hydropsychidae	0.00	30.31	15.25	0.00	34.80	0.00
Leptoceridae	26.36	8.80	1.86	0.01	8.78	0.01
Philopotamidae	0.00	0.00	0.00	0.00	0.00	0.05
Polycentropodidae	0.06	0.11	0.06	0.00	0.34	0.00
Diptera						
Tipulidae	1.07	0.00	0.00	0.13	14.77	2.60
Simuliidae	0.00	0.00	0.00	0.34	0.00	0.00
Ceratopogonidae	13.34	14.89	8.22	5.22	19.32	10.38
Stratyomidae	0.00	0.00	0.00	0.07	0.07	0.22
Xestochironomus	21.24	35.78	19.73	26.63	55.51	12.51
Tanypodinae	6.97	5.50	9.24	6.63	14.99	5.57
Other Chironomidae	19.10	12.34	19.68	10.82	34.10	16.13