

Fast growth and turnover of chironomid assemblages in response to stream phosphorus levels in a tropical lowland landscape

Alonso Ramírez¹

Institute for Tropical Ecosystem Studies, University of Puerto Rico,
P.O. Box 21910, San Juan, Puerto Rico 00931

Catherine M. Pringle

Institute of Ecology, University of Georgia, Athens, Georgia 30602

Abstract

We studied the response of a dominant primary consumer, larval Chironomidae (Diptera), to phosphorus (via a microbial response) across eight detritus-based streams spanning a gradient in soluble reactive phosphorus (range 0.2–8.6 $\mu\text{mol L}^{-1}$) in a tropical landscape in Central America. We predicted that phosphorus would enhance food resources for larval Chironomidae and positively affect their production. A low-phosphorus stream was also experimentally enriched to isolate effects of phosphorus from other solutes present. We found considerable variation in daily growth rates (range 0.09–0.57 $\text{mg mg}^{-1} \text{d}^{-1}$) and annual biomass turnover rates (range 66–126 $\text{mg mg}^{-1} \text{yr}^{-1}$) among streams, both positively related to phosphorus levels. Larval biomass was replaced every 5 d under low-phosphorus and every 3.5 d under high-phosphorus conditions (including the experimentally phosphorus-enriched stream). Annual secondary production (range 793–9,346 $\text{mg m}^{-2} \text{yr}^{-1}$) was variable among streams and negatively related to benthic organic matter, potentially because of low dissolved oxygen. The increase in larval biomass turnover along the phosphorus gradient indicates that a gradient of increasing energy flow exists from detrital-based resources (e.g., fungi) to primary consumers. Larval chironomids matured more rapidly under high phosphorus conditions; this strategy results in (1) similar larval biomass among streams and (2) a potential gradient of increasing energy flow from primary consumers to upper trophic levels as phosphorus increases. Nutrient-enhanced turnover rate of primary consumers can occur without increases in secondary production in stream ecosystems.

The rate of energy flow from basal to upper trophic levels depends on the efficiency of primary consumers in consuming basal resources and making them available to secondary consumers (Cebrian 2004). Therefore, after basal resources (e.g., algae or microbes) are enhanced by nutrients, the response of primary consumers is critical in determining the magnitude of nutrient enrichment effects on ecosystems. Positive responses of primary consumers to nutrient enrichment have been found in detritus-based ecosystems. Studies of soil food webs indicate that nutrient enrichment (e.g., carbon, phosphorus, or nitrogen) can increase basal productivity as well as biomass of primary consumers (Chen and Wise 1997; Mikola and Setälä 1998) and even predators (Chen and Wise 1999). Although there is limited information on the response of insects to enrichment of detritus-based stream ecosystems (but *see* Cross 2004), previous studies have found increases in insect density as a result of nutrient enrichment. For example, nutrient additions to leaf packs

resulted in higher mass loss and higher invertebrate colonization, as compared to leaf packs incubated under ambient nutrient concentrations (Robinson and Gessner 2000; Rosemond et al. 2002). Although most previous studies have assessed consumer response to nutrients in terms of abundance and biomass, consumers can respond in other ways. Pearson and Connolly (2000) found that insects under enhanced nutrient levels had better physiological condition (e.g., more fat storage) than those enhanced under low nutrients. Similarly, Rosemond et al. (2001) found that primary consumers can increase their growth rates in response to increased levels of inorganic phosphorus. These studies show that primary consumers can respond to nutrients in more subtle, but equally important, ways than simply through increased abundance.

Here we study the response of primary consumer secondary production to a gradient of phosphorus levels in streams. We build on results from our previous studies, which examined streams draining a lowland tropical rainforest in Central America. These streams form a natural gradient in phosphorus concentrations (Pringle 1991), which creates a potential gradient in resources for basal trophic levels, because phosphorus is a major limiting nutrient in streams (e.g., Peterson et al. 1985). Experimental enrichment with phosphorus has been found to enhance productivity at several trophic levels in stream food webs (Peterson et al. 1985; Harvey et al. 1998). Previous studies in these same streams have shown that phosphorus concentrations positively affect microbial biomass and activity on leaf litter (Rosemond et

¹ Corresponding author (aramirez@ites.upr.edu).

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al. 2002; Ramírez et al. 2003). Therefore, if primary consumers in these streams can benefit from a microbial response to phosphorus, interstream differences in phosphorus may potentially translate into differences in secondary production of primary consumers.

In this study we assessed the secondary production of a detrital consumer (Chironomidae larvae) in eight streams that varied in phosphorus concentration and drained a tropical landscape in Costa Rica. We hypothesized that in phosphorus-rich streams, larval Chironomidae would grow faster and have higher biomass turnover rates and secondary production than in phosphorus-poor streams.

Materials and methods

Study site—The study streams are within La Selva Biological Station on the Caribbean slope of Costa Rica (10°26'N, 84°01'W). The reserve is adjacent to Braulio Carrillo National Park (area ca. 450 km²), which protects the watersheds of the study streams. La Selva is a tropical wet forest that receives almost 4,000 mm of rainfall a year, with a wet season (>400 mm month⁻¹) occurring from May to November (Sanford et al. 1994).

Geomorphological features of the La Selva landscape result in differential inputs of geothermally modified groundwater to some of the streams, modifying 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. The main signature of modified groundwater is a high solute concentration (e.g., phosphorus, sodium, and chloride; Pringle 1991). Dense riparian vegetation along streams results in light-limited algal communities (Pringle et al. 1986) and detritus-based food webs. Previous studies have shown that phosphorus-rich inputs of geothermally modified groundwater can enhance fungal biomass (Rosemond et al. 2002) as well as microbial activity (i.e., respiration rates; Ramírez et al. 2003) on leaf litter.

For this study we chose eight streams that differed in their inputs of geothermally modified groundwater and that therefore had different solute concentrations (Table 1). Streams formed a gradient in soluble reactive phosphorus (SRP) that ranged from 5 to 267 $\mu\text{g SRP L}^{-1}$. All streams were small (<third order), in close proximity to each other, and drained primary forest. One of the streams, the Carapa, a first-order stream draining into the Sura, was chosen to conduct a whole-stream phosphorus enrichment experiment (Table 1). Dominant substrates were detritus, silt, and clay, with boulders present in some sites. While larger streams at La Selva support diverse assemblages of fishes and shrimps, our study streams contain only a subset of those assemblages. For example, of the >40 fish species recorded at La Selva (Bussing 1994), approximately 10 are found in these study streams (Burcham 1988). In addition, we have found that fishes and shrimps do not appear to control insect assemblage structure in these streams (Ramírez and Pringle 2004).

Chironomidae biomass—Larval Chironomidae were sampled monthly in six study streams for 1 yr (January–December 1998). For the remaining two study streams (Carapa and

Table 1. Annual means and ranges (in parentheses) of major physicochemical variables in the study streams. N:P was calculated as $\text{NO}_3\text{-N}:\text{SRP}$. Experimental SRP is the phosphorus concentration ($\mu\text{g L}^{-1}$) in Carapa after it was enriched with phosphorus.*

	Arboleda	Sura-30	Saltillo-60	Salto-60	Sura-60	Piper	Saltillo-100	Carapa
Discharge ($\text{m}^3 \text{s}^{-1}$)	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)	0.01 (0.0002–0.04)	0.002 (0.0001–0.007)
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)	5.3 (3.6–6.4)	5.4 (3.6–6.4)
Temperature ($^{\circ}\text{C}$)	26 (25–26)	26 (25–27)	25 (25–26)	26 (25–27)	26 (25–26)	26 (25–26)	25 (23–26)	25 (23–26)
SRP ($\mu\text{g L}^{-1}$)	267.3 (190–450)	194.8 (127–288)	99.4 (36–225)	22.6 (15–42)	4.8 (1–20)	4.8 (1–15)	9.8 (<5–17)	6.2 (<5–17)
$\text{NO}_3\text{-N}$ ($\mu\text{g L}^{-1}$)	199.2 (150–247)	219.0 (193–242)	164.4 (125–218)	272.8 (195–470)	212.8 (181–267)	204.6 (183–256)	154.0 (74.5–257.8)	176.0 (131–220)
N:P ratio ($\text{NO}_3\text{-N}:\text{SRP}$)	1.7 (1.0–2.7)	2.5 (1.6–3.7)	3.7 (2.1–12.6)	26.8 (14–48)	97.8 (24–386)	94.8 (40–715)	34.8 (37–100)	62.9 (45–60)
CPOM (Kg AFDM m^{-2})	10.1 (2.9–15.9)	11.9 (1.9–34.5)	18.7 (7.4–42.7)	25.6 (8.4–53.1)	16.3 (2.4–48.5)	19.1 (5.1–45.2)	5.5 (1.8–7.2)	4.1 (2.9–5.6)
Cond. ($\mu\text{S s}^{-1}$)	342 (297–368)	203 (145–268)	146 (73–263)	43 (23–95)	21 (17–26)	23 (21–24)	21 (14.5–56.2)	19 (12.8–55.5)
O_2 litter (mg L^{-1})	4.6	3.9	4.1	1.1	5.4	3.1	3.8	6.1
O_2 water column	6.3	6.6	6.2	7.1	7.6	7.1	6.1	7.1
Experimental SRP								157.0 (90–390)

* SRP, soluble reactive phosphorus; CPOM, coarse particulate benthic organic matter; AFDM, ash-free dry mass.

Saltito-100), we used samples collected for 2 yr (from August 1997 to July 1999) to include 12 months of samples before and after the beginning of the phosphorus enrichment in the Carapa, which we began in July 1998. Saltito-100 was not enriched with phosphorus and served as a reference stream for the Carapa enrichment.

On each sampling date, three benthic core samples (0.006 m² each) were collected in runs in which leaves were the dominant substrate. The core was forced into the substrate, cutting through debris, up to 10 cm in depth. Samples were preserved in formalin (ca. 5%), and insects were removed from organic material using a dissecting microscope at $\times 10$ magnification. Chironomidae were divided into three groups: (1) the genus *Xestochironomus* (found mainly within woody debris); (2) the predator subfamily Tanypodinae; and (3) remaining larvae (mainly collector-gatherers from the subfamily Chironominae). In this study we present data from the last category only, which was dominated by collectors that are more likely to feed on the microbial-detritus complex.

Biomass was estimated by measuring the length of each individual to the closest 0.5 mm and applying a length-mass relationship (Benke et al. 1999). Coarse particulate benthic organic matter (CPOM) associated with each sample was separated, dried at 100°C for 24 h, and ashed at 500°C for 1 hr to determine ash-free dry mass (AFDM).

Phosphorus enrichment—We began the whole-stream phosphorus enrichment in the Carapa in July 1998, and this enrichment was continuously maintained during the entire study. We added phosphoric acid to increase phosphorus concentrations from background levels of $<5 \mu\text{g SRP L}^{-1}$ to $\sim 200 \mu\text{g SRP L}^{-1}$, a mean concentration for streams that receive geothermally modified groundwater inputs at La Selva (e.g., Pringle 1991). A Mariotte bottle was used to continuously add phosphoric acid, according to procedures described by Pringle and Triska (1997) for whole-stream nutrient manipulations. The concentration of phosphoric acid in the bottle and addition rates were adjusted biweekly based on stream discharge to maintain SRP enrichment near the target concentration. Nitrate ($\text{NO}_3\text{-N}$) concentration was measured monthly and SRP levels weekly during this 2-yr study. Nutrient concentrations were measured by collecting two filtered (0.45- μm Millipore filters) water samples from each stream. Samples were frozen until analysis at the University of Georgia. Nitrate ($\text{NO}_3\text{-N}$) and phosphorus (as SRP) concentrations were measured using continuous-flow colorimetry and an Alpkem RFA 300 colorimetric analyzer. The cadmium reduction and ascorbic acid methods were used for nitrate and SRP analyses, respectively (APHA 1992). Oxygen concentration was measured once at each stream and in two locations. First, oxygen was measured under the litter layer by placing the probe under the litter and moving it slowly and then in the water column at 50% water depth. Measurements were done with an YSI Model 58 dissolved oxygen meter.

Growth studies—Chironomid growth rates were measured in the laboratory using chambers (dimensions 8×10 cm) with 90-mm mesh windows that were placed in 12-liter acid-washed plastic tubs filled with stream water and maintained

aerated with air pumps. Stream water was collected the day that experiments were begun and filtered through a coarse filter to remove large organic particles.

Larval Chironomidae for the growth experiments were obtained by placing *Ficus* leaf packs in a nearby fourth-order stream (Sabalo), which was not included in the present study but which has a similar leaf litter insect fauna (Rosemond et al. 2002). Larvae were placed in cold water and measured to the nearest 0.5 mm, using a reference grid, to obtain initial size and biomass and were assigned to one of three size classes: <2 mm, 2–4 mm, and >4 mm. Groups of ca. 20 larvae of a particular size class were placed in each chamber. Thirty conditioned *Ficus insipida* leaf discs cut from leaves incubated in the source stream for 15 d before the experiment were used as food in each chamber. In addition, 30 unconditioned leaf disks were added to each chamber to provide unlimited carbon substrate during the study period. We used *F. insipida* leaves as a food resource because they are commonly consumed by larval Chironomidae in these streams (Rosemond et al. 2001). Instantaneous growth rates (IGR) for each size class and stream were estimated ($n = 4$ chambers) using the equation

$$\text{IGR} = (\ln W_f - \ln W_i)/t$$

where W_i and W_f are the initial and final biomass, respectively, and t is an incubation time of 3 d for our study (Huryn and Wallace 1986). The study streams experience only small changes in temperature throughout the year (Table 1); thus, we conducted only one rearing experiment for each stream. At the beginning of each experiment we collected a water sample for SRP analysis and measured pH, conductivity, and water and air temperature.

Secondary production and P:B ratios—The instantaneous growth method (Benke 1993) was used to determine Chironomidae secondary production. Secondary production was estimated for each size class (i.e., <2 mm, 2–4 mm, and >4 mm) every month by multiplying the average biomass for two consecutive months by the size class-specific growth rate for the stream (Benke 1993). Data for streams along the phosphorus gradient are presented as annual secondary production ($\text{mg AFDM m}^{-2} \text{ yr}^{-1}$) for each stream. Annual turnover rates of biomass (P:B ratios) for Chironomidae were estimated by dividing annual secondary production by mean monthly biomass (Benke 1993). In the phosphorus enrichment experiment, secondary production and P:B ratios for Carapa and Saltito-100 were calculated by month as above but were presented as monthly means (e.g., for production: $\text{mg AFDM m}^{-2} \text{ month}^{-1}$) rather than annual means. Secondary production during the pre-enrichment period in Carapa and Saltito-100 was calculated using growth rates for Saltito-100, as both streams had similar nutrient concentrations and water temperature during that time period (Table 1).

Statistical analyses—Multiple regressions of Chironomidae biomass, growth rates, production, and P:B ratios were conducted using SRP, pH, nitrogen:phosphorus (N:P), CPOM, and discharge (as an indicator of stream size) as independent variables. Monthly data from the phosphorus

Table 2. Growth rates for each size class, biomass, secondary production, and turnover ratios of larval Chironomidae. Streams are ordered by decreasing soluble reactive phosphorus (SRP). Saltito-100a and b refer to the period before and after the enrichment in Carapa. Growth rates in Carapa were determined only during enrichment. SE is the standard error of the calculation and for production it is based on 12 monthly estimates before and after the enrichment.

	Growth rates per size class						Biomass (mg m ⁻²)	SE	Production (mg m ⁻² yr ⁻¹)	SE	P : B (yr)
	<2 mm (mg mg ⁻¹ d ⁻¹)	SE	2–4 mm (mg mg ⁻¹ d ⁻¹)	SE	>4 mm (mg mg ⁻¹ d ⁻¹)	SE					
Arboleda	0.565	0.013	0.377	0.031	0.119	0.009	19.3	5.8	2,283.4		118.4
Sura-30	0.494	0.023	0.376	0.024	0.137	0.021	11.8	3.7	1,220.0		103.3
Saltito-60	0.503	0.042	0.361	0.045	0.097	0.018	19.4	5.5	1,818.4		93.8
Salto-60	0.401	0.042	0.279	0.033	0.155	0.015	10.0	3.4	793.1		79.0
Sura-60	0.495	0.008	0.302	0.040	0.119	0.007	33.9	14.7	2,227.9		65.7
Piper	0.409	0.012	0.344	0.054	0.139	0.022	21.4	7.5	1,861.1		87.0
Saltito-100a							38.4	8.7	4,013.1		104.4
Saltito-100b	0.478	0.006	0.318	0.078	0.158	0.002	64.4	9.1	6,733.6		104.6
Carapa							86.1	27.0	9,345.8	157.0	108.5
Carapa+P	0.472	0.024	0.442	0.036	0.089	0.003	57.2	16.0	7,223.1	107.0	126.4

enrichment stream were analyzed using one-way analysis of variance (ANOVA) with before and after enrichment as treatments. Monthly production in Carapa and Saltito-100 was averaged to obtain mean monthly production and the respective standard deviation before and after the phosphorus enrichment to Carapa. The results of this experiment should be interpreted with caution, as the experiment was not replicated (i.e., phosphorus was added to only one stream). All analyses were conducted in JMP (Version 4.0.4, SAS Institute).

Results

Chironomidae growth—The mixture of Chironomidae individuals used in growth experiments was clearly composed of different species. The subfamily Chironominae was dominant and most individuals had red bodies, indicating the presence of hemoglobin.

The three size classes used in the growth experiment had large and significant differences in their growth rates (Table 2). Small individuals had significantly faster growth rates than large ones (ANOVA, $F_{2,20} = 112.7$, $p < 0.001$). Mean growth rate (mg mg⁻¹ d⁻¹), combining all streams, for individuals in the size class of <2 mm was 0.48 (standard error of the mean [SE]: 0.02), for individuals from 2–4 mm was 0.35 (SE: 0.02), and for individuals >4 mm was 0.13 (SE: 0.01).

Chironomidae growth rates in the two smallest size classes were positively related to SRP (linear regressions, <2 mm: $r^2 = 0.54$, $p = 0.04$; and 2–4 mm: $r^2 = 0.53$, $p = 0.04$). Growth rates in the largest size class (>4 mm) were not related to SRP. Temperature and pH did not vary greatly during the rearing trials and were not related to growth rates. Temperature in the rearing chambers ranged from 25°C to 26°C and pH from 6 to 7.

Chironomidae biomass, production, and P : B—Mean annual Chironomidae biomass was variable among streams, with Saltito-100 and Carapa showing the highest biomass (Table 2). Multiple regression analysis using pH, SRP, N : P,

CPOM, and discharge indicated that CPOM and SRP were negatively related to biomass (CPOM: $r^2 = -0.59$, $p < 0.01$; SRP: $r^2 = -0.77$, $p = 0.05$).

Size class distribution of larval Chironomidae abundance was similar among streams (Fig. 1). The largest percent of individuals were in the 2-mm size class and most were smaller than 4 mm in length. Size class distribution did not appear to be related to phosphorus or stream size (Fig. 1). In terms of biomass, the two smallest size classes accounted for over 70% of the total biomass. Annual secondary production had a pattern similar to that of biomass (Table 2). Annual production was highest in Saltito-100 and Carapa, where production was two to three times higher than in the remaining streams (Table 2). Multiple regression analysis also resulted in CPOM and SRP entering the model, but only CPOM was significant ($r^2 = -0.66$, $p < 0.01$).

Biomass turnover rates (P : B) ranged from 66 in Sura-60 to 126 in Carapa during phosphorus enrichment (Table 2). Multiple regression analysis showed that CPOM and SRP explained variation among streams in Chironomidae P : B ratios (CPOM $r^2 = -0.56$, $p = 0.01$; SRP: $r^2 = 0.81$, $p = 0.02$). In this case, CPOM was negatively related and SPR was positively related to Chironomidae P : B ratios.

The one-time survey of oxygen levels measured 5 cm under the litter showed a clear negative relationship between CPOM and oxygen ($r^2 = -0.58$, $p = 0.02$). Oxygen under the leaf litter ranged from <2 to <6 mg O₂ L⁻¹, while water column levels ranged from 6 to 7.9 mg O₂ L⁻¹ (Table 1).

Phosphorus enrichment—The whole-stream phosphorus addition to Carapa increased SRP concentrations from a background of <5 to ~200 µg L⁻¹ (monthly range 150–250 µg L⁻¹). Phosphorus enrichment to Carapa did not result in increased Chironomidae biomass or monthly secondary production (Fig. 2A,B). Chironomidae biomass and production were, in fact, highest during the year before the enrichment rather than during phosphorus enrichment (Fig. 2A,B). Although we did not measure discharge continuously, monthly measurements had a similar range of values during the year before and after the enrichment (ranging from <0.3 to 4 L

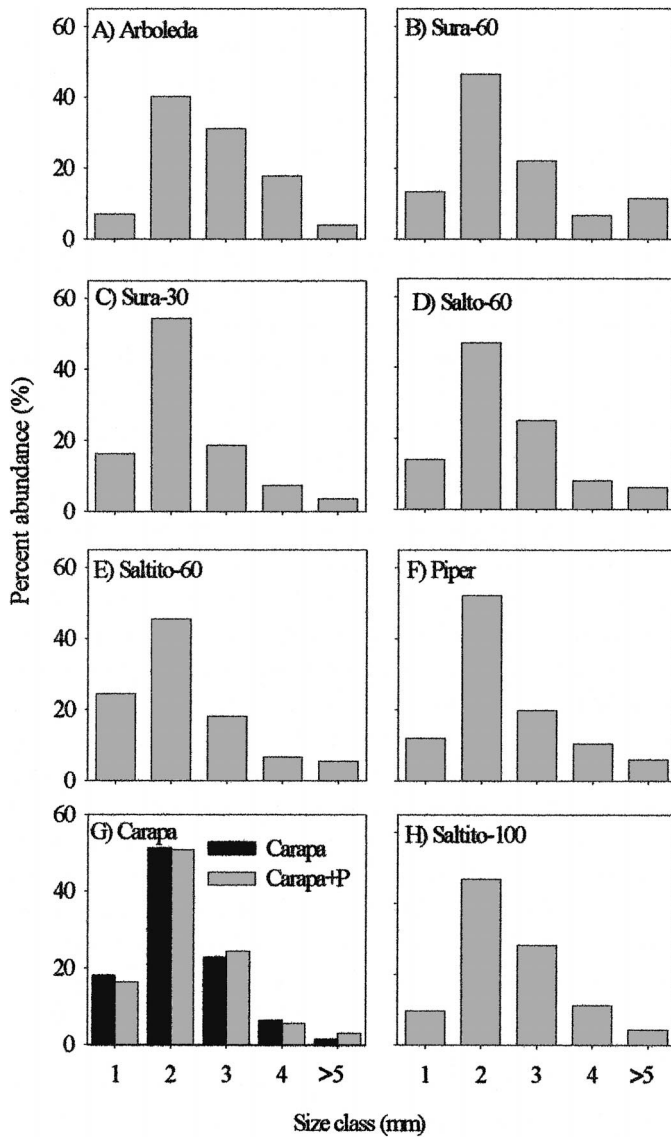


Fig. 1. Percent abundance of larval Chironomidae in each size class and stream. In the Carapa stream (G), size class distribution is shown for before and after the beginning of the phosphorus enrichment.

s^{-1}). In contrast, monthly P:B ratios in Carapa increased significantly during the year of phosphorus enrichment (ANOVA, $F_{3,40} = 11.9$, $p < 0.0001$; Fig. 2C). Saltito-100 contrasted with Carapa in that biomass and production were higher during the second year of study than during the first (Fig. 2A,B). P:B ratios in Saltito-100 were similar to those found in Carapa during the year before the enrichment but were significantly different from those found in Carapa during the enrichment year (Fig. 2C).

Discussion

Insect growth and phosphorus—Small and middle-sized larval Chironomidae in streams with high P exhibited faster growth rates than larval Chironomidae in low-P streams. We

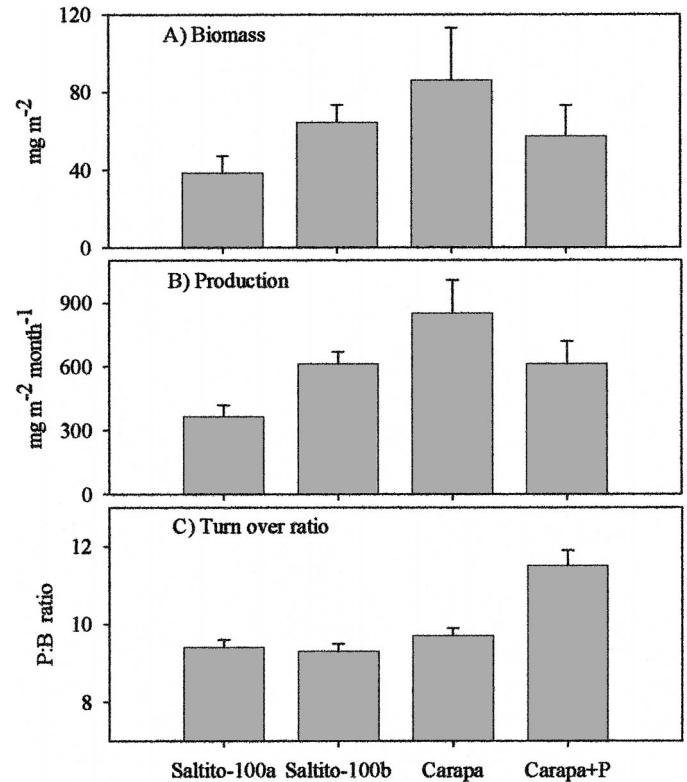


Fig. 2. Average monthly biomass (mg m^{-2}), secondary production ($\text{mg m}^{-2} \text{ month}^{-1}$), and turnover ratio (per month) of larval Chironomidae in Saltito-100 (reference stream) and Carapa (enriched stream). Saltito-100a and Carapa represent conditions before enrichment and Saltito-100b and Carapa+P represent conditions during the period of enrichment in Carapa. Each bar represents the mean of 12 months ($\pm \text{SE}$).

also observed faster growth rates of larval Chironomidae in the stream that was artificially enriched with phosphate (i.e., the Carapa), supporting our hypothesis that phosphorus was a stimulating factor in solute-rich streams. Although a positive response to phosphorus was not observed for the largest Chironomidae size class, this size class accounted for less than 30% of the total biomass. These results indicate a positive effect of phosphorus on the food resources of larval Chironomidae, which in our case were the microbes colonizing leaf litter (Ramírez et al. 2003). Algal communities at the study streams are light limited, with low standing-crop and production rates (Ramírez unpubl. data).

Companion studies at La Selva have clearly demonstrated that phosphorus has a large positive effect on microbial communities on leaf litter. Along a similar phosphorus gradient, both microbial biomass (measured as ergosterol concentrations; Rosemond et al. 2002) and microbial activity (measured as respiration rate; Ramírez et al. 2003) increased with phosphorus. Therefore, larval Chironomidae in our study streams were likely experiencing a gradient in food resources (i.e., microbial biomass) as water phosphorus levels increased. Similarly, Rosemond et al. (2001) found faster growth rates of larval Chironomidae feeding on leaf material and associated microbes under high- versus low-phosphorus conditions at La Selva. Studies in other regions have re-

ported positive responses of microbial communities on leaf litter to water nutrients (e.g., Caraco et al. 1998; Suberkropp 1998) and subsequent positive insect responses to changes in microbial biomass (e.g., Cummins and Klug 1979; Pearson and Connolly 2000). Under laboratory conditions, we showed that phosphorus levels in the water can enhance growth rates of small-sized primary consumers in detritus-based tropical streams.

Measured growth rates of larval Chironomidae in our study are faster than predicted using information from temperate streams, but not as high as those reported for subtropical and other tropical studies. In our study, the smallest larval size class had the fastest growth rates—with a mean of $0.48 \text{ mg mg}^{-1} \text{ d}^{-1}$. While this rate is high compared to predicted values generated from models developed in temperate regions (e.g., Huryn and Wallace 2000), it is lower than the predicted $0.60 \text{ mg mg}^{-1} \text{ d}^{-1}$ using equations in Rosemond et al. (2001) or the $0.60\text{--}0.90 \text{ mg mg}^{-1} \text{ d}^{-1}$ predicted by equations in Hauer and Benke (1991) for a subtropical river. We consider our measured growth rates to be a good estimate of larval Chironomidae growth because they predict a larval life span that is appropriate for our geographic location. Using the mean growth rates that we found for each size class and applying length–mass equations, Chironomidae would be expected to have a larval life span ranging from 23 to 29 d, assuming a hatching size of 0.5 mm and a maximum larval size of 9 mm. This estimation is in general agreement with results reported by Jackson and Sweeney (1995), who obtained a median larval development time of 17–71 d for 13 species of the subfamily Chironominae inhabiting streams in Costa Rica.

Biomass, production, and phosphorus—In contrast with our findings for growth rates, Chironomidae assemblages had variable annual biomass and secondary production among streams. Larval biomass and production were negatively related to CPOM and phosphorus levels in the water. These results conflict with our expectation of a positive effect of phosphorus levels on larval production. Secondary production has two main components: growth and biomass. While we found a positive phosphorus effect on chironomid growth rates, larval biomass was negatively related to CPOM and phosphorus, and it was the reason for the lack of a positive relationship between phosphorus and production. In larger lowland tropical streams, fish predation plays an important role in controlling insect assemblage abundance and biomass (e.g., Pringle and Hamazaki 1998). However, fishes and shrimps in our low-order study streams appear to have negligible effects on insects (Ramírez and Pringle 2004), so they do not explain the lack of differences among streams in insect biomass. In contrast to our results, two previous studies at La Selva have reported increases in insect biomass with phosphorus (Rosemond et al. 2002; Ramírez and Pringle 2004). Both studies were run for a short length of time (i.e., <30 d) and used artificial leaf packs made with a single leaf species as substrate for insect colonization. The use of a homogeneous substrate might facilitate the observation of interstream differences in insect assemblages by potentially reducing variability among streams and could explain the difference in results among studies. Ramírez and

Pringle (2004) also reported the response of insects to phosphorus to be more variable when studied in mixed leaf litter occurring naturally on the stream bottom.

Insect biomass and production have been positively related to the amount of benthic organic matter available in streams (Wallace et al. 1999). The negative relationship we observed could be related to the low oxygen concentrations found under the litter layer. Most larval Chironomidae in the study streams have red bodies (e.g., presence of hemoglobin), indicating adaptations to low-oxygen conditions. Low oxygen could be related to high microbial respiration rates measured even in low-phosphorus streams (Ramírez et al. 2003). Therefore, the observed negative relationship between Chironomidae biomass and production and CPOM could be the result of oxygen conditions within the litter layer and not the amount of benthic litter per se.

Secondary production of larval Chironomidae in our study streams was within the lower range of production values reported in the literature. Tokeshi (1995) considered production values of around $8.0 \text{ g m}^{-2} \text{ yr}^{-1}$ to be moderate for lotic ecosystems. Our estimates ranged from 0.8 to $9.0 \text{ g m}^{-2} \text{ yr}^{-1}$ and are therefore considered low to moderate for lotic ecosystems. Although annual secondary production is low, values are 7 to 85 times higher than those previously reported for a Neotropical stream (Ramírez and Pringle 1998). Ramírez and Pringle (1998) reported secondary production values for Chironomidae of $\sim 0.1 \text{ g m}^{-2} \text{ yr}^{-1}$ for a larger fourth-order stream at La Selva Biological Station that is low in phosphorus (SRP $< 20 \mu\text{g L}^{-1}$). The large difference between the two studies could be a result of nutrient stimulation or intense predation in the larger stream, which is characterized by diverse and abundant predaceous fishes and shrimps (Pringle and Hamazaki 1998; Rosemond et al. 2001).

P : B ratios and phosphorus—Annual P : B ratios of insect assemblages are a measure of biomass turnover in the ecosystem. They indicate the number of times a population replaces its own biomass during a year, a phenomenon mainly controlled by factors affecting individual growth (e.g., temperature, food resources, and life history strategy; Benke 1993). Therefore, it is not entirely surprising to find that larval Chironomidae P : B ratios were positively related to phosphorus in our study streams. We found Chironomidae P : B ratios increasing from 66 in low-phosphorus streams to 118 in Arboleda, the stream with the highest phosphorus concentration (Table 2). These values are considered high, as P : B ratios for Chironomidae are known to range from <1 to 258 (Benke 1998; Huryn and Wallace 2000). These data indicate that larval Chironomidae assemblage biomass was replaced every 5 d under low-phosphorus conditions and every 3.5 d under high-phosphorus conditions. A previous study in a larger stream at La Selva Biological Station reported P : B ratios from 69 to 103 (Ramírez and Pringle 1998), similar to the range reported here. In addition, Jackson and Sweeney (1995) found populations of *Polypedilum epomis* (Chironomidae) from Costa Rica to have larval life spans of around 22 d, which indicates a P : B of 106 (as calculated by Huryn and Wallace [2000]). Although the amount of information about growth and turnover ratios of

aquatic insects in tropical streams is still limited, available studies indicate that Chironomidae have moderate to high growth rates and turnover rates. Extremely high values have been found in other rivers (e.g., Benke 1998), indicating that water temperature is only one of several factors controlling growth and turnover rates of aquatic insects (Huryn and Wallace 2000).

P:B ratios are good indicators of the amount of energy that flows through a particular compartment of a food web (Huryn and Wallace 2000). Chironomidae assemblages are important links in detritus-based food webs; they are small enough to consume microbes and are also an important prey item in the diet of invertebrate and vertebrate consumers (Benke and Wallace 1997; Schmid-Araya and Schmid 2000). Our study shows that larval Chironomidae in phosphorus-rich streams have higher turnover rates than assemblages in phosphorus-poor streams. Fast biomass turnover by primary consumers assures a constant food supply to predators. In our case, the lack of fish effects on insects (Ramírez and Pringle 1998) indicates that riparian predators (e.g., spiders) could potentially benefit from a constant supply of emerging aquatic insects.

High turnover rates in our study streams indicate that larval Chironomidae might take advantage of potentially enhanced food resources under high-phosphorus conditions to reach metamorphosis in a short time. Although we used a community approach, if short life history is a dominant characteristic among chironomids, they would be fit to survive in harsh environments, where prolonged larval life might not be favored. Evidence indicates that warm-water streams that undergo frequent disturbance, such as those studied here (Ramírez and Pringle 1998), have insect faunas dominated by species with short life cycles and fast growth rates (Jackson and Fisher 1986; Benke 1998). Huryn and Wallace (2000) reviewed the life history and production patterns of aquatic insects in many environments and hypothesized that rapid development is a strategy for organisms in environments in which food supplies are abundant and disturbance frequent.

Landscape variation—Most of our knowledge of growth and production of stream insects comes from single-reach studies; we know little about the spatial variation on these factors at the landscape scale. Studies that have assessed insect growth and production among streams show a significant degree of variation among streams (e.g., Huryn 1990). Much of this variation has been related to differences in temperature among streams. Accordingly, models predicting annual secondary production, annual P:B, and growth rates are mainly based on temperature (e.g., Huryn 1990; Benke 1993). Our results also showed considerable variation in larval Chironomidae growth and in annual turnover rates at the landscape scale. However, our study streams do not differ in their temperature regimes, and a large percent of the variation can be explained by differences in phosphorus levels among streams and by stream size. Surface–subsurface interactions can have important effects on the production dynamics of primary consumers through changes in water nutrient concentrations in the tropical lowland streams studied here. These results highlight the importance of understand-

ing the factors affecting consumers in tropical streams and in detritus-based ecosystems in general. We show that primary consumers can respond to increases in phosphorus and that they can potentially move significant amounts of energy to upper trophic levels, not by producing more biomass but by replacing it at high rates.

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