

Invertebrate drift along a longitudinal gradient in a Neotropical stream in Serra do Cipó National Park, Brazil

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Received 1 March 2004; in revised form 19 July 2004; accepted 14 September 2004

Key words: diversity assessment, drift, invertebrates, longitudinal gradients, neotropical stream

Abstract

The diversity and composition of drift invertebrate assemblages were evaluated along a longitudinal gradient of an altitudinal stream in southeastern Brazil. The main goal of this study was to evaluate the influence of seasonality, stream order, and some abiotic factors on invertebrate drift and the use of drifting invertebrate assemblages to assess aquatic invertebrate diversity. Drift samples were collected over a 24 h period using nets (open area of 0.08 m²; mesh 0.250 mm), partially submerged (60%) in the water column. Taxonomic richness, Pielou evenness (J), Shannon–Wiener diversity (H'), and total density of drift invertebrate assemblages were used in unpaired *t*-tests, Kruskal–Wallis and stepwise multiple regression analysis. The results showed a high taxonomic richness of aquatic invertebrates, with 91 *taxa* found. Chironomidae and Ephemeroptera represented together c. 80% of the total density of drift organisms. The drift approach allowed the collection of new and rare *taxa*, besides the knowledge of pupae stage of several chironomid genera. Significant differences in the taxonomic richness and diversity of drift invertebrate assemblages were found between the rainy and dry periods, indicating a significant influence of seasonality. An increase in water flow and electrical conductivity were associated with the increase in the taxonomic richness and diversity in the rainy period. No significant differences were found among the other abiotic variables among the stream orders.

Introduction

Lotic ecosystems present unidirectional and continuum water movement responsible for the maintenance of several processes, such as organic matter transport, sediment deposition and formation of longitudinal gradients within drainage basins (Vannote et al., 1980; Allan, 1995). Those factors influence directly or indirectly the resident biological communities (Ward et al., 1995). This fluvial continuity allows the dispersion of immature stages of aquatic invertebrates, and thus, the colonization of river reaches downstream from their original habitats. This dispersion process occurs through the downstream transport of these invertebrates (by means of passive or active enter

in the water column), in a phenomenon known as drift (Brittain & Eikeland, 1988).

Drift of invertebrates is a common phenomenon in aquatic ecosystems (Allan, 1995), and can be the result of various factors, such as: (1) increased flow and water velocity, leading to a dislodgment of the resident benthic fauna caused by physical disturbance of the substrate (Poff & Ward, 1991); (2) presence of benthic predators, causing the entry of benthic prey in the water column for predator avoidance (Huhta et al., 2000); (3) modifications in water physical and chemical characteristics (Brittain & Eikeland, 1988); and (4) redistribution of invertebrates populations in function of competitive pressures (Brittain & Eikeland, 1988).

Several authors have reported that there is not a pattern of taxonomic composition, and the most common organisms found in drift are derived from the benthic communities and belong to immature forms of Chironomidae and Simuliidae (Diptera), Trichoptera, Ephemeroptera and Plecoptera (Matthaei et al., 1998; Pringle & Ramirez, 1998). Various studies have focused on the taxonomic composition and determinant factors of invertebrate drift in the temperate region, but those concerning tropical regions are scarce (e.g., Ramirez & Pringle, 1998, 2001).

The major aim of this study was to evaluate the diversity and composition of drift invertebrate assemblages along a longitudinal gradient in a Neotropical stream, in southeastern Brazil. The following questions were addressed: (1) Are there differences in the diversity and composition of drift invertebrate assemblages among the river reaches (2nd up to 5th order)? (2) Does the seasonality (rainy and dry periods) influence the diversity and composition of these assemblages? (3) What are the main abiotic factors related to invertebrate drift? (4) Can the evaluation of drifting invertebrate assemblages be used as tool in the assessment of aquatic invertebrate diversity?

Methods

Study area

Serra do Cipó is located in the central part of the Minas Gerais State (19°–20° S; 43°–44° W), dividing two important watersheds: São Francisco River and Doce River. The vegetation is composed of savanna (locally called “cerrado”) in the lower altitudes (from 700 m a.s.l. up to 1000 m a.s.l.), rock fields (locally called “campos rupestres”) in the highest zone (above 1000 m a.s.l. up to the highest elevations, at 1860 m a.s.l.), and riparian forest in the humid valleys along the rivers. The typical soil in the region is latosoil, deep and low fertility (Giulietti et al., 1987). The climate is classified as “Cwb” (Köppen, 1931), with rainy summers and dry winters, and an annual median of precipitation about 1500 mm (Galvão & Nimer, 1965). The Serra do Cipó National Park is located in the southern part of

Espinhaço Cordillera, enclosing an area of about 33.800 ha and 154 km perimeter.

Samples were collected during the dry (June and August) and rainy (October and December) periods of 2001, from 2nd to 5th order river reaches of Indaiá Stream. This stream belongs to the headwaters of the Doce River basin (Fig. 1), situated inside the limits of the Serra do Cipó National Park and is practically in “pristine” condition (Galdean et al., 2000). Indaiá Stream has good water quality (dissolved oxygen of 9.0–10.7 mg/l, >90% saturation; specific conductivity <15.0 μ S/cm; total alkalinity <10.0 μ Eq/CO₂; low concentration of total and dissolved nutrients (total-P: 1.32 up to 27.95 μ g/l; total-N: 145.1 up to 589.9 μ g/l; P-PO₄ <10 μ g/l; N-NH₄⁺ <970 μ g/l) and high diversity and density of benthic macroinvertebrates (H' 3.36–3.66; ~60,000 ind/m²) (Galdean et al., 2000). This stream has bedrock along its extension, with gravel/sand and fine/coarse particulate organic matter deposits, presence of filamentous algae and small macrophytes in the pools; mosses (*Andreaea* – *Andreaeaceae*), angiosperms (*Eriocaulaceae*) and algae biofilm over bedrock in rapid reaches. This situation is clearly observed on the 2nd and 5th order reaches, while in the 3rd and 4th orders, the streambed is covered by cobbles and pebbles. The riparian vegetation has an open canopy in the 2nd and 5th orders reaches, being composed mainly by rock field elements (e.g., *Vellozia* spp.). On the other hand, in the 3rd and 4th reaches the canopy covers the river bed since a forest is formed and composed mainly by *Miconia chartacea* Triana (*Melastomataceae*) and *Podocarpus sellowii* Klotzsch ex Endl (*Podocarpaceae*).

Physical and chemical variables in the water column

The following variables were measured *in situ* using a multiprobe HORIBA®: temperature (°C), dissolved oxygen (mg/l), specific conductivity (μ S/cm), pH and water turbidity (NTU). Water current velocity (m/s) was measured with a Global-water fluxometer before and after net fixing, and flow (m³/s) was calculated by multiplying the net submerged area, water current velocity and total sampling time.

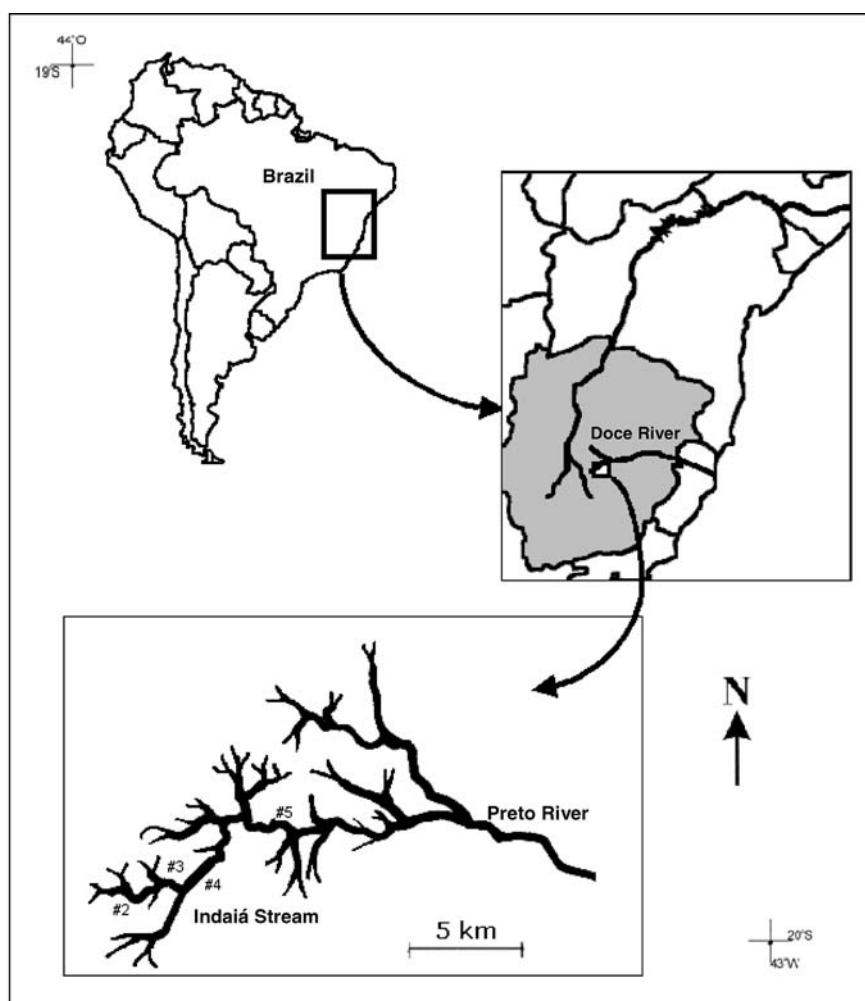


Figure 1. Map of the study area.

Drift samples

The drift samples were collected using nets (open area of 0.08 m²; mesh 0.250 mm), partially submerged (60%) in the water column. One net was set in each studied reach, and removed after a 24-h period.

The entire collected material was fixed in 10% formalin, and washed under 0.250 mm sieve in the laboratory, sorted and the identified organisms (Wiggins, 1977; Merritt & Cummins, 1988; Pérez, 1988; Dominguez et al., 1992) deposited in the Reference Collection of Benthic Macroinvertebrates of the Institute of Biological Sciences in the Federal University of Minas Gerais, according to

Callisto et al. (1998). The Chironomidae larvae (Diptera) were identified according to Wiederholm (1983), Cranston (2000b), Epler (2001), and Trivinho-Strixino & Strixino (1995), using an optical microscope (400 ×), after being previously treated with 10% lactophenol solution (Wiederholm, 1983).

Data analysis

Taxonomic richness was estimated as the total number of different taxa found in each sample. The assemblage diversity and evenness were calculated using the Shannon–Wiener and Pielou indices, respectively (Magurran, 1991). The

Kruskal–Wallis test was applied to test for differences in the diversity, taxonomic richness, evenness and total density of the drift invertebrate assemblages.

Differences in the composition and diversity of the drift invertebrate assemblages were evaluated through *t*-tests, using taxonomic richness, diversity, evenness and total density of invertebrates as dependent variables. The same test was used to evaluate seasonal differences in physical and chemical variables. A stepwise multiple regression was performed in order to determinate the main variables related to invertebrate drift. The statistical program used in all analyses was Statistica (version 5.0, Statsoft 1997).

Results

Abiotic features

The studied stream reaches were characterized by low depths (0.05–0.28 m, in the dry period and 0.09–0.35 m, in the rainy period), slightly acid waters, with the pH varying between 5.31–6.58 (dry period) and 3.87–4.28 (rainy period). High concentrations of dissolved oxygen (6.67–9.71 mg/l, in the dry period and 6.96–9.82 mg/l, in the rainy period) and low values of specific conductivity ($< 20.0 \mu\text{S}/\text{cm}$ in the dry period and $< 40.0 \mu\text{S}/\text{cm}$ in the rainy period) were also found. The temperature was significantly different between the two sampling periods ($t_{(14; 0.05)} = 3.3333$; $p < 0.005$), varying between 14.09–19.5 °C in the dry period and 17.0–23.31 °C in the rainy period. Regarding the water flux, strong seasonal differences were found in relation to water current velocity ($t_{(14; 0.05)} = 4.6440$; $p < 0.0004$) and water flow ($t_{(14; 0.05)} = 6.3173$; $p < 0.00002$), with higher values of both variables in the rainy period.

Drift invertebrates

The drift invertebrate assemblages along the longitudinal gradient in Indaiá Stream were basically composed of aquatic insects (the raw data are available from the authors on request). Among the 91 identified *taxa*, Chironomidae–Diptera (33 genera), Trichoptera (18 genera) and Ephemero-

ptera (13 genera) showed the highest taxonomic richness values. Besides that, 8 Heteroptera genera, 5 families of Coleoptera, 2 families of Plecoptera and 6 Diptera families were also identified.

Comparing with previous benthic collections in the study area (Galdean et al., 1999, 2000, 2001), several *taxa* identified in this study represent new records for the local biodiversity (e.g., within the chironomids, 15 new genera were added).

Chironomidae and Ephemeroptera represented together c. 80% of the total density of drift organisms. Among the other *taxa*, the Trichoptera (7.95%), Heteroptera (3.81%) and Simuliidae–Diptera (3.81%) also presented high densities. Regarding the longitudinal distribution of drift invertebrates, the chironomids predominated in all river reaches in both periods, except by the 2nd order in the dry season, that was dominated by mayfly nymphs, mainly baetids (Fig. 2).

Variations in taxonomic richness, evenness and invertebrate diversity were observed along the longitudinal gradient in Indaiá Stream (Fig. 3). The taxonomic richness and invertebrate diversity, represented by the Shannon–Wiener diversity index, showed a marked difference between the sampling seasons, with higher values being found in the rainy season, especially in October (Fig. 3). Taxonomic richness varied between one *taxon* (2nd order reach, dry period, June) and 64 *taxa* (3rd order reach, rainy period, October). Invertebrate diversity index varied between $H' = 0$ (2nd order reach, dry period, June), and $H' = 3.361$ (5th order reach, October).

On the other hand, density values showed little variations between the sampling seasons, except by the 2nd order reach, which presented a very low value in June, followed by a peak in August (Fig. 3). The densities varied between 1276 ind/cm³ (2nd order reach, dry period, June) up to 162,490 ind/cm³ (2nd order reach, dry period, June).

Determinant factors of diversity and total density of drift invertebrates

Seasonality strongly influenced the diversity of the drift invertebrate assemblages along the longitudinal gradient in Indaiá Stream. Significant differences were found between the dry and rainy periods in the taxonomic richness ($t_{(14; 0.05)} = 3.724721$; $p < 0.003$) and Shannon–Wiener diversity

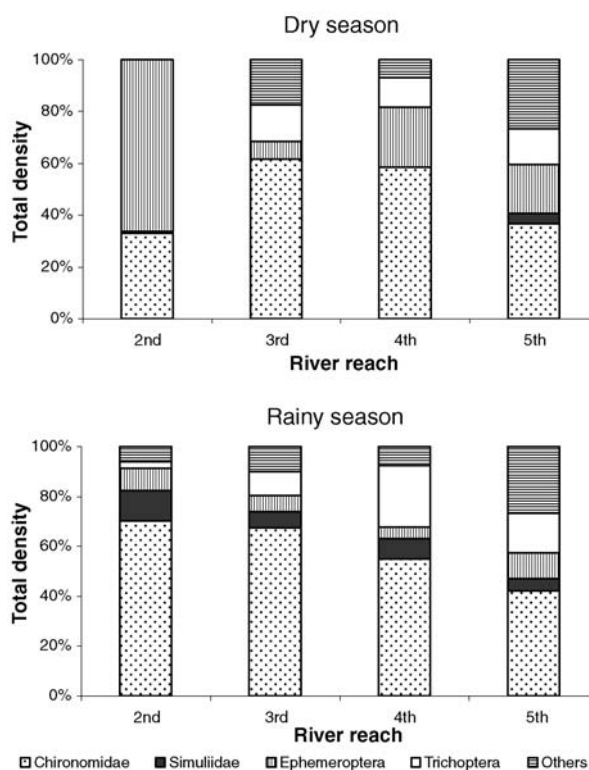


Figure 2. Invertebrate drift composition (%) in dry and rainy seasons along the longitudinal gradient in Indaiá Stream, Serra do Cipó National Park.

index ($t_{(14; 0.05)} = 2.05453$; $p < 0.05$), with higher values found in the rainy period. However, no significant differences were found in the Pielou evenness values ($t_{(14; 0.05)} = 0.517377$; $p = 0.61297$) and total density values ($t_{(14; 0.05)} = 1.415617$; $p = 0.17875$).

Among the studied variables the water flow ($\beta = 0.52039$; $p < 0.02$) and the specific conductivity ($\beta = 0.43259$; $p < 0.04$) were the main factors that influenced the taxonomic richness of drift invertebrates. Significant positive relations were found between these variables ($R^2 = 0.7572$; $p < 0.0007$), indicating that an increase in water flow and specific conductivity was associated with an increase in taxonomic richness of drift invertebrates (Fig. 4). However, only the water flow ($\beta = 0.48455$; $p < 0.05$) affected the diversity of drift invertebrates. Significant positive relations between these two variables were found ($R^2 = 0.23479$; $p < 0.05$), being observed only a slight increase in the Shannon–Wiener diversity

index values with the increase of water flow (Fig. 4). No significant relations were found between the values of total density and Pielou evenness and abiotic variables ($p > 0.05$).

Discussion

Drift invertebrates

The dominant organisms in the drift invertebrate assemblages were the chironomids and the baetids. Several studies about the composition of the drift fauna in tropical (Pringle & Ramirez, 1998; Ramirez & Pringle, 1998, 2000) and temperate regions (Allan, 1987; Koetsier et al., 1996; Gayraud et al., 2000) have found the same results regarding the dominance of these two groups.

The large density and taxonomic richness of chironomids in drift may be related with phenological factors (life cycle stage), life habit, and body morphology. In contrast to most aquatic

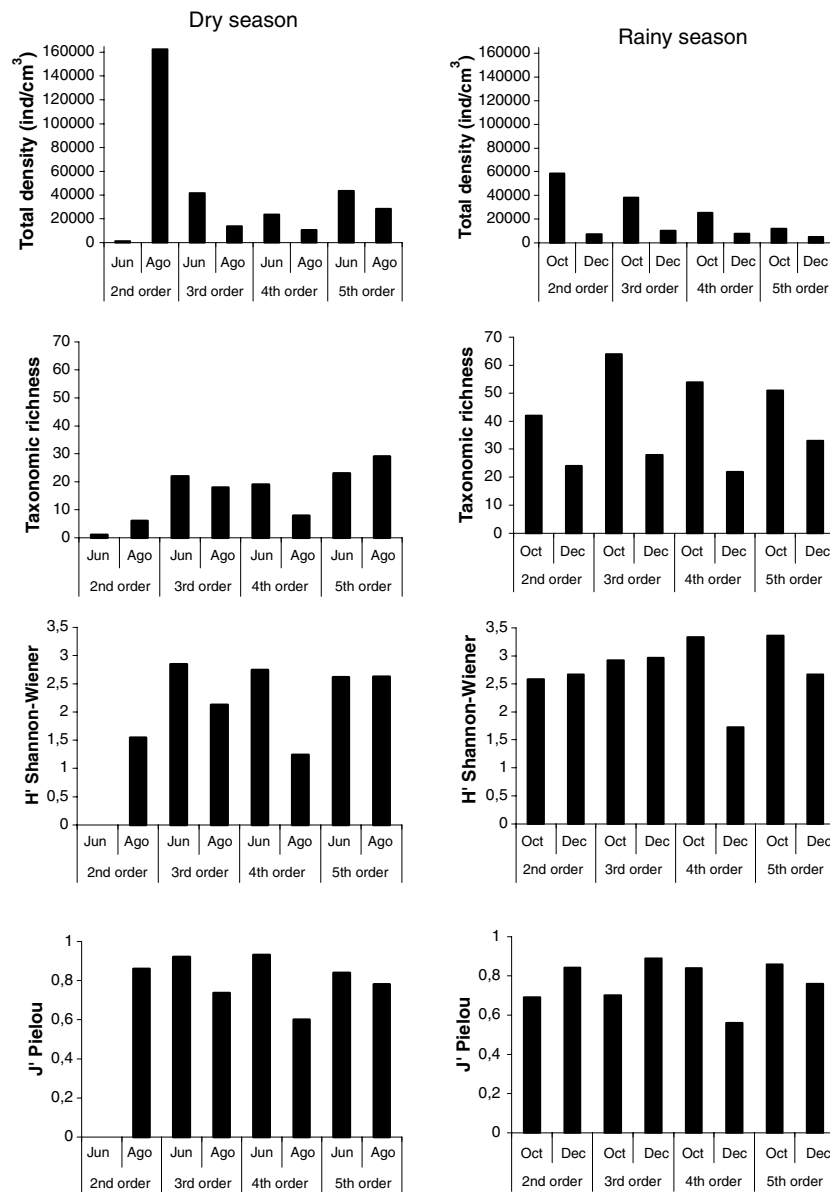


Figure 3. Total density, taxonomic richness, Shannon–Wiener diversity and Pielou evenness of the drift invertebrate assemblages along the longitudinal gradient in Indaiá Stream, during the dry (June and August) and rainy (October and December) seasons in the Serra do Cipó National Park (MG).

insects, these organisms have the tendency to leave the sediment and enter the water column during their pupae phase being dragged by the water current several meters along the surface, until adult emergence (Cranston, 2000a). The Chironomidae pupae are also characterized by low mobility (Vergon & Bourgeois, 1993), and by the absence of morphological adaptations to water

flow increase, thus, being more prone to the displacement from the substrate (Gayraud et al., 2000). Some larvae also live in the water surface layer, attaching themselves to the surface by a thin silk filament (Ward, 1992), and are susceptible to the downstream dislodgment as a function of water flow variation. Gayraud et al. (2000) suggest that the absence of morphological adaptations for

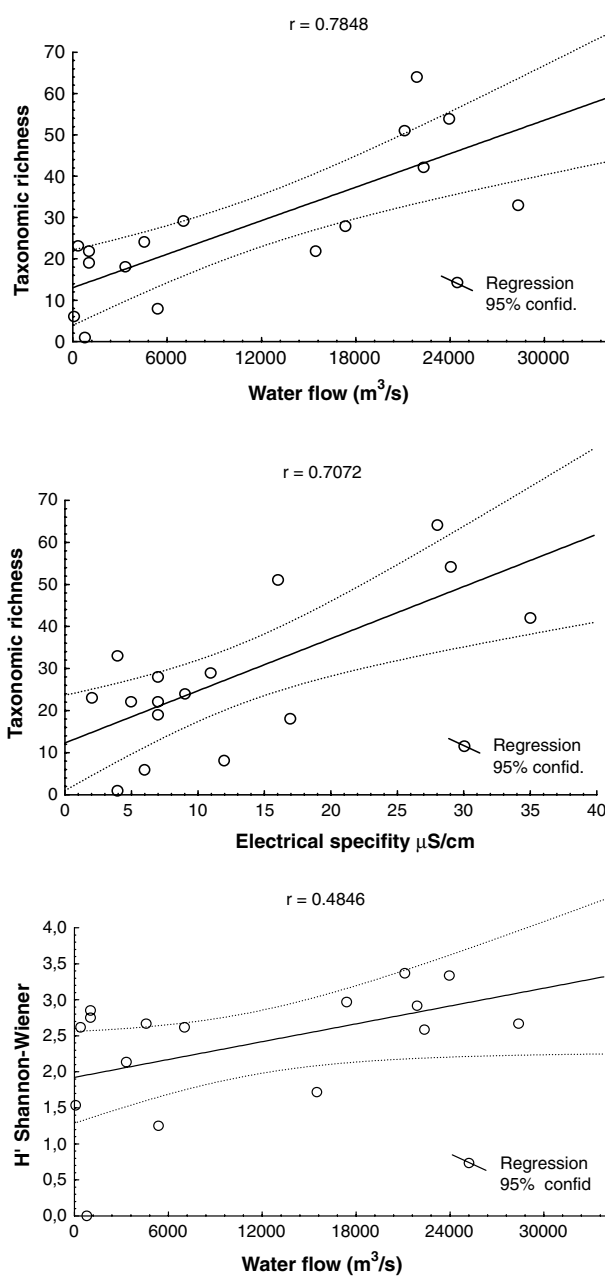


Figure 4. Relationship between taxonomic richness and Shannon–Wiener diversity of the drift invertebrate assemblages and water flow (m^3/s) and specific conductivity ($\mu\text{S}/\text{cm}$) along the longitudinal gradient in Indaiá Stream, Serra do Cipó National Park (MG).

resistance to hydraulic stress in the free-living Chironomidae expose them to a high probability of dislodgment during water flow disturbance.

The drift of Baetidae nymphs seems to be related to behavioral rather than catastrophic events. In adverse situations (e.g., predators

present), these organisms detach rapidly from the substrate and enter the water column (McIntosh et al., 2002). This drift habit is also related to the life cycle stage, being frequent in mature nymphs (Corkum & Pointing, 1979) and during foraging activities (Pescador, 1997).

On the other hand, these two groups are extremely abundant in the Serra do Cipó aquatic ecosystems, specially in Indaiá Stream, where they can account together for c. 38% of the total density of the benthic macroinvertebrate communities (Callisto et al., 2004). Considering that the drift habit can be viewed as a active phenomenon of populations redistribution, as pointed out by other authors, we assumed that the dominance of these groups is possibly related to their benthic densities. However, it must be outstanding that new studies, with simultaneous benthic and drift samples collections are needed in order to confirm that information.

Major factors affecting taxonomic richness and diversity of aquatic invertebrate drift assemblages

Seasonality had a major influence on the diversity and taxonomic richness of these assemblages. The rainy period in the Serra do Cipó region is characterized by strong storms that influence the whole aquatic biota, with a rapid increase of water current velocity and flow, raising the water level up to 5 m above the regular values in some areas.

Changes in discharge result in different hydraulic conditions within the stream channel. This factor may cause sediment scouring, revolving the benthic substrates and causing direct mechanical damage and removal of benthic organisms increasing the number of invertebrate *taxa* in the drift (Brittain & Eikeland, 1988; Gore, 1994). Non-scouring flood events may also cause a large effect on benthic macroinvertebrate assemblages. Imbert & Perry (2000) assessed the effect of stepwise and abrupt changes in non-scouring flow in gravel bed experimental streams, and found that, in both cases, there were significant increases in taxonomic richness of drifting fauna.

Regarding the density values, we observed that contrary to an increase in the rainy period, there was a decrease in dry period. It should be noted that even observing an increase in the total number of drifting invertebrates, density values decreased due to the increase in water flow, and thus a dilution of the numbers.

Our results also show that most of the physical and chemical characteristics of the water column exert little influence in the diversity and density of drifting invertebrate assemblages along the

longitudinal gradient in Indaiá Stream. In addition to flow, only specific conductivity positively influenced the taxonomic richness. Euliss et al. (1991) studying an aquatic Heteroptera (water boatman) in agricultural drainwater evaporation ponds in California, found through regression models a positive relationship between specific conductivity, density and biomass. Specific conductivity in aquatic ecosystems generally increases, as a result of the lack of dilution and increased evaporation and groundwater inputs (Caruso, 2002). Every year in Serra do Cipó, with the beginning of the rainy period, is observed an increase of the input of allochthonous organic matter by the semi-deciduous riparian vegetation along the streams. The sediment runoff coming from the adjacent drainage basin during this period carries ions to the streams, resulting in higher values of specific conductivity in October. We assume that the positive relationship between specific conductivity and drift taxonomic richness values is due to the increase of water flow in the rainy period (mainly October).

Drift sampling as a tool in the assessment of aquatic invertebrate diversity

Diversity assessment of aquatic invertebrate assemblages is usually made by the collection of benthic samples and utilization of artificial substrates. Recently, Pringle & Ramirez (1998) suggested the utilization of the drift technique to evaluate aquatic invertebrate assemblages in bio-assessment protocols in tropical streams. According to these authors, the utilization of this technique aggregates several advantages. For instance, they represent an integrated sample of various habitats, and provide critical information about the presence of migratory components in the invertebrate assemblages.

Our results show that the use of the drift technique is an efficient complementary tool in the assessment of aquatic invertebrate assemblages. This methodology allowed the collection of some *taxa* that normally would not be sampled using traditional benthic sampling techniques (e.g. *Microvelia*, *Rhagovelia* – Veliidae; and *Halobatopsis* – Gerridae) due to their life habit (nektonic organisms), and rare taxa, as already suggested by other authors (e.g., Pringle & Ramirez, 1998).

Moreover, it added several new *taxa* to the invertebrate diversity in Serra do Cipó region, especially among the Chironomidae family (e.g., *Parametriocnemus* and *Onconeura*). Also, it made possible the collection of a large number of chironomid exuviae, which are normally not collected in benthic samples. According to Cranston (2000a), the chironomid exuviae represent important historic records of the biodiversity of freshwater ecosystems and also may represent the sampling of some *taxa* that were not collected in former benthic samples (Galdean et al., 1999, 2000, 2001) and neither in the larvae drift samples.

Acknowledgments

The authors are especially grateful to the valuable comments and suggestions provided by Dr J. L. Attayde and language review by Mr L. Cota. The logistic support offered by IBAMA, financial support by Brazilian National Research Council (Grants 462185-001 and 472328-018), FAPEMIG, and CAPES scholarship funds are appreciated. M. Goulart was a master student in the Graduation Program in Ecology, Conservation and Management of Wildlife – Federal University of Minas Gerais, maintained by the US Fish and Wildlife Service. This program contributes to the implementation of the Convention on Nature Protection and Wildlife Preservation in the Western Hemisphere (1940) and the Ramsar Convention on Wetlands (Ramsar, Iran, 1971).

References

- Allan, J. D., 1987. Macroinvertebrate drift in a rocky-mountain stream. *Hydrobiologia* 144: 261–268.
- Allan, J. D., 1995. Stream ecology: structure and function of running waters. Chapman & Hall, New York.
- Brittain, J. E. & T. J. Eikeland, 1988. Invertebrate drift – a review. *Hydrobiologia* 166: 77–93.
- Callisto, M., F. A. R. Barbosa & J. A. Vianna, 1998. Qual a importância de uma coleção científica de organismos aquáticos em um projeto de biodiversidade? IV Simpósio de Ecossistemas Brasileiros 1: 432–439.
- Callisto, M., M. Goulart, A. O. Medeiros, P. Moreno, & C. A. Rosa, 2004. Diversity assessment of benthic macroinvertebrates, yeasts and microbiological indicators along a longitudinal gradient in Serra do Cipó, Brazil. *Brazilian Journal of Biology* 65: in press.
- Caruso, B. S., 2002. Temporal and spatial patterns of extreme low flows and effects on stream ecosystems in Otago, New Zealand. *Journal of Hydrology* 257: 115–133.
- Corkum, L. D. & P. J. Pointing, 1979. Nymphal development of *Baetis vagans* McDunnough (Ephemeroptera, Baetidae) and drift habits of large nymphs. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 2348–2354.
- Cranston, P. S., 2000a. August Thienemann's influence on modern chironomidology – an Australian perspective. *Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen* 27: 278–283.
- Cranston, P. S., 2000b. Electronic Guide to The Chironomidae of Australia. (<http://entomology.ucdavis.edu/chiropage/index.html>)
- Dominguez, E., M. D. Hubbard & W. L. Peters, 1992. Clave para ninfas y adultos de las familias y generos de Ephemeroptera (Insecta) sudamericanos. *Biología Acuática* 16: 39 p.
- Epler, J. H., 2001. Identification Manual for the Larval Chironomidae (Diptera) of North and South Carolina. North Carolina Department of Environmental and Natural Resources – Division of Water Quality. North Carolina.
- Euliss, N. H., R. L. Jarvis & D. S. Gilmer, 1991. Standing crops and ecology of aquatic invertebrates in agricultural drain-water ponds in California. *Wetlands* 11: 179–190.
- Galdean, N., M. Callisto & F. A. R. Barbosa, 1999. A proposed typology for the rivers of Serra do Cipo (Minas Gerais, Brazil) based on the diversity of benthic macroinvertebrates and the existing habitats. *Travaux Museum History Natural Grigore Antipa* 41: 445–453.
- Galdean, N., M. Callisto & F. A. R. Barbosa, 2000. Lotic Ecosystems of Serra do Cipó, southeast Brazil: water quality and a tentative classification based on the benthic macroinvertebrate community. *Journal of the Aquatic Ecosystem Health & Management* (in press).
- Galdean, N., M. Callisto & F. A. R. Barbosa, 2001. Biodiversity assessment of benthic macroinvertebrates in altitudinal lotic ecosystems of Serra do Cipó (MG, Brazil) *Brazilian Journal of Biology* 61: 239–248.
- Galvão, M. V. & E. Nimer, 1965. Clima. *Geografia do Brasil-Grande Região Leste*, IBGE, Rio de Janeiro 5: 91–139.
- Gayraud, S., M. Philippe & L. Maridet, 2000. The response of benthic macroinvertebrates to artificial disturbance: drift or vertical movement in the gravel bed of two Sub-Alpine streams? *Archiv für Hydrobiologie* 147: 431–446.
- Giulietti, A. M., N. A. Menezes, J. R. Pirani, M. Meguro & M. G. L. Vanderley, 1987. Flora da Serra do Cipó: caracterização e lista de espécies. *Boletim de Botânica* 9: 1–151.
- Gore, J. A., 1994. Hydrological change. In Calow P. & G. E. Pets (eds), *The Rivers Handbook: Hydrological and Ecological Principles*, Blackwell Scientific Publications, London.
- Huhta, A., T. Muotka & P. Tikkanen, (2000). Nocturnal drift of mayfly nymphs as a post-contact antipredator mechanism. *Freshwater Biology* 45, 33–42.
- Imbert, J. B. & J. A. Perry, 2000. Drift and benthic invertebrate responses to stepwise and abrupt increases in non-scouring flow. *Hydrobiologia* 436: 191–208.
- Koetsier, P., G. W. Minshall & C. T. Robinson, 1996. Benthos and macroinvertebrate drift in six streams differing in alkalinity. *Hydrobiologia* 317: 41–49.

- Köppen, W., 1931. *Climatologia*. Fondo de Cultura Económica, Buenos Aires.
- Magurran, A. E., 1991. *Ecological Diversity And Its Measurement*. Chapman & Hall, London.
- Matthaei, C. D., D. Werthmuller & A. Frutiger, 1998. An update on the quantification of stream drift. *Archive für Hydrobiologie* 143: 1–19.
- McIntosh, A. R., B. L. Peckarsky, B. W. Taylor, 2002. The influence of predatory fish on mayfly drift: extrapolating from experiments to nature. *Freshwater Biology* 47: 1497–1513.
- Merritt, R. W. & K. W. Cummins, 1988. *An introduction to the aquatic insects of North America*. 2nd. edn. Kendall/Hunt, New York.
- Pérez, G. P., 1988. *Guía para el estudio de los macroinvertebrados acuáticos del departamento de Antioquia*. Editorial Presencia Ltda., Bogotá.
- Pescador, M. L., 1997. General Ecology of Mayflies: adaptations, reproductive strategies and trophic categories. In *Taller Internacional sobre sistemática y bioecología de Ephemeroptera como bioindicador de calidad de agua*. Santiago de Cali, Colombia: 10 pp.
- Poff, N. L. & J. V. Ward, 1991. Drift responses of benthic invertebrates to experimental stream flow variation in a hydrologically stable stream. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 1926–1936.
- Pringle, C. M. & A. Ramirez, 1998. Use of both benthic and drift sampling techniques to assess tropical stream invertebrate communities along an altitudinal gradient, Costa Rica. *Freshwater Biology* 39: 359–373.
- Ramirez, A. & C. M. Pringle, 1998. Invertebrate drift and benthic community dynamics in a lowland neotropical stream, Costa Rica. *Hydrobiologia* 386: 19–26.
- Ramirez, A. & C. M. Pringle, 2001. Spatial and temporal patterns of invertebrate drift in streams draining a Neotropical landscape. *Freshwater Biology* 46: 47–62.
- Trivinho-Strixino, S. & G. Strixino, 1995. *Larvas de Chironomidae (Diptera) do Estado de São Paulo: Guia de Identificação e Diagnoses dos Gêneros*. Universidade Federal de São Carlos, São Paulo.
- Vannote, L. R., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130–137.
- Vergon, J. P. & C. Bourgeois, 1993. Les larves de Diptères Chironomidae: I. Caractères généraux et clés d'identification des tribus. *Bulletin of the Linnean Society* 8: 36–50.
- Ward, D., N. Holmes & P. José, 1995. *The New Rivers & Wildlife Handbook*. RSPP, NRA e The Wildlife Trusts, Bedfordshire.
- Ward, J. V., 1992. *Aquatic Insect Ecology: 1. Biology and Habitat*. John Wiley & Sons, New York.
- Wiedenbrug, S., 2000. *Studie zur Chironomidenfauna aus Bergbach von Rio Grande do Sul, Brasilien*. Ph.D. Theses, Munchen, Germany: 444 pp.
- Wiederholm, T., (ed.), 1983. *Chironomidae of the Holarctic region. Keys and diagnoses. Part 1. Larvae*. *Entomologica Scandinavica* 19: 457.
- Wiggins, G. B., 1977. *Larvae of the North American Caddisfly Genera (Trichoptera)*. University of Toronto Press, Toronto.