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Seasonal, discharge-driven patterns of mayfly assemblages in an intermittent Neotropical stream

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SUMMARY

1. Streams in the seasonal wet and dry tropics have highly dynamic discharge regimes. Our study stream, located in mid-western Brazil, drains into the Pantanal, South America's largest wetlands, and is characterized by frequent spates in the rainy season and several weeks of interrupted flow in the dry season.
2. In order to understand how these seasonal flow patterns influence the aquatic fauna, floating litter was studied because: (i) this habitat is exposed to the current, and thus is likely to be most affected abiotically and biotically by changes in flow; and (ii) this habitat is abundant in unaltered tropical streams. Studies were conducted in a third- and a fourth-order reach. Mayflies were chosen as study organisms because they were frequent and species-rich on floating litter, and because they should to be responsive to changes in current velocity.
3. In the course of 15 months, covering one rainy and two dry seasons, mayflies showed pronounced seasonal patterns at family and genus level, which were evidently driven by discharge. Two periods of high mayfly densities were observed in the course of one year. One maximum coincided with the peak of the rainy season, the other with the peak of the dry season, and both were distinct in faunistic composition. At high current velocities the leptophlebiid *Farrodes* sp. was dominant and *Leptohyphes* sp., *Acerpenna* sp. and *Paracloeodes* sp. were frequent. In the dry season, when the river was reduced to isolated standing waters, 86–93% of all mayflies were *Caenis* sp.
4. Altogether sixteen mayfly genera from the families Baetidae, Caenidae, Leptohyphidae, Leptophlebiidae and Oligoneuriidae were recorded. Two genera are new to science, the baetid *Aturbina* was recently described (among others, from material from our study river), *Acerpenna* and *Paracloeodes* are new records for South America, and *Miroculis* and *Terpides* are recorded for the first time south of the Amazon.

Introduction

This study on mayflies from the Rio Bento Gomes, an intermittent river which drains into the Pantanal, is the first survey on insect assemblages from any of the many tributaries of South America's largest wetlands. The Pantanal lies in the catchment area of the upper Paraguay River and is part of the second largest drainage system of South America. No basic ecological features are known for the Paraguay River or any of its countless tributaries (Di Persia, 1986; Bonetto & Wais, 1995; Por, 1995), and only some rough hydrological data have been compiled from its catchment area (EDIBAP, 1979; RADAM Brasil, 1982), which covers some 980 000 km^2 in the seasonal tropics, extending from 14 to 27°S. Because in the tropics seasonality is marked by annual variation of rainfall, the discharge regime of streams and rivers is highly dynamic. In the section of the catchment area where our studies were conducted (16°S), the surface flow of rivers ceases for some time in the dry season in the upper and middle reaches, while in the rainy season frequent spates are common in the headwaters, resulting in extensive inundations of floodplains in the lower reaches.

The aim of this study was to understand how these seasonal flow patterns affect the aquatic fauna of the headwaters. For this purpose we studied mayfly assemblages attached to floating litter. Mayflies were among the most frequent and species-rich insects among floating litter. Floating litter is an abundant habitat in the upper and middle reaches of our study river, as it is in general in tropical lowland rivers, that are fringed by gallery forest and have channels with high retention characteristics when little impacted by human activities (Fittkau, 1976). Because floating litter is exposed to the current it is likely to be affected, both abiotically and biotically, by changes in flow. Mayflies are often sensitive to current velocity, so we expected they would be responsive to seasonal flow patterns, indicating changes of habitat conditions. Their abundance dynamics and assemblage composition on floating litter was studied over a period of 15 months, covering one rainy and two dry seasons.

Materials and methods

Study area

The Rio Bento Gomes is an intermittent river in the lowlands of central-western Brazil, in Mato Grosso state. It drains $\approx 2500\ km^2$ of savannah woodland, which is mainly used for extensive cattle breeding where no larger settlements are present. After some 200 river km (60 km bee-line) it flows into the Pantanal (16°20′S, 56°32′W; Fig. 1).

The river′s flow regime depends strongly on local precipitation, and is highly dynamic and particularly well defined because of the seasonality of the tropical climate, with 80% of annual rain falling from November to March. In 1992–93 (May to May) annual rainfall was 1580 mm, and in 1993–94 it was 1145 mm (recorded at 'Fazenda Campo Alegre', a main spring of the Bento Gomes). Our studies are the first ever undertaken in the upper reaches of the Bento Gomes, thus long-term records of environment conditions are not available. Average annual rainfall (75 years of records) for Cuiabá, the closest meteorological station 80 km east of our study area, is 1380 mm (EDIBAP, 1979). During the rainy season, in particular during the first weeks of its onset, floods are frequent (at intervals of 10 days or less), often sudden, short events, lasting a few hours only. Subsequently the upper Bento Gomes (first- to third-order reaches) enters full spate, while the water level in the lower reaches (fifth- and sixth-order) rises more or less continuously, inundating gallery forests and savannahs. In the dry season, surface flow generally ceases some time between July and October.

Almost the entire course of the Bento Gomes, down to the reaches where it opens into the Pantanal, is bordered by gallery forest, providing the river with a considerable amount of litter. The gallery forest produces litter throughout the year, however there is a pronounced litterfall peak in the late dry season (August, September; Haase, in press). Floating litter, retained by roots and twigs sticking out into the water, consisted mainly of leaves, and included twigs, fruits and floral debris. It was particularly abundant in the river′s upper and middle reaches, and included litter from the trees *Alchornia castaneiflora* (Willd.) A. Juss. (Euphorbiaceae), *Ficus gomelleira* Kth. et Bouché (Moraceae), *Inga uruguensis* Humb. et. Arn. (Leguminosae), *Licania parvifolia* Huber (Chrysobalanaceae), *Mouriri guianensis* Aubl. (Melastomataceae), and the shrub *Compretum lanceolatum* Pohl (Compretaceae).

We studied litter-associated mayflies at two sites in the middle reaches of the Bento Gomes ($\approx$ 180 m a.s.l.). Site 1 lay in a third-order reach, near a small settlement of some ten huts called 'Filisterra'. Site 2, located on a property called 'Sitio Periquito' some 10 river km downstream from site 1, lay in a fourth-order reach. At site 1 the maximum bank-full width of the river was 5.1 m, at a depth of 60 cm, and with a 2.5 m high cutbank. The gallery forest was thinned out by the local people, and floating litter was less abundant than at site 2. At site 2 the channel was broader and shallower, with a maximum width of 10.2 m at a depth of 35 cm, and low cutbanks (< 1 m) covered with forest. Maximum non-spate current velocity was the same at both sites ($65\ cm\ s^{-1}$), although at site 2 discharge was generally 1.5–2 times higher than at site 1. In the dry season of 1993 flow ceased for between 1 and 2 months at site 1, and between 2 and 3 months at site 2. The remnant pools were 50–100 m long at both sites, and deeper at site 1, but still less than 10 cm in depth. They were separated by broad

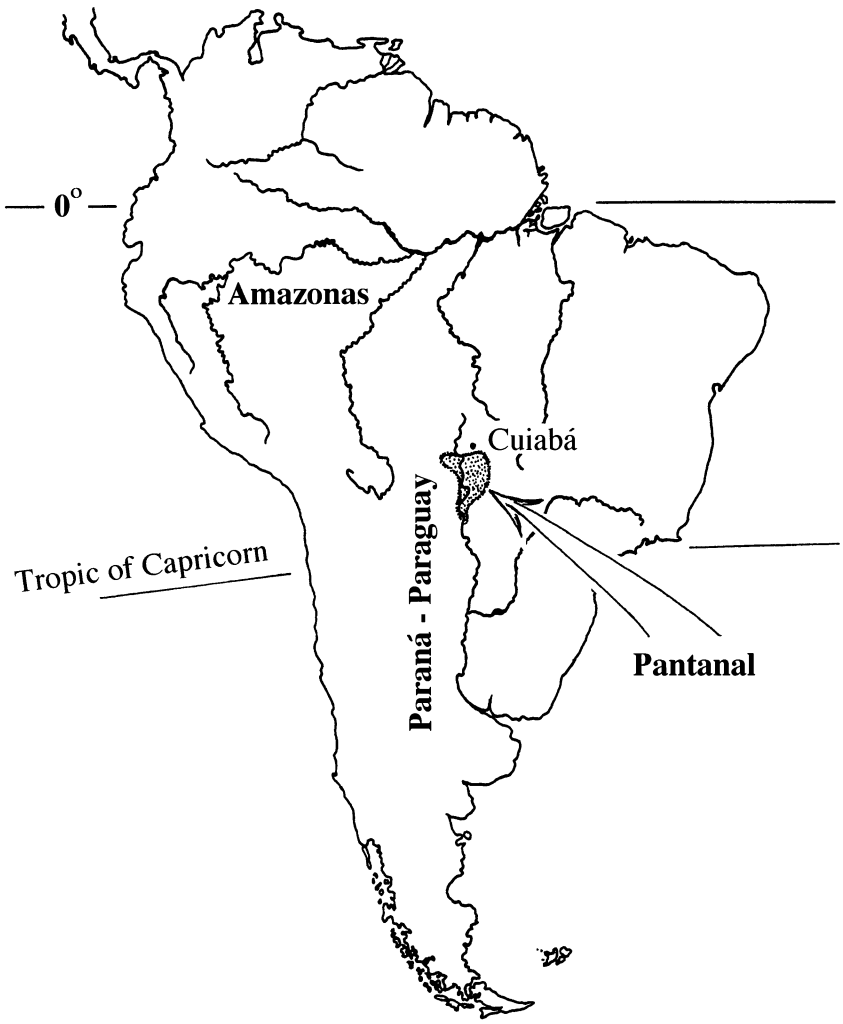

Fig. 1 Location of the study area. The Bento Gomes River drains into the northern Pantanal, the biggest wetland of South America, and part of the catchment of the Paraguay River.

riffles of approximately the same length. Annual mean water temperature was 25 °C (n = 15). A maximum of 29 °C was reached in the rainy summer season (January–March), and a minimum of 17 °C occurred for a few days in the dry winter season (July–August), when cold fronts come up from Patagonia. Conductivity ranged from 80 to 250 and 80 to 290 µS cm^{-1} (at 25 °C) at sites 1 and 2, respectively, and was highest in the dry season. The pH was circumneutral at both sites, and sediment load was highest in the rainy season, particularly after thunderstorms.

Methods

From May 1993 to August 1994 samples were taken every 4 weeks, a total of eighteen sampling occasions over 15 months. Floating litter packs and the attached fauna were collected by hand (one handful each sample) by putting a dip net (125 µm mesh size) underneath the sample when lifted from the water surface. The material was preserved immediately in pure ethanol (diluted by the water the sample contained), and stored until sorted under a dissecting microscope (×25). On each date and at each site, five replicates were taken, with the exception of the first two pilot sampling occasions (no replicates), results of which are included in this study.

Current velocities were always measured across the entire river width (every 50 cm) and water column (every 5 cm), employing a dip rod according to Jens (1968) (Tauchstab nach Jens, Hydro-Bios, Kiel, Germany), which counterbalances the torque on the rod induced by the current (accuracy of 5%). These data also allowed the calculation of total discharge at a given time. Current velocities measured in this way certainly differed from those present among floating litter to which the attached fauna was subjected. However, as the flow regime of a river is the 'pace-maker' for flow changes in all stream habitats, the recorded values depict the prevailing flow dynamics throughout the seasons.

All mayfly larvae were sorted and allocated to the lowest taxonomic level possible (genus, except for Baetidae). We were not able to relate all baetid larvae to genera, thus family level was used for quantitative analyses. Baetidae, Leptohyphidae, Leptophlebiidae and Oligoneuriidae were identified by W.P. McCafferty and C. Lugo-Ortiz, Purdue University, Indiana, U.S.A., and Caenidae by P. Malzacher, Ludwigsburg, Germany. Voucher material is deposited at the Entomological Collection of Purdue University, U.S.A., and at the Zoologische Staatssammlung München, Germany.

To standardize sample size, all litter collected was dried for 48 h at 80 °C and weighed (accuracy of 0.01 g). The abundance of larvae per sample was expressed as individuals/10 g litter dry weight (DW). Sample weights ranged from 4.3 to 11.4 g DW. This standardization technique neglects litter features such as surface area, texture and degree of decomposition, which may be important habitat qualities for the colonizing fauna (e.g. Hax & Golladay, 1993; Phillips & Kilambi, 1994). However, composition and surface quality of floating litter was more or less the same over time.

Relationships between standardized densities of mayfly taxa and current velocity were investigated by calculating product–moment correlation coefficients (Fowler & Cohen, 1990).

Results

From 11 May 1993 to 31 August 1994, the discharge of the Bento Gomes varied from 0 l s^{-1} in August and September to 853 l s^{-1} at site 1 and 1290 l s^{-1} at site 2 in February, when the river was bankfull along its third- and fourth-order stretch. During spates, discharge was estimated to exceed 2000–3000 l s^{-1}. This means that the Bento Gomes changed its flow patterns fundamentally through the seasons, becoming alternately a running and standing water (Fig. 2).

Altogether sixteen mayfly genera from five families were collected from the litter samples, among which twelve genera from four families occurred at both sites (Table 1). Baetidae (seven genera) and Leptophlebiidae (four genera) were most diverse, followed by Leptohyphidae (two genera) and Caenidae (one genus). Oligoneuriidae (two genera) were rare and occurred only at site 2.

The composition of the mayfly assemblages showed a pronounced seasonality associated with the well-defined discharge regime of the river. Among the eleven genera recorded in lotic situations, *Farrodes* sp., *Leptohyphes* sp., *Acerpenna* sp. and *Paracloeodes* sp. were most abundant. Four genera, dominated by *Caenis* sp., occurred in lentic situations, and *Cloeodes* sp. was found in both. Table 1 shows each taxon along with the ranges of current velocities within which 85% or more of its larvae were collected. *Lachlania* sp., Oligoneuriidae gen. n. and *Farrodes* sp. were most abundant at current velocities higher than 35 cm s^{-1}, while *Leptohyphes* sp. and *Terpides* sp. occurred over a broad range of flow patterns (3–64 and 9–64 cm s^{-1}, respectively). *Caenis* sp., *Callibaetis* sp., *Tricorythodes* spp. and *Ulmeritoides* sp. appeared when flow ceased and the river transformed into a series of standing waters. Among the rheophilous taxa only *Farrodes* sp. and *Leptohyphes* sp. showed significant correlations between abundance and current velocity (*Farrodes*: $r = 0.79$, $P < 0.01$; *Leptohyphes*: $r = 0.49$, $P < 0.05$).

Two periods of high mayfly density were observed in the course of one year. One maximum coincided with the peak of the rainy season, when current velocities were high, though variable (37–64 cm s^{-1}, January–March, 1994; Figs 3 and 4). The other maximum was achieved rapidly at the peak of the dry season after flow had ceased for 4–8 weeks. At this time, densities were half as high again as in the rainy season (28 September 1993, 31 August 1994; Fig. 4). Dry season maxima were recorded only at site 2, where the stream channel was broad and shallow, and where pools formed earlier and lasted longer than at site 1 (Fig. 2).

Figs 3 and 4 show mayfly densities recorded over 15 months at sites 1 and 2, along with relative abundances of individual families and the maximum current velocity recorded at the respective site and date. Basic assemblage patterns in time were the same at both sites, however they were clearer at site 2 (Fig. 4).

Abundance at site 2

Studies began in May, i.e. in the transition period from the wet to the dry season, when little rain fell so that the river's discharge and current velocity were

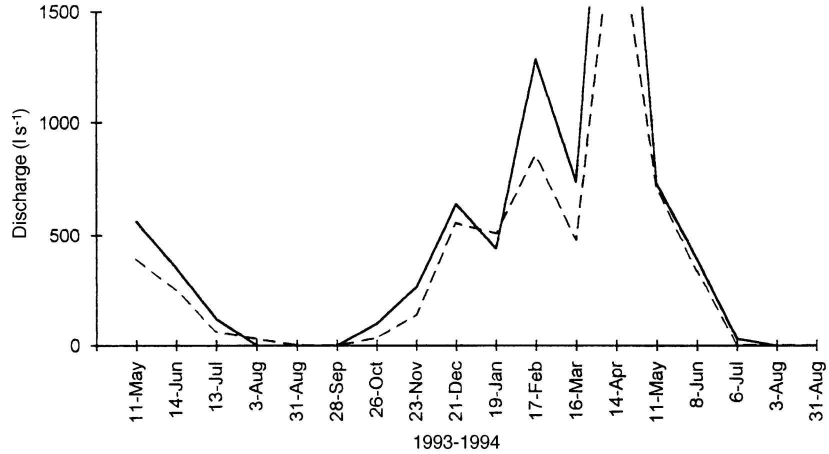

Fig. 2 The discharge pattern measured at site 1 (third-order; dotted line) and site 2 (fourth-order; solid line) in the Bento Gomes River from May 1993 to August 1994.

Table 1 Mayfly genera collected from floating litter in a third- (site 1) and fourth-order reach (site 2) of the Bento Gomes river in 1993–94, along with the range of current velocity within which more than 85% of all larvae of a given genus were collected. *Not quantified due to difficulties in identifying all larvae; –, genus not present. Current velocities were measured in the stream, not among the litter packs (see text)

	Current velocity (cm s^{-1})	
Taxa	Site 1	Site 2
Baetidae		
Acerpenna sp.	Lotic*	Lotic*
Aturbina georgei	Lotic*	Lotic*
Callibaetis sp.	0	0
Cloeodes sp.	0–51	0–45
Camelobaetidius sp.	–	Lotic*
Paracloeodes sp.	Lotic*	Lotic*
Baetidae n.gen., n.sp.	Lotic*	Lotic*
Caenidae		
Caenis sp.	0	0
Leptohyphidae		
Leptohyphes sp.	3–48	19–64
Tricorythodes spp.	0	0
Leptophlebiidae		
Farrodes sp.	27–65	35–64
Miroculis sp.	14–48	–
Terpides sp.	14–51	9–64
Ulmeritoides sp.	0	0
Oligoneuriidae		
Lachlania sp.	–	44–64
Oligoneuriidae n.gen., n.sp.	–	45–64

decreasing steadily (Figs 2 and 4). The number of mayflies on floating litter also decreased continuously, from 131 larvae/10 g DW, to seventy-three, sixty-six, thirty-nine and eight larvae/10 g. During this period the relative abundance of Leptophlebiidae, in particular of *Farrodes* sp., decreased, while that of Baetidae increased (Fig. 4).

When flow ceased in early August, Caenidae appeared and built up a dense population during the next 8 weeks, attaining maximum densities of 494 larvae/10 g litter DW (± 218, n = 5) in late September, with many mature larvae present. In the now isolated pools, thick litter packs touched the bottom. Besides the dominant *Caenis* sp., the assemblage consisted of *Cloeodes* sp., *Callibaetis* sp., some larvae of *Ulmeritoides* sp. and two species of *Tricorythodes*.

In the first week of October, heavy rain ended the dry season, and subsequent thunderstorms between 19 and 24 October turned the Bento Gomes into running water again. On 26 October, maximum current velocity was 22 cm s^{-1} and discharge was 100 l s^{-1} at site 2 (Figs 2 and 4). Floating litter was present, but the attached fauna consisted solely of a few chironomids and beetles, and no mayflies were found (Fig. 4).

The next torrential downpours occurred between 6 and 16 November, causing the first spates in the rainy season of 1993–94. From then on, discharge and current velocity increased—although not continuously (Figs 2–4)—until April 1994, including several spate events in the upper and middle reaches of the river (most of them not directly observed at sites 1 and 2). On 14 April 1994, the river was in spate and high discharge (≈ 3000 l s^{-1}) prevented us from taking samples. This was the last spate in the rainy season of 1993–94. With increasing current velocity the number of mayflies increased in November and December

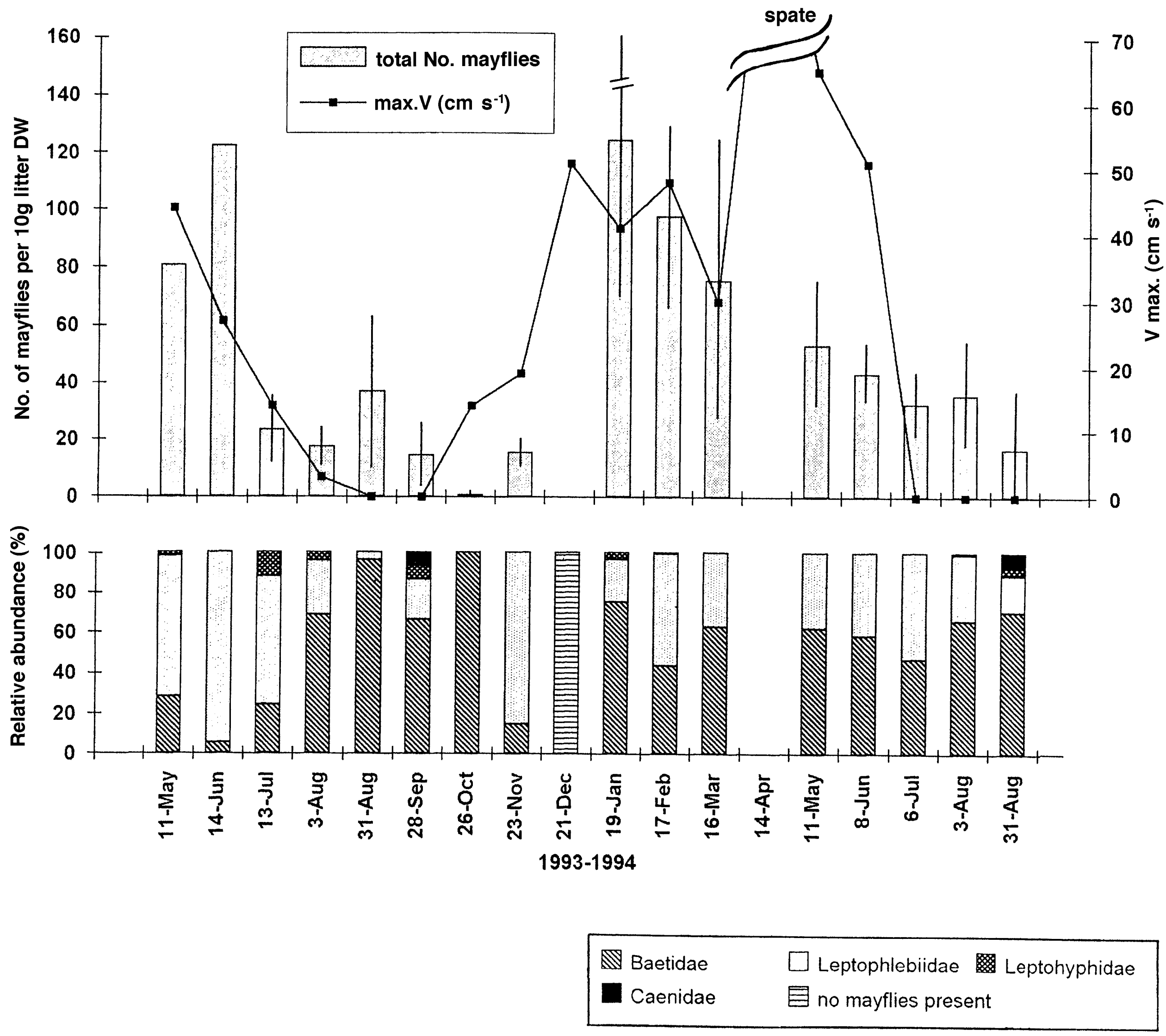

Fig. 3 Mean number (± SD) of mayflies recorded on floating litter (per 10 g litter dry weight) during 1993–94 at site 1, with the maximum current velocity (V_{max}, cm s^{-1}) and the relative abundances of the mayfly families.

and remained high for the next 2 months (Fig. 4). After the onset of flow, Caenidae were no longer evident (occasional *Caenis* sp. larvae were observed on 21 December and 19 February). Baetidae (*Acerpenna* sp., *Paracloeodes* sp.) and Leptophlebiidae (*Farrodes* sp. and *Terpides* sp.) appeared first (23 November), followed by Leptohyphidae (*Leptohyphes* sp.) and Oligoneuriidae (*Lachlania* sp.) (21 December). The latter were never abundant (one to three larvae per sample), but were present throughout the rainy season. The second species of Oligoneuriidae (gen. n. sp. n.) occurred only sporadically. With increasing current velocity, the relative abundance of Baetidae decreased, while that of Leptophlebiidae increased (Fig. 4).

The next dry season commenced suddenly and discharge and current velocity dropped sharply (Figs 2 and 4). Mayfly densities were lower than in the rainy season, although higher than during the dry season of the previous year, and Baetidae again became relatively more abundant as current velocity declined (Fig. 4). In early July, when discharge had almost stopped, Baetidae made up 86–95% of all mayflies, and their absolute and relative abundances continued to increase until flow ceased in early August. As in

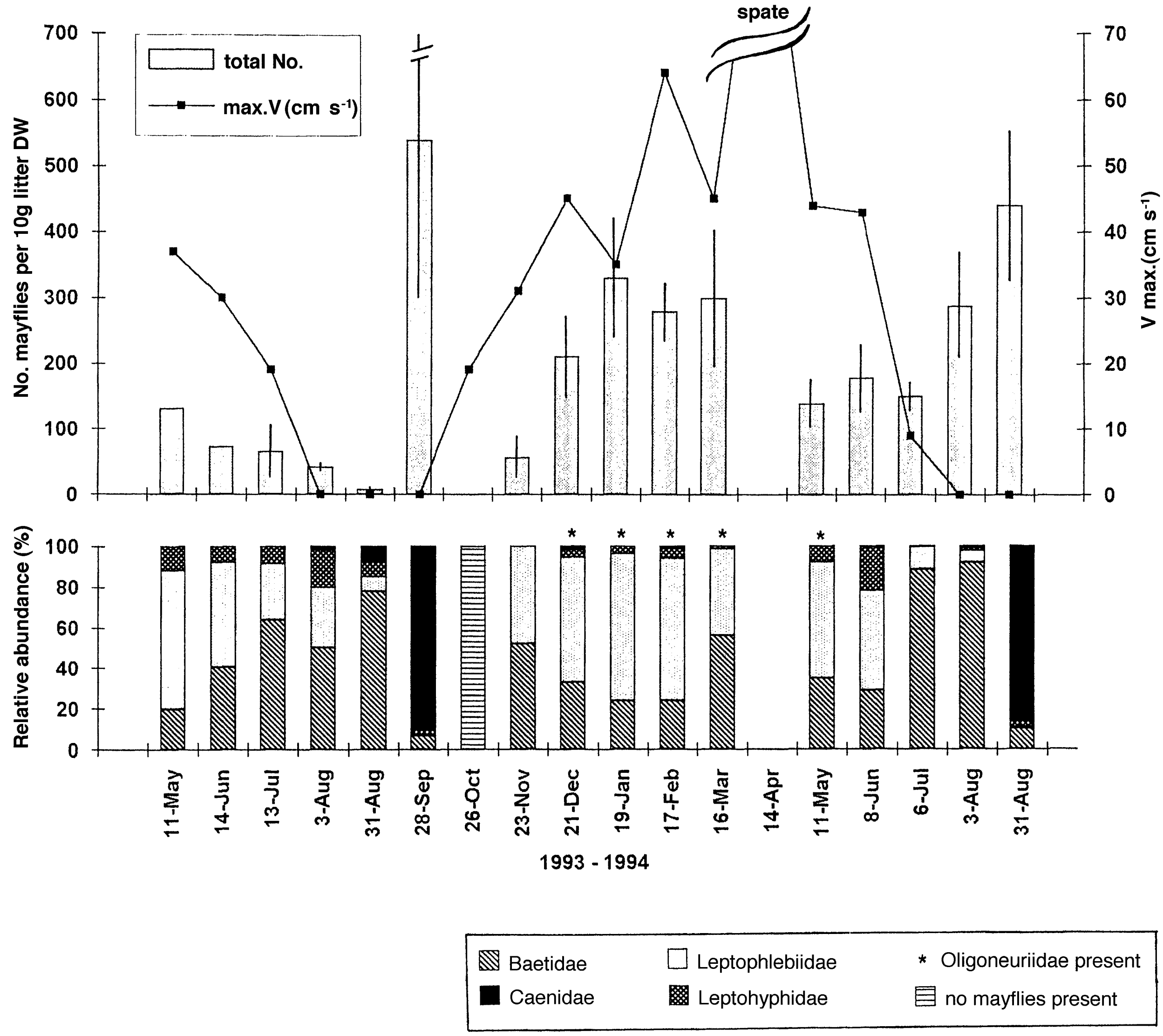

Fig. 4 Mean number (± SD) of mayflies recorded on floating litter (per 10 g litter dry weight) during 1993–94 at site 2, with the maximum current velocity (V_{max}, cm s^{-1}) and the relative abundances of the mayfly families.

the previous dry season, *Caenis* appeared in the now standing waters, and attained densities of up to 381 larvae/10 g litter DW (± 98, $n = 5$), i.e. 86% of the mayfly fauna in the next 4 weeks (Fig. 4).

Abundance at site 1

Basically the same dynamic picture emerged at site 1, although at lower mayfly densities and with less pronounced changes in the faunistic composition (Fig. 3). At the end of the rainy season, when current velocity decreased continuously, the total number of mayflies also decreased. Concurrently, the relative abundance of Leptophlebiidae decreased while that of Baetidae increased. When flow ceased, Caenidae appeared (September 1993, August 1994), and then disappeared with the onset of flow after the first rain. Then, with rising current velocity, mayfly densities increased rapidly and Leptophlebiidae again became more abundant (Fig. 3).

Our data show that the seasonal change of the Bento Gomes from a lotic to a lentic system, and vice versa, resulted in alternating structures of the mayfly assemblages (Figs 3 and 4). This biotic response was particularly clear when considered at the genus level, for example by the abundance dynamics of *Farrodes*

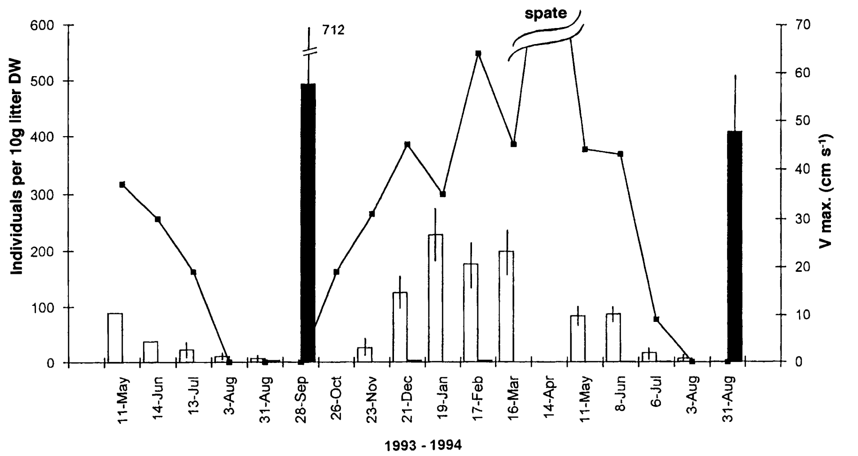

Fig. 5 Densities (mean ± SD) of *Farrodes* sp. (open bars) and *Caenis* sp. (closed bars), with the maximum current velocity (V_{max}, cm s^{-1}) recorded at site 2 during 1993–94.

sp. and *Caenis* sp., the most frequent genera in lotic and lentic situations, respectively (Fig. 5).

Discussion

Studies on Neotropical macrobenthos are very rare, and much observational work is still needed, in particular over longer periods because much of our present knowledge, at least on Neotropical low-order streams, is based on data taken during short visits (Lowe-McConnell, 1988). Because our observations come from a pioneering field study, no further information is available from the Paraguay River catchment area for direct comparison. The principal finding, that the particularly well-defined flow regime of the Bento Gomes River resulted in a pronounced seasonality of the litter-associated mayfly fauna, is described for the first time. Reviews of the literature on the Paraguay–Paraná-de la Plata system (Di Persia, 1986; Bonetto & Wais, 1995) show that nothing is known about its northern, tropical section, where our study river is situated. This area is drained by the 2250 km long Paraguay, with an annual mean discharge of 4.3 million l s^{-1} before it meets the Paraná River (EDIBAP, 1979). Por (1995) reviewed the available information about the Pantanal, the 150 000 km^2 large wetlands into which the Bento Gomes River drains, and mentioned 820 papers, mainly informal reports on botany, agriculture and cattle breeding by governmental institutions, among which eight deal with invertebrates, none of them with insects.

The mayflies

In this region, limno-entomological studies have started only recently (Nolte, 1995; Cranston & Nolte, 1996; Nolte, Tietböhl & McCafferty, 1996; Serrano & Nolte, 1996), so it is not surprising that among the sixteen collected mayfly genera, two were new, undescribed genera (W.P. McCafferty, pers. comm.), the baetid *Aturbina* was recently described (among others, from material from our study river; Lugo-Ortiz & McCafferty, 1996), and two other baetids, *Acerpenna* and *Paracloeodes*, are new records for South America (Dominguez, Hubbard & Peters, 1992). For the leptophlebiids *Miroculis* and *Terpides*, both Neotropical genera known only from northern South America and the Antillas (Dominguez *et al.*, 1992), the Bento Gomes River is the southernmost record.

The Baetidae was the most abundant and diverse family, as it is in many running waters (Hutchinson, 1993). It occurred throughout the year, though in low numbers in the dry season. It includes a high variety of life forms, such as species with very short life cycles, particularly in the Tropics (Jackson & Sweeney, 1995), high mobility (Mackay, 1992) and drought tolerance (Nolte *et al.*, 1996). Leptophlebiidae, the mayfly family with the highest number of described genera in South America (Dominguez *et al.*, 1992), was also abundant and diverse. Leptophlebiidae and Leptohyphidae were present during most of the year, whereas Oligoneuriidae appeared only at times with high current velocities, and Caenidae primarily when flow had ceased. Jacobi & Benke (1991) reported similar time-limited occurrences of the latter two families from a subtropical lowland river, where Oligoneuriidae appeared mainly in the cooler months, and Caenidae in summer and early autumn. As the cooler months coincided with high discharge and the summer months with low discharge patterns, these observations match well with our findings, although Jacobi & Benke

(1991) attributed the temporary appearance of the two families more to prevailing temperatures than flow patterns.

The habitat

Allochthonous litter is known as a well-colonized habitat and a significant nutrient source for aquatic systems (e.g. Mackay, 1969; Webster & Benfield, 1986; Richardson, 1992). There have been numerous experiments on litter colonization and decomposition (e.g. Chergui & Pattee, 1991; Hax & Golladay, 1993; Philips & Kilambi, 1994). Nevertheless, little information is available on freshly fallen, naturally structured, non-conditioned litter (i.e. washed, dried, packed in litter bags). Early studies on non-manipulated (probably 'older', submerged) litter as a habitat were conducted in a shallow, intermittent Canadian creek (Mackay, 1969; Mackay & Kalff, 1969) and showed that litter supported the most diverse fauna among five habitats monitored throughout one year. The main feature of freshly fallen, floating litter, in contrast to older, submerged litter, is that it is a transient habitat, whose existence is determined by the time until it is saturated with water and sinks, and also the flow patterns, particularly in the rainy season. Fittkau (1976), who studied the fauna associated with drifting organic matter in Amazonian waters, introduced the term 'kinal' (from Greek *kin* = move, drift) for such floating habitats, by which he stressed 'the dynamic and very often unstable character' of this abundant habitat, which is 'easily destroyed or displaced'. Fittkau (1976) mentions the presence of mayflies in the kinal, especially in the middle reaches of streams (rhithral), but there are no detailed data available on the fauna from such floating habitats, either from tropical or temperate streams.

Seasonal patterns as clear as we recorded for the mayfly assemblages on floating litter are rarely reported from insect communities in intermittent streams. This may be attributed to the comparatively constant qualities of the studied habitat, caused by steady replacement of sinking leaves by freshly fallen litter. In comparison, bottom sediments, the commonly studied habitats in stream ecology, are more or less permanent substrata, thus easily subject to temporal changes. Boulton & Lake (1992a) showed, by multidimensional analyses of bottom data from intermittent streams, that the broader the scale of included substrata, the more the seasonal faunal patterns became masked by variations caused by habitat differences over time.

The seasonal cycle

Our study began in the transition period from the rainy season to the dry season, when we observed a continuous decline of mayfly densities. In streams with seasonally high discharge fluctuations, a decrease of insect densities when discharge decreases is a common pattern (e.g. Hynes, 1975; Outridge, 1988; Boulton & Lake, 1992b). It is generally interpreted as being a consequence of increased predation and competition in the now physically more stable, and eventually shrinking habitat (Pearson, Benson & Smith, 1986; Boulton *et al.*, 1992; Dudgeon, 1992). We observed an increase in numbers of predators, mainly beetles and triclads, when mayfly densities decreased in the shrinking stream, which fits this scenario. Decreasing mayfly densities may also be attributed to a larger amount of litter available for colonization at this time, as in the northern Pantanal litterfall peaks in gallery forests in the dry season (Haase, in press), and litter accumulates in the now standing waters. The initially decreasing densities, however, contrast with the occurrence of a growing population of *Caenis* sp. which reversed the decline of total mayfly densities in the isolated stream segments in the peak of the dry season. At least at site 2, mayfly abundances attained much higher densities at this time than in the wet season (Fig. 4), indicating favourable ambient conditions in the receding pools.

Subsequent to an initial phase in November, when mayfly densities built up, densities were high in the rainy season (December–April). The increasing discharge and current velocity resulted in increasing proportions of Leptophlebiidae and the steady presence of Oligoneuriidae (Fig. 4). This shows that the frequent short-term spates between the individual sampling occasions did not disturb underlying seasonal patterns, which conforms with observations from intermittent streams with seasonally determined discharge patterns in south-eastern Australia (Boulton & Lake, 1992a,b). Contrasting patterns were reported by Flecker & Feifarek (1994) from an intermittent Andean piedmont stream, also subject to a seasonal wet–dry climate, but with apparently high interannual discharge variations. Flecker & Feifarek (1994) observed strongly fluctuating mayfly densities during the rainy season that were negatively correlated with monthly rainfall.

The rain which ended the dry season in early October 1993 was the only event in 15 months that affected mayfly assemblages in a salient way. At this time the river was far from being in spate, but with the abrupt change from a lentic to a lotic system, high mayfly densities dropped to zero and almost no mayflies were found on floating litter about 1 week after flow resumed. Four weeks later, rheophilous species from two families were established, though in low densities compared with both those recorded before flow had resumed and those in the subsequent rainy season when current velocity was high. From our field data it cannot be decided whether densities stayed low due to lower current velocity on 23 November, or whether floating litter had only recently entered the water and was yet to be colonized by more animals. The same consideration applies to the composition of the mayfly assemblages. In permanent streams, Baetidae are known to recover on artificially disturbed substrata patches within 3–14 days (see review by Mackay, 1992; Matthaei *et al.*, 1996), whereas in an intermittent stream in Arizona species of *Baetis*, *Leptohyphes* and *Tricorythodes* were observed to re-establish within 22–35 days (Fisher *et al.*, 1982). The post-flood situation in the Arizona desert stream was similar to flow onset in our study stream in that no nearby sources of colonizers existed, and our data match the 3–5 week colonization times observed by Fisher *et al.* (1982). Similar drastic effects of abrupt flow onset on the fauna have been documented from intermittent streams in Australia (e.g. Bunn, Edward & Lonergan, 1986; Outridge, 1988).

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References

Bonetto A.A. & Wais I.R. (1995) Southern South American streams and rivers. *Ecosystems of the World*, Vol. 22. *River and Stream Ecosystems* (eds C.E. Cushing, K.W. Cummins and G.W. Minshall), pp. 257–293. Elsevier, Amsterdam.

Boulton A.J. & Lake P.S. (1992a) The ecology of two intermittent streams in Victoria, Australia. II. Comparisons of faunal composition between habitats, rivers and years. *Freshwater Biology*, **27**, 99–121.

Boulton A.J. & Lake P.S. (1992b) The ecology of two intermittent streams in Victoria, Australia. III. Temporal changes in faunal composition. *Freshwater Biology*, **27**, 123–138.

Boulton A.J., Peterson C.G., Grimm N.B. & Fisher S.G. (1992) Stability of an aquatic macroinvertebrate community in a multi-year hydrologic disturbance regime. *Ecology*, **73**, 2192–2207.

Bunn S.E., Edward D.H. & Lonergan N.R. (1986) Spatial and temporal variation in the macroinvertebrate fauna of streams of the northern Jarrah forest, Western Australia: community structure. *Freshwater Biology*, **16**, 67–92.

Chergui H. & Pattee E. (1991) An experimental study of the breakdown of submerged leaves by hydromycetes and invertebrates in Morocco. *Freshwater Biology*, **26**, 91–100.

Cranston P.S. & Nolte U. (1996) *Fissimentum*, a new genus of drought-tolerant Chironomini (Diptera: Chironomidae) from the Americas and Australia. *Entomological News*, **107**, 1–15.

Di Persia D.H. (1986) Zoobenthos of the Paraná system. *The Ecology of River Systems* (eds B.R. Davies and K.F. Walker), pp. 589–598. Dr W. Junk, Dordrecht.

Dominguez E., Hubbard M.D. & Peters W.L. (1992) Clave para ninfas y adultos de las familias y generos de Ephemeroptera (insecta) sudamericanos. *Biologia Acuatica*, **16**, 1–32.

Dudgeon D. (1992) Patterns and processes in stream ecology. A synoptic review of Hong Kong running waters. *Die Binnengewässer*, **29**, 1–147.

EDIBAP (Empresa de Desenvolvimento Integrado da Bacia do Alto Paraguai) (1979) *Estudo de desenvolvimento integrado da bacia do alto Paraguai*, Vol. 2. Ministério do Interior, Brasília.

Fisher S.G., Gray L.J., Grimm N.B. & Busch D.E. (1982) Temporal succession in a desert stream following flash flooding. *Ecological Monographs*, **52**, 93–110.

Fittkau E.J. (1976) Kinal und Kinon, Lebensraum und Lebensgemeinschaft der Oberflächendrift am Beispiel amazonischer Fließgewässer. *Biogeographica*, **7**, 101–113. [in English: Fittkau E.J. (1977) Kinal and kinon, habitat and coenosis of the surface drift as seen in Amazonian running waters. *Geo-Eco-Trop*, **1**, 9–20.]

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

Fowler J. & Cohen L. (1990) *Practical Statistics for Field Biology.* Open University Press, Philadelphia.

Haase R. (in press) Litterfall and nutrient return in eight forests of the Pantanal, Mato Grosso, Brazil. *Journal of Tropical Ecology.*

Hax C.L. & Golladay S.W. (1993) Macroinvertebrate colonization and biofilm development on leaves and wood in a boreal river. *Freshwater Biology*, **29**, 79–87.

Hutchinson G.E. (1993) *A Treatise on Limnology*, Vol. 4 (ed. Y.H. Edmondson). Wiley & Sons, New York.

Hynes J.D. (1975) Annual cycles of macro-invertebrates of a river in southern Ghana. *Freshwater Biology*, **5**, 71–83.

Jackson J.K. & Sweeney B.W. (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.

Jacobi D.I. & Benke A.C. (1991) Life histories and abundance patterns of snag-dwelling mayflies in a blackwater Coastal Plain river. *Journal of the North American Benthological Society*, **10**, 372–387.

Jens G. (1968) Tauchstäbe zur Messung der Strömungsgeschwindigkeit und des Abflusses. *Deutsche Gewässerkundliche Mitteilungen*, **12**, 90–95.

Lowe-McConnell R.H. (1988) Tropical perspective for future research in river ecology. *Journal of the North American Benthological Society*, **7**, 527–529.

Lugo-Ortiz C.R. & McCafferty W.P. (1996) *Aturbina georgei* gen et sp. n.: a small minnow mayfly (Ephemeroptera: Baetidae) without turbinate eyes. *Aquatic Insects*, **18**, 175–183.

Mackay R.J. (1969) Aquatic insect communities of a small stream on Mont St. Hilaire, Quebec. *Journal of the Fisheries Research Board of Canada*, **26**, 1157–1183.

Mackay R.J. (1992) Colonization by lotic macro-invertebrates: a review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 617–628.

Mackay R.J. & Kalff (1969) Seasonal variation in standing crop and species diversity of insect communities in a small Quebec stream. *Ecology*, **50**, 101–109.

Matthaei C.D., Uehlinger U., Meyer E.I. & Frutiger A. (1996) Recolonization by benthic invertebrates after experimental disturbance in a Swiss prealpine river. *Freshwater Biology*, **35**, 233–248.

Nolte U. (1995) From egg to imago in less than seven days: *Apedilum elachistus* (Chironomidae). *Chironomids: From Genes to Ecosystems* (eds P.S. Cranston), pp. 7–184. CSIRO Publications, East Melbourne.

Nolte U., Tietböhl R.S. & McCafferty W.P. (1996) A mayfly from tropical Brazil capable of tolerating short-term dehydration. *Journal of the North American Benthological Society*, **15**, 87–94.

Outridge P.M. (1988) Seasonal and spatial variations in benthic macroinvertebrate communities of Magela Creek, Northern Territory. *Australian Journal of Marine and Freshwater Research*, **39**, 211–223.

Pearson R.G., Benson L.J. & Smith R.E.W. (1986) Diversity and abundance of the fauna in Yuccabine Creek, a tropical rain forest stream. *Limnology in Australia* (eds P. De Decker and W.D. Williams), pp. 329–342. CSIRO/ W. Junk Publishers, Melbourne/Dordrecht.

Phillips E.C. & Kilambi. V. (1994) Utilization of coarse woody debris by Ephemeroptera in three ozark streams of Arkansas. *The Southwestern Naturalist*, **39**, 58–62.

Por F.D. (1995) The Pantanal of Mato Grosso (Brazil). *World's Largest Wetlands. Monographiae Biologicae.* Kluwer Academic Publishers, Dordrecht.

RADAM Brasil (1982) *Levantamento de recursos naturais* 26: Cuiabá. Departamento Nacional da Produção Mineral, Rio de Janeiro.

Richardson J.S. (1992) Food, habitat, or both? Macroinvertebrate use of leaf accumulations in a montane stream. *Freshwater Biology*, **27**, 169–176.

Serrano M.A.S. & Nolte U. (1996) A sit-and-wait predatory chironomid from tropical Brazil: *Fittkauimyia crypta* sp. n. (Diptera: Chironomidae). *Entomologica Scandinavica*, **27**, 251–258.

Webster J.R. & Benfield E.F. (1986) Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics*, **17**, 567–594.

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