

# Composition and diversity of Ephemeroptera (Insecta) nymph communities in the middle section of the Jacuí River and some tributaries, southern Brazil

Ana Emilia Siegloch<sup>1</sup>, Claudio Gilberto Froehlich<sup>1</sup> & Carla B. Kotzian<sup>2</sup>

1. Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, 14040-901 Ribeirão Preto, SP, Brazil. (siegloch@usp.br, cgfroeh@usp.br)
2. Departamento de Biologia, Universidade Federal de Santa Maria, Caixa Postal 5057, 97105-900 Santa Maria, RS, Brazil. (mickey@ccne.ufsm.br)

**ABSTRACT.** The taxonomic composition and diversity of assemblages of Ephemeroptera nymphs of four lotic environments in the central region of State of Rio Grande do Sul, a subtropical area in southern Brazil, were evaluated. Samplings were done monthly, with a Surber sampler, from June 2001 to May 2002, in the Jacuí River and three of its tributaries. The total number of nymphs collected in the four sampling sites was 11,007 in five families and 19 genera, of these, 11 are new records for the State. The highest diversity occurred in Point 4 ( $H' = 2.41$ ) and the lowest in Point 2 ( $H' = 1.69$ ). Point 4 had the highest environmental stability, conservation of the riparian vegetation and the lowest anthropic impact, while Point 2 presented a large environmental simplification due to a direct anthropic influence (e.g. domestic sewerage, trampling by cattle). The diversity of nymphs observed in the total area is high, compared to the estimated maximum theoretical diversity; a result of the high evenness and richness recorded. Rarefaction curves, calculated for a sample of 1,018 specimens, showed a similar expectation of richness for the four sampling sites. This result seems to be associated with the overall environmental homogeneity of the region caused by long-term alterations (land use and deforestation). In summary, higher diversity of Ephemeroptera nymph assemblages seems to be associated with habitat complexity, a good vegetation cover and a lower anthropic influence.

**KEY WORDS.** Ephemeroptera, nymphs, taxonomic composition, diversity, southern Brazil.

**RESUMO.** Composição taxonômica e diversidade das comunidades de ninfas de Ephemeroptera (Insecta) do curso médio do Rio Jacuí e afluentes, sul do Brasil. Foram analisadas a composição taxonômica e a diversidade das ninfas de Ephemeroptera de quatro ambientes lóticos localizados na região central do Rio Grande do Sul, região subtropical do sul do Brasil. As coletas foram realizadas mensalmente entre junho de 2001 e maio de 2002 no Rio Jacuí e em três afluentes, com um amostrador do tipo Surber. Foram coletadas 11.007 ninfas, distribuídas em cinco famílias e 19 gêneros, sendo 11 novos registros para o Estado. A maior diversidade foi encontrada no Ponto 4 ( $H' = 2,41$ ) e a menor no Ponto 2 ( $H' = 1,69$ ). O Ponto 4 apresenta maior estabilidade ambiental, conservação da vegetação ciliar e menor ação antrópica; enquanto o Ponto 2 possui grande simplificação ambiental, proveniente da influência antrópica direta no local (e.g. esgoto doméstico, pisoteio de gado). A diversidade de ninfas na área total foi alta, comparada com a diversidade teórica máxima estimada, resultante da alta riqueza e equidade registradas. As curvas de rarefação evidenciaram expectativa de riqueza relativamente semelhante para os pontos, em uma amostra comparável de 1.018 indivíduos. Este resultado provavelmente está associado à semelhança dos locais devida à continuada alteração ambiental da região (uso do solo e desmatamento). No geral, a maior diversidade das comunidades de ninfas de Ephemeroptera parece ser resultante da complexidade do hábitat, maior cobertura vegetal e menor ação antrópica.

**PALAVRAS-CHAVE.** Ephemeroptera, ninfas, composição taxonômica, diversidade, sul do Brasil.

Ephemeroptera nymphs are important components of freshwater benthic communities both by their abundance and diversity as by the wide variety of habitats they occupy (MERRITT & CUMMINS, 1996; SALLES *et al.*, 2004b; DOMÍNGUEZ *et al.*, 2006). About 3,000 species of mayflies in ca. 375 genera are known worldwide (DOMÍNGUEZ *et al.*, 2006). Mayflies are very diverse in the Neotropical Region, their nymphs being commoner in low to medium-order streams with stony bottoms. From Brazil, 66 genera and 170 species have been reported. The best known regions are the Southwest and North, followed by the South (SALLES *et al.*, 2004b; DIAS *et al.*, 2005; SIEGLOCH *et al.*, 2006; POLEGATTO & BATISTA, 2007).

Among published papers, most emphasize taxonomic aspects, but more recently several important contributions have been made on the ecology of running waters invertebrate communities, including the Ephemeroptera (MELO *et al.*, 2002; FROELICH & OLIVEIRA, 1997; OLIVEIRA *et al.*, 1997; OLIVEIRA & FROELICH, 1997;

BISPO *et al.*, 2001; BAPTISTA *et al.*, 2001, 2006). For the State of Rio Grande do Sul, no studies on Ephemeroptera nymph communities have been made. Previous studies concern macroinvertebrate communities of the Rio dos Sinos basin (STERNERT *et al.*, 2002; SANTOS *et al.*, 2003), of the Rio Tainhas and Rio Taquara (BUENO *et al.*, 2003), all in the northeast of the State, and in streams of the middle Jacuí River basin, in the central part of the State (AYRES-PERES *et al.*, 2006). In this area, ecological studies on the communities of Heteroptera (NERI *et al.*, 2005) and Trichoptera (SPIES *et al.*, 2006) have also been done.

In this context, considering the importance of faunistic surveys for obtaining basic information for biological and ecological studies and the poor knowledge of the mayfly fauna of State of Rio Grande do Sul, the aims here were to ascertain the taxonomic composition and the diversity of the mayfly nymph communities of the middle course of the Jacuí River basin.

## MATERIAL AND METHODS

The area is located in the central region of State of Rio Grande do Sul, in the transition zone between the physiographic regions known as the Lower northeastern Slope and the Central Depression, with altitudes varying from 50 to 500 m a.s.l. (PEREIRA *et al.*, 1989). The climate is humid subtropical with hot summers (Cfa of Köppen) (MALUF, 2000), with a rather uniform rainfall along the year, oscillating between 1,500 and 1,750 mm and the mean annual temperature varies between 18 and 20°C, with lowest temperatures in June and July (PEREIRA *et al.*, 1989). The vegetation of the Jacuí River valley and its tributaries belongs to the Seasonal Deciduous Forest, part of the Atlantic Forest Domain (MARCUSO *et al.*, 1998). At present this vegetation is much degraded and in different succession stages, from low shrubs to secondary growths distributed sparsely; likewise, along rivers, the riparian wood (DURLO *et al.*, 1982; LONGHI *et al.*, 1982; MARCHIORI *et al.*, 1982).

In the middle course of the Jacuí River a dam (U.H.E. Dona Francisca, 29°26'50"S, 53°16'50"W) was built and began operating in October 2000. The reservoir flooded 1,337 ha of land, increasing environmental stress.

Samplings were done monthly from June 2001 to May 2002 in the Jacuí River and three of its tributaries within the area close to the reservoir (Fig. 1). The sampling points are: Point 1 (29°42'29"S, 53°17'02"W) – Jacuí River,

at an altitude of 70 m and ca. 2 km downstream of the dam in a 7th order stretch, in Agudo municipality. A few samplings were done in a bay formed in the left bank during high waters. Daily fluctuations in water level, caused by the dam operations, are a peculiarity of this point. The area is open, with sparse riparian shrubs. Point 2 (29°28'03"S, 53°13'28"W) – Lajeado do Gringo River, a 4th order tributary at an altitude of 136 m, Ibarama municipality. Riparian vegetation is restricted to one bank and the stretch has been much altered by human occupation; the point stands at the back of a farm house. Point 3 (29°22'57"S, 53°12'08"W) – Lajeado da Gringa River, a 3rd order tributary at an altitude of 100 m, Ibarama municipality. A narrow riparian shrubby vegetation is present at both banks and, in the river, the stony substratum is frequently covered by the macrophyte *Podostemum* (Podostemaceae). Point 4 (29°21'17"S, 53°09'13"W) – Carijinho River, a 4th order tributary at an altitude of 111 m, Arroio do Tigre municipality. The riparian vegetation is in a relatively good state and *Podostemum* occurs attached to cobbles in the river.

For characterizing the degree of anthropic influence a scale of three subjective steps was used: 1 – low, 2 – medium, 3 – high intensity; for the vegetation cover a similar scale was used: 1 – relatively good conditions, 2 – shrub present on both banks, 3 – greatly altered (OLIVEIRA *et al.*, 1999). For turbidity, a scale from 1 – low to 2 – high, was based on a subjective evaluation (Tab. I). The hydrologic classification followed STRAHLER (1957).

Nymphs were collected in riffles with a Surber sampler of 0.36 m<sup>2</sup> in area and a 1 mm mesh. In each point three sampling units were taken, two near the bank and one at the centre, except in Point 1, where the units were collected near the left bank or, when the water level was high, in a bay. When the macrophyte *Podostemum* was attached to stones in the sampling area, it was scraped off and preserved in ethanol at 80%. Sampled material was sorted in the laboratory, identified with the aid of a stereomicroscope and counted. For the identification of the nymphs were used the keys of DOMÍNGUEZ *et al.* (2006) and SALLES *et al.* (2004a). Nymphs of Leptohiphidae were identified to species with the aid of a specialist and specialized bibliography.

Voucher specimens are deposited in the Invertebrate Collection of the Zoology Section of the Department of Biology, Federal University of Santa Maria (UFSM), State of Rio Grande do Sul, and in the Museum of Zoology, University of São Paulo (MZSP), State of São Paulo.

The diversity was evaluated by Shannon-Wiener (H') Diversity Index and by Pielou's Evenness Index (E), utilizing programs *Biodiversity Pro* and *Ecological Methodology* (McALECEE *et al.*, 1997; KREBS, 1999). The genera richness among the sites was compared by *T* test, described by POOLE (1974), utilizing program *Past 1.34* (HAMMER *et al.*, 2003).

Rarefaction curves were built for the sampling points utilizing a method similar to those of HURLBERT (1971) and SIMBERLOF (1972) that selected randomly *K*

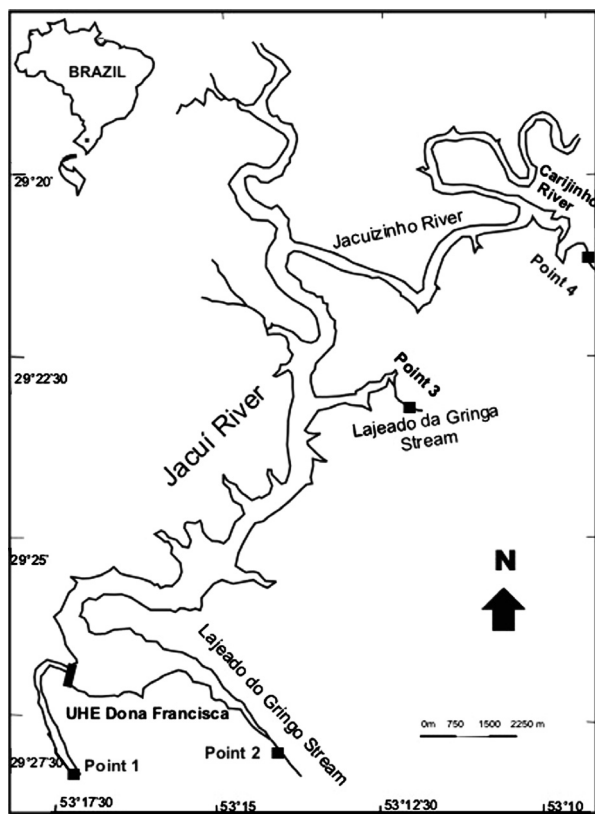


Fig.1. Map of the study area indicating the sampling points in the Jacuí River middle section and in three tributaries, situated in central region of the State of Rio Grande do Sul.

individuals from the samples. The number of genera was estimated for K individuals and the procedure was iterated 1,000 times. The mean of the number of genera obtained was considered as the estimated richness for K individuals. The method also allows to calculate the variance and confidence intervals, in this case at 95% significance. The program *EcoSim7* (GOTELLI & ENTSMIGEN, 2003) was used.

The accumulated species richness was estimated by collector curves by Coleman method (COLEMAN, 1981), obtained from 100 curves generated by random addition of samples, with help of the program *EstimateS 7* (COLWELL, 2004). According to COLWELL & CODDINGTON (1994), this method avoids fluctuations in the curves when samples are added and is excellent to evaluate how much the survey approaches the total richness of the area. Obtained species richness depends not only on the characteristics of the area but also on sampling effort. When an increase in the sampling effort does not result in an increase in the number of species, the total richness of the area has been attained (SANTOS, 2003).

## RESULTS

A total of 11,007 nymphs were collected, belonging to 19 genera in five families (Tab. II). Some Leptohiphidae were identified to species: *Leptohiphes plaumanni* Allen, 1967, *Tricorythodes santarita* Traver, 1959, *Tricorythopsis yacutinga* Molineri, 2001 and *Tricorythopsis gibbus* Allen, 1967.

The lowest abundance was presented by Point 1 (1,018 individuals) and the highest by Point 3 (4,920 individuals). It is important to emphasize that in July 2001 no sampling was done in Point 1 due to a spate. The richness obtained for the four sites was very similar, but was slightly higher in Point 4 (17 genera) and lower in Point 2 (14 genera) (Tab. II).

Leptophlebiidae presented the largest number of genera, eight, and also a good proportion of collected nymphs, 27.8%. Leptohiphidae and Baetidae had four genera each, and their share of collected nymphs were 38.85 and 31.38%, respectively.

There was no strong dominance of any genus. The most abundant were *Traverhypthes* Molineri, 2001 (13.37% of the total), *Baetodes* Needham & Murphy, 1924 (13.35%) and *Americabaetis* Kluge, 1992 (12.94%); the rarer ones were *Asthenopus* Eaton, 1871 (0.02%), *Hydrosmilodon* Flowers & Domínguez, 1992 (0.01%) and *Massartella* Lestage, 1930 (0.01%).

The overall diversity of mayfly nymphs ( $H' = 2.47$ ) represented 87.28% of the maximum theoretical diversity ( $H'_{max} = 2.83$ ). Point 4 had the largest diversity index and evenness values ( $p < 0.05$ ) (Tab. III). Along the year, diversity and evenness values oscillated strongly, especially those of Points 1 and 2; these points, on the whole, showed the lowest values and a sharp drop in November (Point 1), and in October and November (Point 2). Point 4 kept the highest values, except in April and May (Figs. 2, 3).

Rarefaction curves calculated for 1,018 individuals (total abundance of Point 1) showed an expected richness of 16 genera for Point 1, 15.7 genera for Point 4, 15.2 genera for Point 3 and 14 genera for Point 2. Even with the lower expected value for Point 2, the expected genera richness for all points were similar, especially when considering the confidence intervals (Figs. 4, 5).

Examining the genera accumulation curves, it may be seen that only the curve of Point 2 stabilized from January 2002 on. For the other points the asymptote was not reached, particularly for Point 1, and that the confidence intervals maintained large values to the end (Fig. 6).

Table I. Physical characterization of the four sampling points between June 2001 and May 2002 in the middle section of the Jacuí River and tributaries, southern Brazil. (1, low; 2, medium; 3, high intensity for the vegetation cover and anthropic influence; for turbidity, a scale from 1, low to 2, high intensity).

Point	Sites	Order of stream	Degree of canopy cover	Degree of anthropic influence	Degree of turbidity
1	Jacuí River	7 <sup>a</sup>	1	3	2
2	Lajeado do Gringo	4 <sup>a</sup>	2	3	1
3	Lajeado da Gringa	3 <sup>a</sup>	2	2	1
4	Carijinho River	4 <sup>a</sup>	3	1	1

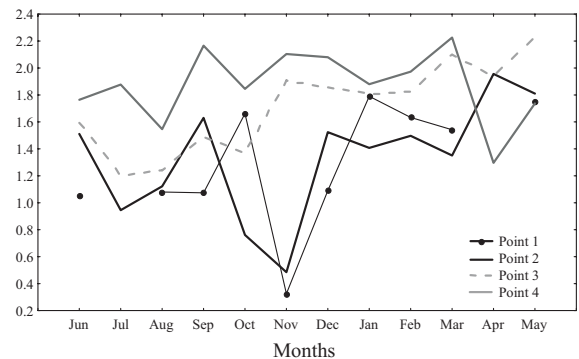


Fig. 2. Diversity index of Shannon-Wiener registered between June 2001 and May 2002 in the middle section of the Jacuí River and tributaries, southern Brazil.

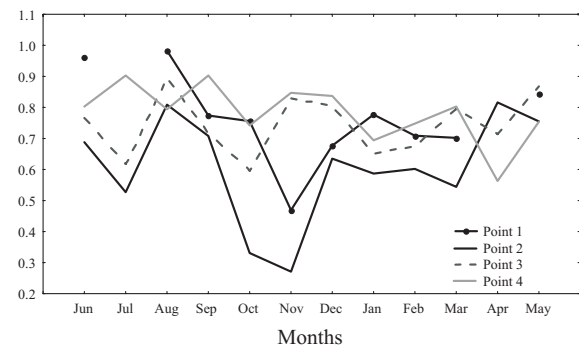


Fig. 3. Evenness index registered between June 2001 and May 2002 in the middle section of the Jacuí River and tributaries, southern Brazil.

Table II. Taxonomic composition and genera abundance of the Ephemeroptera nymphs communities sampled between June 2001 and May 2002 in the Jacuí River and three tributaries, southern Brazil (\* new genera registered for State of Rio Grande do Sul).

Taxa	Point 1	Point 2	Point 3	Point 4	Total
<b>BAETIDAE</b>					
<i>Americabaetis</i> Kluge, 1992	19	82	1049	274	1424
<i>Baetodes</i> Needham & Murphy, 1924*	17	823	440	189	1469
<i>Camelobaetidium</i> Demoulin, 1966	33	14	172	168	387
<i>Cloedes</i> Traver, 1938*	43	35	45	51	174
<b>CAENIDAE</b>					
<i>Caenis</i> Stephens, 1835	1	11	120	11	143
<b>LEPTOHYPHIDAE</b>					
<i>Leptohyphes</i> Eaton, 1882*	1	307	149	158	615
<i>Traverhyphes</i> Molineri, 2001*	351	55	779	287	1472
<i>Tricorythodes</i> Ulmer, 1920	23	23	765	77	888
<i>Tricorythopsis</i> Traver, 1958	26	17	588	671	1302
<b>LEPTOPHLEBIIDAE</b>					
<i>Farrodes</i> Peters, 1969*	147	22	39	85	293
<i>Homothraulius</i> Demoulin, 1955*	215	20	49	238	522
<i>Hydrosmilodon</i> Flowers & Domínguez, 1992*	1	0	0	0	1
<i>Massartella</i> Lestage, 1930	0	0	0	1	1
<i>Needhamella</i> Domínguez & Flowers, 1989	43	15	39	63	160
<i>Thraulodes</i> Ulmer, 1920*	28	578	303	213	1122
<i>Ulmeritoides</i> Traver, 1959*	0	0	8	101	109
<i>Ulmeritus</i> Traver, 1956*	0	66	373	413	852
<b>POLYMITARCYIDAE</b>					
<i>Asthenopus</i> Eaton, 1871*	2	0	0	0	2
<i>Campsurus</i> Eaton, 1868	68	0	2	1	71
<b>Total</b>	<b>1018</b>	<b>2068</b>	<b>4920</b>	<b>3001</b>	<b>11007</b>

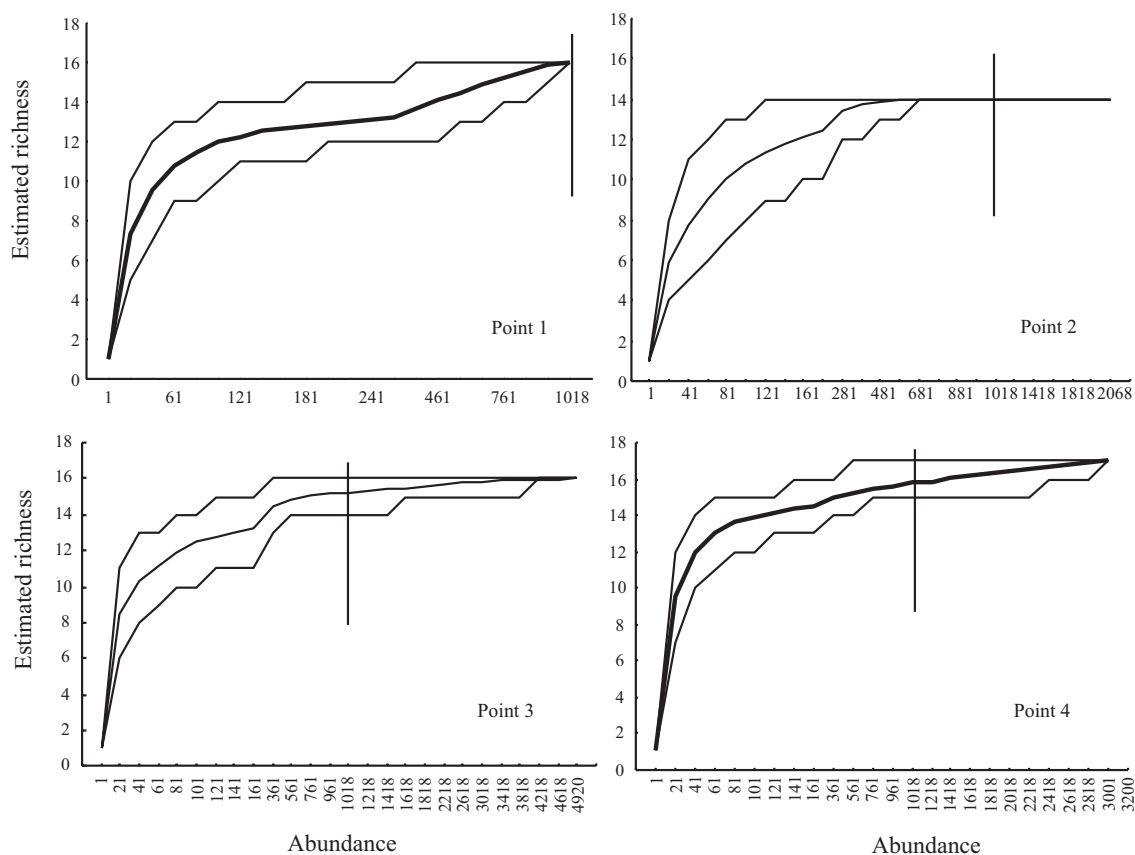


Fig. 4. Rarefaction curves of Ephemeroptera nymphs genera registered between June 2001 and May 2002 in the Jacuí River middle section and in three tributaries, southern Brazil. The upper and lower lines indicate confidence intervals (95%) computed for each point, and the bars represent a sub-sample of the 1,018 individuals.

Table III. Diversity index ( $H'$ ),  $H_{max}$ , Evenness (E) and Richness calculated for the four sampled stations and the total of the site in the middle section of the Jacuí River and tributaries, State of Rio Grande do Sul, based from data obtained between June 2001 and May 2002.

Index	Point 1	Point 2	Point 3	Point 4	Total
Shannon-Wiener ( $H'$ )	1.98	1.69	2.24	<b>2.41</b>	2.47
$H_{max}$	2.71	2.64	2.77	2.77	2.83
Evenness (E)	0.73	0.64	0.81	<b>0.87</b>	0.87
Richness	16	14	16	17	19

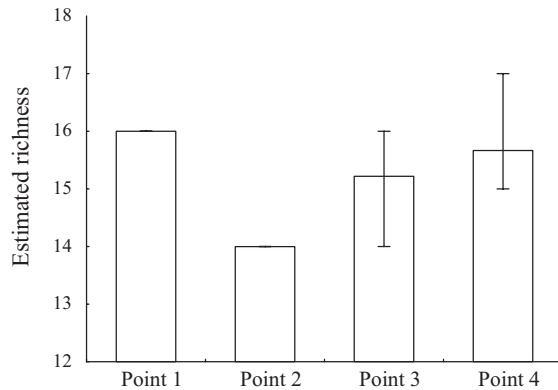


Fig. 5. Estimated richness comparison for 1,018 individuals sampled between June 2001 and May 2002 for Ephemeroptera nymphs assemblages in four sites studied in the Jacuí River and effluents, southern Brazil; for points 3 and 4 the confidence intervals (95%) are indicated.

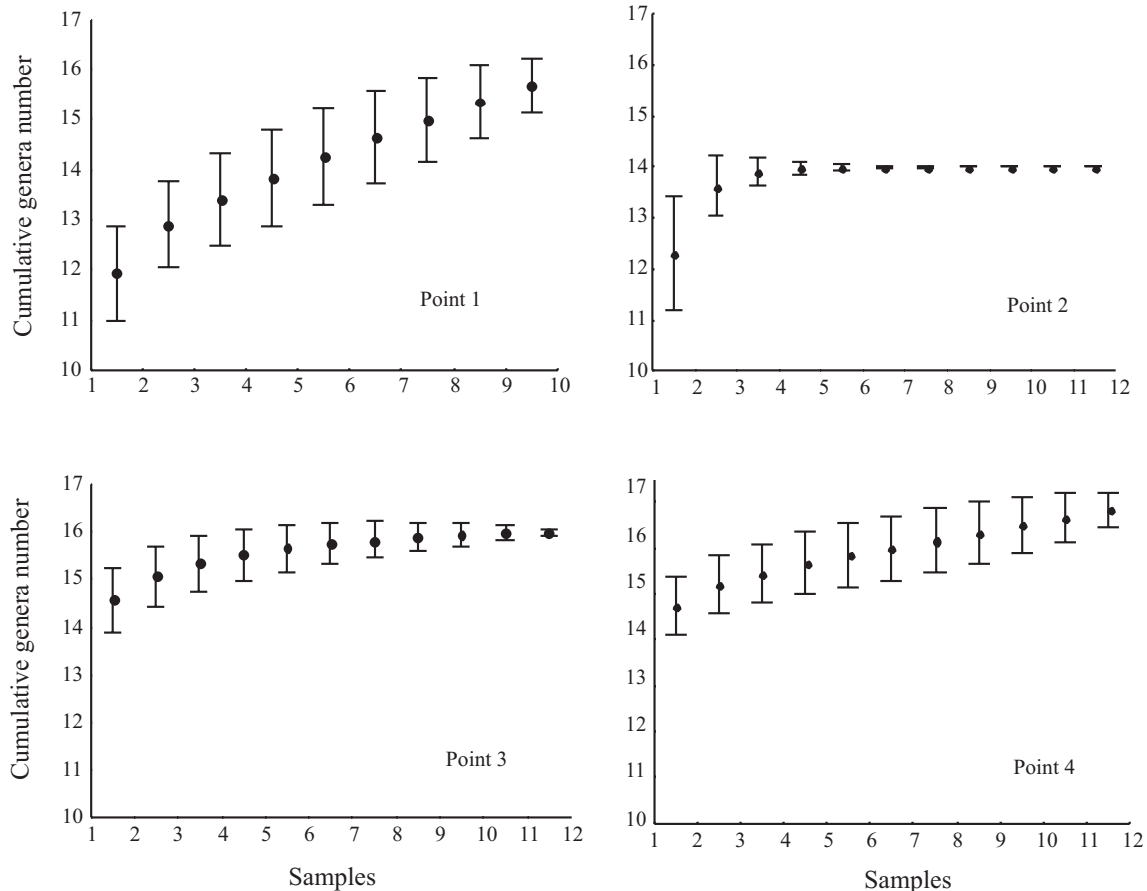


Fig. 6. Accumulation curves of genera for the four Ephemeroptera communities in the middle section of the Jacuí River and tributaries, southern Brazil, built from data obtained between June 2001 and May 2002. The level bars indicate confidence intervals (95%) computed for each point.

## DISCUSSION

Brazilian Ephemeroptera were, until the 1980s, poorly known in all aspects, taxonomic (HUBBARD, 1982), biological and ecological (e.g., FROELICH, 1969). Since 1990 there has been an increasing number of important contributions, chiefly taxonomic (e.g., DA-SILVA, 1992; LOPES *et al.*, 2003; MOLINERI & DOMÍNGUEZ, 2003). Biological and specially ecological studies are still scarce, what may be due to the lack of faunistic surveys, except for a few isolated ones, in the vast hydrographic system of the country (SALLES *et al.*, 2004b).

Of the 66 genera reported for Brazil, 19 (28.8%) were collected in the studied area, of which 11 are new records for State of Rio Grande do Sul. Sixteen genera were previously reported for the state (SANTOS, 2003; SALLES *et al.*, 2004b), of which 9 were found in the study area. For the States of Rio de Janeiro and São Paulo, better surveyed, the numbers are 28 and 30 respectively (SALLES *et al.*, 2004b). Three of the four identified species of Leptohiphidae (*Leptohiphes plamanni*, *Tricorythodes santarita* and *Tricorythopsis gibbus*) are also new records for the state.

The family Leptophlebiidae is widely distributed but attains its maximum diversity in the Southern Hemisphere with the subfamily Atalophlebiinae. In the Neotropics, there are more than 50 described genera and they are a very characteristic element of streams (SAVAGE,

1987; HUBBARD, 1990). In Brazil, Leptophlebiidae and Baetidae are the most numerous families, each with 20 genera (61% of all genera); this is a consequence both of the richness of these families and of the emphasis given to them in taxonomic studies (SALLES *et al.*, 2004b). In this study, the Leptophlebiidae were the most diversified family, with eight genera. Notwithstanding the number of genera of Baetidae occurring in Brazil, only four taxa were found. This may be due to the method used, that sampled predominantly riffles. The genera *Baetodes*, *Cloeodes* Traver, 1938 and *Camelobaetidius* Demoulin, 1966, found in this study, occurred also in riffles in the Intervalas State Park, in the State of São Paulo (Bispo, pers. comm.). *Americabaetis*, on the other hand, occurs widely in many habitats, including impacted ones.

Leptohiphidae presents six genera in Brazil (DIAS *et al.*, 2005, 2006). Here four genera were collected and the family was the most abundant. Leptohiphidae nymphs are common at the margins of streams, where they live preferentially in depositional areas. In this study, two of the three sampling units were taken at the margins, where water flows slower, allowing a greater deposition of organic matter. Where *Podostemum* was present, probably the retention of fine organic particles was enhanced, increasing the food supply to these collector-gatherer nymphs. The macrophytes also offer shelter against the water current (EDMUNDS *et al.*, 1976). The presence of these characteristics probably explain the richness and abundance of Leptohiphidae in Points 3 and 4.

Nymphs of all genera collected had a relatively even abundance distribution, except *Hydrosmilodon*, *Massartella* and *Asthenopus*, collected only occasionally. Of these three genera, there is not enough information about *Hydrosmilodon*; *Massartella* nymphs are widely distributed and more often found in leaf packs in depositional places (FROELICH & OLIVEIRA, 1997) while *Asthenopus* nymphs are burrowers in fallen wood, in roots and in stems of macrophytes, habitats not sampled in this study.

Richness and evenness are key elements in the evaluation of diversity and, with the same richness, communities in which there are no dominant species have a higher diversity. Here the lowest diversity index was obtained in Lajeado do Gringo River (Point 2), that has low values of richness and evenness, the latter due to high numbers of *Baetodes*. This point is located near a farmstead and is subjected to direct human influence with domestic sewerage and trampling by cattle that causes local instability and a reduction of the riparian vegetation. In this stretch the stream is open to the sunlight, is shallow and suffers organic enrichment, conditions that promote the development of periphyton and favour the dominance of *Baetodes*, a scraper that lives on the surface of stones (EDMUNDS *et al.*, 1976).

The largest diversity index was obtained in Carijinho River (Point 4), that presented also the largest richness and evenness. This point has better environmental conditions, better kept riparian trees and more food resources (SPIES *et al.*, 2006), which permitted the occurrence of a diverse fauna. The presence of a riparian wood and also the presence of macrophytes

adhered to the stones probably contributed to give the stretch a higher stability and better offer of food resources. The trees contribute with allochthonous resources and, as the stretch is partially open, the autochthonous primary production is also good. Besides, the macrophytes provide shelter for the animals. It should be noted that this stream receives also sewage effluents upstream, but as it is turbulent and at a sufficient distance, it arrives at the sampling point well self-depurated.

Looking at the temporal variation in diversity, the sharp fall in November in Point 1 was due to the low abundance and richness, while that in October-November in Point 2 was due to the rise in abundance of *Baetodes* what decreased evenness and, in consequence, diversity.

The high diversity of mayfly nymphs in the middle course of the Jacuí River, as compared with the theoretical maximum for the area, reflects the high richness and evenness found. According to CONNELL (1978), a greater diversity should be found in environments subject to intermediate disturbance level, what would allow the coexistence of a great variety of taxa. HILDREW & TOWNSEND (1987) state that these environments, together with a high productivity, permit that highly competitive species but inefficient colonizers coexist with poorly competitive species but good colonizers. In the studied area, disturbance factors such as a sparse riparian vegetation, soil use in the valley, input of organic sewage, although depurated in the studied points, could have enhanced a high productivity and availability of organic particles and as a consequence the high diversity.

Diversity indexes are important for comparing environments, both for an evaluation of their status as for conservation measures, but it is recommended that richness and abundance should be considered separately (GOTELLI & GRAVES, 1996). Here, to evaluate richness alone, the rarefaction method was used. The rarefaction curves showed, on the whole, a similar expected richness for all points, probably a consequence of the general alteration of the whole region. In spite of local differences such as size of the river, presence of riparian vegetation and anthropic influence, and the fact that some samplings in the 7th order Jacuí River were done in a bay when the river was full, all points were similar as regards substrata and other environmental descriptors. The lower expected richness found in Point 2 mirrors the large local environmental simplification determined by immediate human influence.

Collector curves were worked out to see if the sampling effort was adequate to ascertain the richness of the four points. In Point 2 the curve stabilized, an indication that the sampling effort was adequate. This rarely happens in tropical ecosystems due to their large diversity (SANTOS, 2003). The result for Point 2 points to the environmental simplification of the place that does not offer the ecological requirements for a higher diversity. For the other points collector curves showed that a more intensive effort was needed to sample all the fauna, specially for Point 1, where two distinct spots were sampled, the channel and a bay. Obviously if other mesohabitats besides stony bottoms were sampled, richness would be higher.

In conclusion, in the studied area mayfly nymph communities presented a high richness, probably a consequence of the availability of food resources. The expected richnesses estimated by the rarefaction method for the four sampling points were on the whole similar, probably a consequence of the alteration and simplification to which the whole region has long been subjected, as well as by the homogeneity of the substrata and environmental factors. Local differences such as size of the river, presence of riparian vegetation and anthropic impact were not important enough to cause differences in the composition of genera. Point 4, however, with its better environmental conditions and a slightly higher diversity, may be showing a dampening of the impacts.

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