Universidade Federal de São Carlos
Centro de Ciências Biológicas e da Saúde
Programa de Pós Graduação em Ecologia e Recursos Naturais

Padrões de diversidade e organização temporal de Chironomidae (Diptera) em um córrego tropical

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Dissertação apresentada ao Programa de Pós Graduação em Ecologia e Recursos Naturais da Universidade Federal de São Carlos, como parte dos requisitos para obtenção do Título de Mestre em Ecologia.

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RESUMO

Neste estudo nós investigamos a dinâmica temporal de Chironomidae em um córrego florestado localizado no sudeste do Brasil. Primeiro, nós analisamos alguns padrões de diversidade através da descrição de duas relações macroecológicas (tamanho do corpo-riqueza de espécies e tamanho do corpo-abundância) e também testamos se essas relações variavam na escala intra-anual. Segundo, nós analisamos a fenologia da emergência usando uma série temporal de 48 coletas semanais. De maneira geral, ambas a riqueza de espécies e a abundância apresentaram um pico nos tamanhos intermediários, além disso, estas relações mostraram ser variáveis nesta escala intra-anual; a emergência de Chironomidae não foi estacional, e também não foi relacionada a nenhuma variável ambiental medida; por outro lado, as espécies mais persistentes (*Caladomyia* sp. 1, *Endotribelos* sp. 4, *Caladomyia* sp. 2, e *Corynoneura* sp. 1) parecem apresentar alguma estrutura temporal na emergência, provavelmente relacionada ao fotoperíodo e a temperatura mínima do ar respectivamente; não houve sincronia na emergência das espécies, com a maioria dos taxa emergindo juntos ao longo do ano; a riqueza de espécies assim como a composição taxonômica não mudaram ao longo do tempo.

Palavras-chave: Córregos tropicais, Fenologia, Insetos aquáticos, Macroecologia.

ABSTRACT

In this study we investigated the temporal dynamics of a chironomid assemblage in a forested stream located in southeastern Brazil. First, we analyzed some diversity patterns of this assemblage by describing two macroecological relationships (body size-species richness and body size-abundance) and by testing with they vary in an intra-annual scale. Second, we analyzed the emergence phenology using a time series of 48 weekly samples. In general, both species richness and abundance peaked on intermediate body sizes, moreover these relationships showed to be variable in this intra-annual scale; Chironomidae emergence was not seasonal, neither was related to any environmental variables measured; on the other hand, the most persistent species (*Caladomyia* sp. 1, *Endotribelos* sp. 4, *Caladomyia* sp. 2, and *Corynoneura* sp. 1) appeared to have some temporal structure on emergence, probably associated with photoperiod and minimum air temperature respectively; there was no synchrony in species emergence with most taxa emerging together through the year; species richness as taxonomic composition did not change over time.

Key-words: Aquatic insects, Macroecology, Tropical streams, Phenology.

SUMÁRIO

1- INTRODUÇÃO GERAL

A teoria ecológica por muito tempo tem considerado a diferenciação do nicho como o principal mecanismo de coexistência entre espécies em ambientes heterogêneos (MacArthur, 1958; MacArthur & Levins, 1967; Kronfeld-Schor & Dayan, 2003). Geralmente, a separação de nichos envolve o habitat, os recursos alimentares, o eixo do tempo, ou uma combinação destes. Segundo Gotelli & Graves (1996), o tempo representa um eixo de recurso importante, o qual pode ser dividido por uma comunidade de espécies coexistentes.

Variações estacionais na floração de plantas e no período de atividade de insetos constituem uma evidência primária da divisão do tempo pelas espécies. Por exemplo, animais que forrageiam em diferentes horas do dia podem reduzir a competição por um recurso limitado e plantas que florescem em diferentes épocas do ano podem reduzir a competição por animais polinizadores (Stiles, 1977).

Historicamente, o debate dedicado ao papel das forças que controlam as dinâmicas populacionais tem sido centrado em três temas (Bjørnstad & Grenfell, 2001): *i*) a importância relativa de controles bióticos e abióticos nas flutuações animais (influência estocástica em pequena escala versus fatores climáticos versus interações entre indivíduos da mesma espécie ou de diferentes espécies); *ii*) o impacto de processos intrínsecos (intraespecíficos) contra o impacto de processos extrínsecos (interações no nível comunidade) e *iii*) a dimensão das flutuações populacionais, uma vez que as populações estão "dentro" de comunidades ricas e são afetadas numerosas interações, será que modelos simples que envolvem uma ou poucas espécies são capazes de capturar padrões de flutuações?

Essas considerações nos fazem remontar a uma das questões mais antigas da ecologia ou mesmo da história natural: *Por que o número de espécies e indivíduos de uma dada comunidade varia no tempo?*

Esta questão que pode até parecer uma pergunta faustosa, tem fascinado ecólogos e observadores da natureza desde muito tempo. Por um século ou mais, pesquisas têm sido direcionadas para estudar ciclos de populações, sejam eles periódicos, aleatórios ou caóticos (Cazelles & Stone, 2003) e foi através dessa pergunta que tentamos estruturar todo o nosso trabalho. Portanto, nesta dissertação nós analisamos e discutimos a variação temporal de uma comunidade animal de um ambiente bem preservado.

A solução para responder a pergunta acima é complexa e requer que tenhamos antes respostas de outras perguntas mais simples. Segundo Wiegert (1988), de uma maneira simplista, uma área do conhecimento pode ser vista passando por três estágios ao longo de seu amadurecimento: “O que?”, “Como?” e “Por quê?”. O primeiro estágio é fortemente descritivo e voltado ao estabelecimento do fenômeno de interesse; o segundo estágio diz respeito à maneira como os objetos estão arranjados e como eles funcionam; já o estágio “Por quê?” é aquele onde se desenvolve o entendimento de um mecanismo. Sendo assim, uma parte deste trabalho é voltada à descrição de padrões ainda pouco compreendidos para região Neotropical.

Assim como é feito na maioria dos estudos ecológicos, nós trabalhamos com um recorte da comunidade, já que é logisticamente inviável analisar todas as populações de uma área. Para tal, decidimos utilizar um grupo taxonômico, a família Chironomidae (Ordem Diptera), como fonte de dados de nossa investigação.

Através da análise de um componente da fenologia reprodutiva destes organismos, a emergência dos adultos, nós examinamos alguns dos atributos e relações mais estudados em ecologia de comunidades (ex. abundância de indivíduos, riqueza de espécies, tamanho do corpo e a relação entre essas variáveis) ao longo de uma série temporal em um córrego tropical. A fenologia reprodutiva é propriedade chave de uma população (Kaspari *et al.*, 2001), pois assim como as plantas necessitam ajustar seu tempo para floração, frutificação e germinação (Stiles, 1977), os insetos também necessitam ajustar seu tempo para encontrar condições adequadas para, por exemplo, emergir, encontrar um parceiro ou um local para ovopositar.

Isso gera um potencial conflito. Para aqueles organismos que vivem em regiões de clima temperado, mudanças estacionais no clima são simples fatos da vida. Estações frias alternam com estações quentes, períodos chuvosos com períodos secos e as oportunidades para o crescimento podem durar apenas algumas semanas ou meses do ano (Kaspari *et al.*, 2001). Quanto mais alta a latitude, menor é a estação de crescimento, isto é, o período do ano em que o ambiente oferece condições necessárias para a alimentação e reprodução. As estações climáticas tendem a se traduzir em uma periodicidade nas atividades dos organismos (Wolda, 1992). São numerosos os trabalhos que descrevem os aspectos estacionais dos ciclos de vida de insetos do Hemisfério Norte (Wolda, 1988).

No entanto, consideremos a região Neotropical. Mudanças estacionais na temperatura tendem a ser mínimas ou mesmo ausentes. As oportunidades para o crescimento podem ocorrer durante o ano todo, uma vez que é a temperatura que constringe a fenologia atuando na atividade fisiológica do organismo (Precht *et al.* 1973). Isto não quer dizer que nos trópicos não existem estações climáticas bem definidas. Nestes, os períodos chuvosos tendem a alternar com um ou dois períodos de estiagem a cada ano (Wernstedt, 1972). As estações secas (ou de estiagem) podem ser expressas como estações “mais” secas ou mesmo podem ser completamente ausentes.

Estudos sobre os padrões de emergência de insetos aquáticos em ambientes tropicais ainda são escassos e os fatores que controlam este fenômeno são pobremente entendidos (Flint & Masteller, 1993). Alguns autores têm mostrado que nos trópicos ocorrem desde padrões altamente estacionais até correlações fracas entre emergência e clima, mas nenhum necessariamente não-estacional (Coffman & de la Rosa, 1998; McElravy *et al.*, 1982; Wolda & Fisk, 1981).

Tem sido sugerido que a precipitação e o fotoperíodo seriam os fatores chave na regulação dos padrões de emergência nestes ambientes (Anderson & Sedell, 1979; Coffman *et al.*, 1971). Entretanto, é reconhecido que as fases da lua influenciam a emergência de algumas espécies de Ephemeroptera e outros insetos aquáticos nos trópicos (Corbet, 1958, 1964; Wolda & Flowers, 1985). A lua controla o movimento das marés e geralmente propicia alguma iluminação. No lago George (Uganda), não foi detectado nenhum tipo de estacionalidade na emergência de *Procladius brevipetiolatus* Goetghebuer, mas uma clara periodicidade lunar pode ser observada, com abundâncias mais altas durante o primeiro quarto do ciclo lunar (McGowan, 1975). Apesar de periodicidades lunares na emergência ocorrerem em diversas espécies de Chironomidae tropicais, não há trabalhos que investigem o fenômeno e os mecanismos que o controlam ainda não foram elucidados (Armitage, 1995).

Dados coletados ao longo de uma série temporal, na maioria das vezes, são compostos em duas classes de elementos (Legendre & Legendre, 1998): a tendência (mudanças determinísticas) e a estacionalidade (variabilidade periódica). O primeiro pode ser um componente linear ou não linear que muda ao longo do tempo e não se repete, ou pelo menos não é capturado pelo intervalo de tempo amostral (por ex. um “platô” seguido por um período de crescimento exponencial). Já o segundo, pode ser igual ao exemplo anterior, porém ele se repete em intervalos sistemáticos ao longo do tempo.

Na natureza é possível que os dois componentes citados acima existam ao mesmo tempo em um conjunto de dados, o que pode gerar confusão na análise e interpretação dos resultados. Quando isso acontece, um padrão que existe em uma escala menor (por ex. ciclos lunares) pode não ser detectado devido à presença de uma tendência em uma escala maior (por ex. variação intra-anual). Neste caso, a solução é extrair a tendência dos dados (Legendre

& Legendre, 1998) e então prosseguir na análise da série temporal. Por esse e pelos outros motivos já citados, nosso planejamento amostral foi construído para contemplar a detecção de um possível ciclo lunar na emergência de Chironomidae.

1.1 Considerações sobre o grupo

Os insetos da família Chironomidae (ordem Diptera) estão entre os mais abundantes e diversos em ambientes aquáticos continentais (Cranston, 1995). Em condições ambientais extremas como baixos níveis de oxigênio dissolvido, suas larvas podem ser os únicos insetos presentes no sedimento.

Espécimes de Chironomidae podem ser encontrados desde as mais altas montanhas (5600 m) no Himalaia (Saether & Willassen, 1987) até regiões abissais a 1000 m de profundidade no Lago Baikal (Cranston, 1995). Segundo este mesmo autor, em termos geográficos, os quironomídeos são o grupo de insetos holometábolos mais amplamente distribuído no mundo.

Algumas estimativas apontam que possa existir mais de 15000 espécies de Chironomidae (por ex. Coffman, 1995), entretanto, a base de dados destas estimativas merece ser analisada criticamente. Assim como em outros grupos de insetos, a fauna do Hemisfério Norte (Europa e Estados Unidos principalmente) é melhor conhecida. Com exceção do "Guia de identificação e diagnose de larvas de Chironomidae do Estado de São Paulo" (Trivinho-Strixino & Strixino, 1995) e algumas revisões de gêneros, não existem manuais de identificação que contemplem outros estágios de vida dos Chironomidae no Brasil.

Certamente os Chironomidae são habitantes ubíquos de locais enriquecidos organicamente, porém a visão "popular" que este é o ambiente mais comum, ou mesmo o único para estes animais está longe de ser verdade. A amplitude de habitats que suas larvas podem ocupar vai desde ambientes lóticos (rios e córregos), lênticos (represas e lagoas) e o mar até locais inesperados como poças temporárias, plantas em que haja acúmulo de água (por ex. bromélias) além daqueles que são terrestres. Além disso, as larvas de Chironomidae não são restritas ao sedimento ou outras superfícies expostas à água, muitas habitam águas intersticiais, troncos em decomposição, raízes de plantas e até mesmo frutos caídos.

Neste contexto, nosso objetivo nesta dissertação foi compreender como a emergência e a composição de Chironomidae em um córrego tropical variam no tempo. Para atingirmos nosso objetivo trabalhamos em dois temas complementares, no primeiro analisamos e discutimos a fenologia reprodutiva de Chironomidae, considerando três escalas temporais: semanal, mensal e estacional; já no segundo tema descrevemos e discutimos alguns padrões macroecológicos (relação tamanho do corpo-riqueza de espécies e tamanho do corpo-abundância de indivíduos) em Chironomidae e analisamos se estes padrões variam na escala intra-anual. Esses temas são discutidos separadamente em dois capítulos em formato de artigos científicos para publicação, já que as revistas que escolhemos para submetê-los são estrangeiras, eles estão escritos em inglês. Segue abaixo uma súmula dos principais aspectos que foram desenvolvidos nos dois capítulos.

Capítulo I: Relação entre riqueza de espécies, abundância e tamanho do corpo de uma assembléia tropical de Chironomidae: em busca de padrões.

A Macroecologia utiliza uma abordagem que enfatiza a existência de padrões nas comunidades, que refletem a operação de princípios ou leis naturais. Apesar da complexidade dos ecossistemas, alguns fenômenos parecem ditar como alguns atributos ecológicos mudam com o tamanho do corpo. Por exemplo, parece que a riqueza de espécies e a abundância de indivíduos estão fortemente relacionadas com o tamanho do corpo destes indivíduos. Enquanto as relações entre as espécies e o ambiente tendem a ser mais fracas, em muitos casos o tamanho do corpo ainda é o melhor preditor que temos na análise da variação de parâmetros ecológicos que envolvam muitas espécies. Portanto, analisar essas relações em uma comunidade pode nos ajudar a compreender como a diversidade de espécies está estruturada. Neste capítulo exploramos essa abordagem para descrever e analisar pela primeira vez no Brasil os padrões macroecológicos citados acima para os Chironomidae. Além disso, testamos se os padrões encontrados variavam na escala intra-anual, uma vez que alguns autores consideram essas relações como propriedades estáveis dos sistemas.

Capítulo II: Padrões de emergência de uma diversa assembléia tropical de Chironomidae: existe apenas aleatoriedade?

Muitas áreas do conhecimento como a biologia, ecologia e metereologia investigam fenômenos que oscilam no tempo. Na ecologia, geralmente os pesquisadores estão interessados em mudanças que ocorrem periodicamente e isto se deve ao fato de que muitos fenômenos ecológicos são fortemente influenciados por ritmos geofísicos e também por ritmos endógenos dos organismos. Estudos sobre a fenologia de populações se dedicam a investigar algum componente do ciclo de vida dos indivíduos ao longo de uma série temporal. A fenologia pode ser moldada por uma mistura de fatores abióticos, bióticos e históricos, os quais podem dizer muito sobre a estrutura das populações estudadas. A emergência pode ser considerada um componente essencial da fenologia de insetos aquáticos, uma vez que é através deste fenômeno que acontece a transição do meio aquático para o aéreo, onde ocorre a reprodução destes organismos. Neste capítulo, nós examinamos a emergência de Chironomidae em um córrego tropical através da análise deste fenômeno ao longo de uma série temporal.

1.2 Considerações sobre a área de estudo e o procedimento amostral

O córrego em que realizamos nosso experimento (Córrego do Fazzari) está inserido na microbacia do Rio Monjolinho, bacia do Rio Tietê, estado de São Paulo (Figura 1). O clima da região é do tipo tropical de altitude (Cwa na classificação de Köppen), com verão chuvoso e inverno seco. A estação mais seca vai de Junho até Agosto e a chuvosa de Setembro a Maio.

O segmento estudado localiza-se em uma reserva legal na área não urbanizada do *campus* da Universidade Federal de São Carlos. A vegetação ripária deste córrego (Figura 2) foi classificada por Roque & Trivinho-Strixino (2005) como sendo Floresta Atlântica semi-decídua (Morellato & Haddad, 2000).

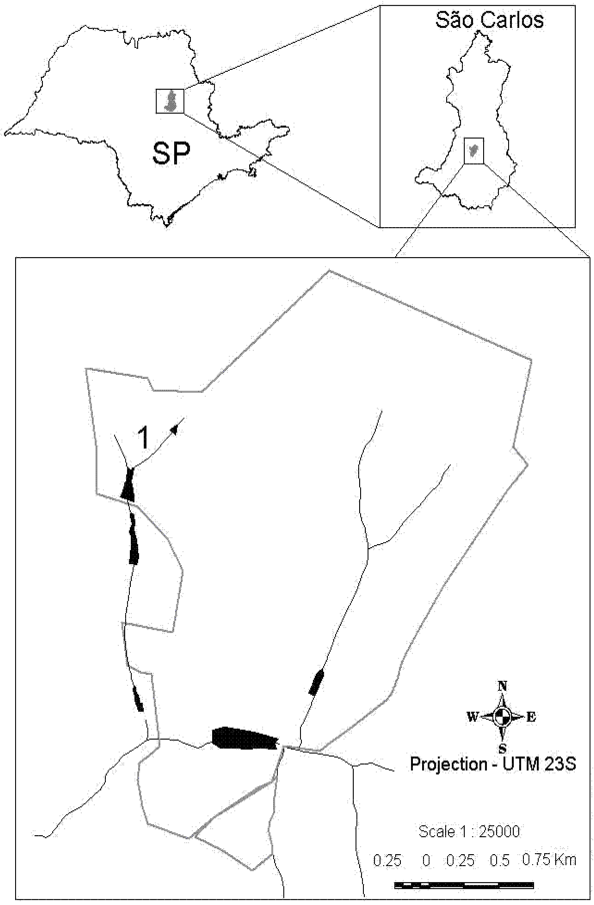

Figura 1. Mapa com a localização do Córrego do Fazzari (1) na cidade de São Carlos, SP. Fonte: A. Fushita.

Figura 2. Vista geral da vegetação ripária do Córrego do Fazzari. Fonte: T. Siqueira.

O córrego do Fazzari possui elevado teor de oxigênio dissolvido, baixa condutividade elétrica, ausência de macrófitas e o substrato é caracterizado pela predominância de trocos e folhas (Figura 3). As características gerais do segmento estudado estão apresentadas na tabela I.

Figura 3. Aspecto geral do substrato (folhas e troncos) do Córrego do Fazzari. Fonte: S. Trivinho-Strixino.

Tabela I. Principais características físicas e químicas do córrego do Fazzari.

Inclinação	Baixa
Profundidade (m)	< 0,5
Largura (m)	<1,5
Condutividade (μS cm $^{-1}$)	0,003
pH	4,75
O_2 dissolvido (mg^{-1})	6,95
Salinidade	0
Substrato	Lodoso

Neste estudo nós optamos pela utilização da coleta de exúvias de pupas, pois o uso desta metodologia para a análise da emergência oferece algumas vantagens em relação aos adultos. Segundo Coffman & Ferrington (1996) as vantagens desta técnica são bem documentadas e incluem todas as espécies que emergem na superfície da água; a maioria dos táxons pode ser mais facilmente separada e identificada em comparação com os adultos; grande número de espécimes pode ser coletado em curto espaço de tempo; como as coletas são realizadas na superfície ou na coluna d'água, os substratos não ficam sujeitos a perturbações; a maioria das espécies emergindo pode ser obtida independentemente do microhabitat larval e as exúvias permanecem flutuando por pelo menos um dia.

Segundo os mesmos autores, diferenças morfológicas são mais fáceis de serem reconhecidas em espécies congenéricas, utilizando-se exúvias, do que seus adultos correspondentes. Isso é muito importante principalmente em sistemas aquáticos tropicais, onde muitos gêneros são representados por espécies simpátricas muito similares (Coffman & de la Rosa, 1998).

Além disso, como as exúvias não possuem tecidos, o processo de diafanização na confecção de lâminas torna-se desnecessário, permanecendo as características diagnósticas da pupa perfeitamente discerníveis nos espécimes montados entre lâmina e lamínula. Em alguns exemplares, a exúvia da larva, ou o adulto farado podem permanecer presos nas exúvias possibilitando a adequada associação entre as três fases (larva, pupa e adulto) e permitindo uma correta identificação da espécie.

Procedimento amostral

Considerando a complexidade espacial e temporal do fenômeno da emergência seria metodologicamente e logisticamente inviável contemplar todas as escalas espaciais e temporais do fenômeno sem perder robustez analítica. Assim optamos por um desenho amostral que, pelo menos exploratoriamente, nos permitisse uma visão geral do processo contemplando os nossos objetivos.

Nós selecionamos um segmento de córrego que foi seccionado em três trechos de mesmo tamanho e visualmente similares, sendo que cada um deles continha uma corredeira e um remanso. No limite dos trechos foi disposta uma rede de deriva (“drift”) tipo Brundin com abertura de malha de 200 µm (Figura 4) e deixada no local por uma hora. Após esse tempo, utilizamos uma rede de mão (200 µm) para coletar as exúvias que naturalmente estivessem acumuladas em remansos, troncos ou em qualquer local em que houvesse acúmulo de material.

As coletas foram realizadas sempre dois dias após o início de cada fase da lua (crescente, cheia, minguante e nova) durante um ano, totalizando 48 amostras. Nós optamos por sistematizar as datas de coleta, ao invés de aleatorizar, pois desta maneira o possível efeito do ciclo lunar seria igual para todas as amostras.

O material retido nas redes foi acondicionado em recipientes plásticos contendo água e transportado para o laboratório onde se procedeu a triagem das exúvias em bandejas de polietileno sobre fonte de luz (bandejas transluminadas). As exúvias, assim obtidas, foram preservadas em álcool a 70%.

Figura 4. Rede de deriva tipo "Brundin" instalada no córrego do Fazzari durante procedimento de coleta. Fonte: T. Siqueira.

Realizamos a identificação das exúvias sob lupa e/ou microscópio com o auxílio de chaves de identificação (Borkent, 1984; Coffman & Ferrington, 1996; Wiederholm, 1986), descrições originais e consultas a especialistas. Os exemplares foram depositados na coleção de Chironomidae do Laboratório de Entomologia Aquática da Universidade Federal de São Carlos.

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Capítulo I

Relação entre riqueza de espécies, abundância e tamanho do corpo de uma assembléia tropical de Chironomidae: em busca de padrões.

2. SPECIES RICHNESS, ABUNDANCE, AND BODY SIZE RELATIONSHIPS FROM A TROPICAL LOTIC CHIRONOMID ASSEMBLAGE: LOOKING FOR PATTERNS.

Abstract

We investigated two of the most studied relationships in the macroecological research program (species richness vs. body size and abundance vs. body size) of a local chironomid assemblage from southeastern Brazil. Although numerous studies have examined these relationships, few have investigated how they vary at different temporal scales. We used data from a forested stream to document and examine these relationships at an intra-annual scale. Both the body size distribution and the abundance-body size relationship varied temporally. In some months the body size distribution was skewed to the right, whereas in others it approached normality. We found both linear relationships, with different values of slopes, and polygonal patterns in the abundance-body size relationships. Our results point out that body size relationships seem to be non-stable properties of this chironomid assemblage at an intra-annual scale.

Key words: Aquatic insects, macroecology, streams, temporal variation

2.1 Introduction

A major goal of ecology is to understand what determines the spatial and temporal patterns of species richness and the relative abundances of these species in a community (e.g. MacArthur, 1965; May, 1986; Brown, 1995; Gaston, 2000).

Species richness, species abundance, and body size are closely correlated (Hutchinson and MacArthur, 1959; Lawton, 1990; Blackburn and Gaston, 1994; Russo *et al*. 2003), but the process and mechanisms by which these patterns arise have not been fully elucidated (Gardezi and da Silva, 1999; Kozlowski and Gawelczyk, 2002; Gaston and Blackburn, 2000). Body size is of particular interest because it is correlated with most animals' traits, such as metabolic rate, assimilation efficiency, generation time, reproductive rate, diet, predators, and perception of heterogeneity (Peters, 1983; Brown, 1995; Gaston and Blackburn, 2000). Moreover, body size appears to be associated to ecological parameters such as habitat range (Diniz-Filho *et al*. 2004) and total production (McClain, 2004), and it is an important variable in evolutionary research (Blackburn and Gaston, 1994). Therefore, understanding the processes controlling size frequency distributions in a community and how body size is related to abundance may give insights into the determinants of diversity and how we can conserve them.

It has been observed that frequency distributions of body size generally exhibit a characteristic right-skew pattern (Blackburn and Gaston, 1994; McClain, 2004); most species small-bodied, and only a few large-bodied (Kozlowski and Gawelczyk, 2002). In the case of abundance versus body size tree basic forms of relationships are reported in the literature: (1) linear relationships, with most showing a negative but a few exhibiting a positive slope, (2) polygonal pattern with weak relationship between variables and where intermediate-sized taxa are most abundant, and (3) combination features of the previous two (Blackburn and Gaston, 1997; Griffiths, 1998; Storch and Gaston 2005).

The main criticisms of these studies are that (i) the data are not samples of real assemblages, but tend to be compilations from different situations varying from being “snapshots” of a single day sampling effort to data from weekly, monthly, or yearly surveys (Blackburn *et al.*, 1993); (ii) most studies emphasize the variation that occurs at different spatial scales (see Gaston and Blackburn, 2000) and assumed that these relationships are a stable characteristic of the system studied (Stead *et al.*, 2005), but few have investigated how these patterns vary temporally (Schmid *et al.*, 2002; Stead *et al.*, 2005). In addition, there is an enormous bias in the publication record from which the theoretical background has been constructed. Most studies come from temperate regions and focus on vertebrates and terrestrial ecosystems (Gaston and Blackburn, 1999). Documenting the relationships through a wide range of taxonomic groups, regions, habitats, and scales remains necessary to identify the generality of the patterns.

Here we examine the frequency distribution of number of species as a function of body size and body size-abundance relationships for a local chironomid assemblage in the Neotropical region. We analyze these relationships for the data agglomerated into annual and then for each month separately. Our study focuses on the following questions: (i) does the distribution of taxon richness with body size fit the commonest right-skewed pattern? (ii) what form does the relationship between abundance and body size take within this local stream rich assemblage? (iii) are the above relationships temporally invariant?

Among the aquatic groups, the dipteran family Chironomidae is a good one to explore relationships among species richness, abundance and body size because it represents one of the most speciose and abundant group in any aquatic environment in the world and the larvae play different trophic roles

2.2 Materials and methods

Study organisms

Studying patterns and relationships between body size and other variables within insects may produce some bias in the results; this is partially due to the variation in body length among different stages and larval instars. To avoid overestimation of species richness and abundance and misinterpretations on body size distributions we decided to analyze a single stage of the individuals' cycle – the pupa – by collecting chironomid floating pupal exuviae.

According to Coffman and de La Rosa (1998) the advantages offered by the collection of pupal exuviae are well documented and include: all species emerge at the water surface, the exuviae remain floating for at least a day, large numbers of specimens can be rapidly collected, species from all microhabitats are included, and discrimination of species/morphoespecies is usually more readily made than with either larvae or adults. To these advantages may be added the ethical and non-destructive nature of the sampling of inanimate cast cuticles (Hardwick *et al*., 1995). Furthermore, since the chironomid adults are short-lived and most of them do not feed, the size of the pupal stage reflects all the energetic gains of the insects' life. This method, moreover, avoids autocorrelation bias related to temporal field sampling, causing no interference on population dynamics.

Study area and data analyses

We worked within the Fazzari stream, a first order forested stream located in the State of São Paulo, southeastern Brazil (21°59'S - 47°54'W, ~910 m a.s.l.). Regional climate is Cwa (Köppen classification), with wet summer and dry winter. The dry season goes from June to August and the wet season, from September to May. Annual rainfall and mean temperature lie around 1,595 mm and 21.7 °C, respectively.

The stream is surrounded by a well preserved riparian forest, with tree canopy covering more than 70% of the channel, low deep (< 50 cm), absence of macrophytes, water with high level of dissolved oxygen, low conductivity, temperature ranging from 15-23°C and the streambed is characterized by predominance of organic material (wood and leaves). Fazzari stream is one of the most intensely sampled stream in southeastern Brazil for chironomids (see Roque *et al.* 2003) and many of the new chironomid species descriptions from Brazil in the last decade have come from this site.

We carried out weekly quantitative samples in three stream segments with similar riffle/pool areas from April 2004 to March 2005. In each segment (10-20m) we used hand nets (200 µm mesh size) to collect natural accumulations of floating pupal exuviae from behind stream flow blocks (e.g. logs) and drift nets (200 µm mesh size) to intercept exuviae that were possible induced to drift in the main flow by the disturbance caused by hand netting. Despite Hardwick *et al*. (1995) have found diurnal variation in exuvial drift in second order streams of tropical Australia we believe that our samples included not only exuviae from immediate adult emergence but also those from at least two days before (Wilson & Bright, 1973). Moreover, since our study site is a small stream with a sinuous channel and low water flow, probably pupal exuviae accumulated near the place of adult emergence.

In the laboratory the material was sorted and the chironomids counted and identified to the lowest taxonomic level possible. In cases in which species identification was not possible, we separated individuals into morphotypes. For the analyses of body size distributions we used the male pupa size as a surrogate measure of the species, each specimen was measured from the front of the cephalothorax to the tip of the abdomen.

Instead of pooling the number of species into body size classes as usual in most studies, we used all the observations for producing normal probability plots, which according to Williamson and Gaston (2005) is easier and more efficient than using histograms. The distributions of body size were analyzed using Shapiro-Wilk tests and when the distribution departs from normality, skewness was tested with a one-sample t-test (Sokal and Rohlf, 1995). Given that most studies use the logarithmic scale we performed the above analysis on both untransformed and log-transformed data. Acho que deveria usar somente escala log.

Abundance-body size relationships for the annual data and for each month separately were analyzed using Ordinary Least Squares regression in accordance with previous freshwater and terrestrial studies (Cyr *et al.*, 1997).

2.3 Results

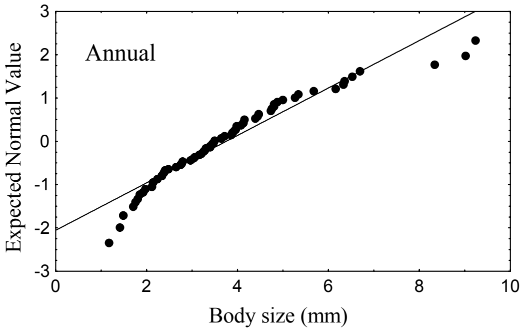
We obtained a total of 16, 551 individuals representing 71 chironomid species/morphospecies (Table I) for the 12 months of sampling, of which 47 taxa belonged to Chironominae, 14 Tanypodinae, and 9 Orthocladiinae. Body size data were available for all of them except one species, *Tanytarsus impar* Trivinho-Strixino and Strixino, which was infeasible to measure given the bad state of the pupal exuviae.

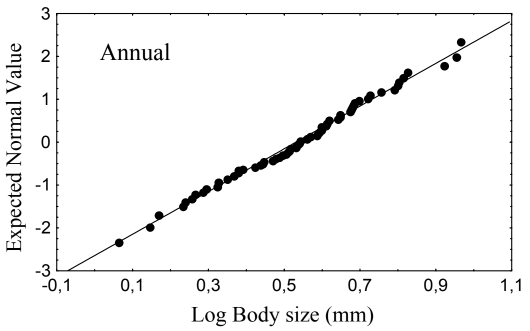
Body size distributions

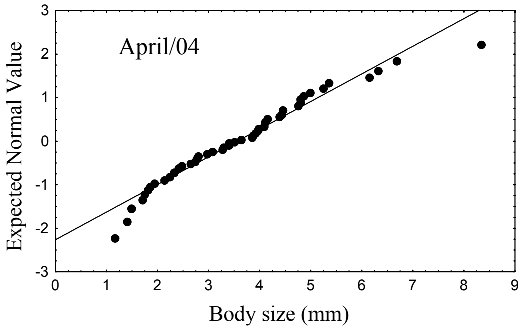
When the species richness of all the 12 months samples were summed and analyzed together untransformed annual body size distributions deviated from normality and were significantly right-skewed (Fig. 1 a) ($W = 0.915$, $P < 0.0001$; skew = 1.145, SE = 0.286, $t_s = 3.912$, $P < 0.001$). However, when we set the body size frequencies on the logarithmic scale, the right-skewed pattern was not maintained ($W = 0.981$, $P = 0.689$).

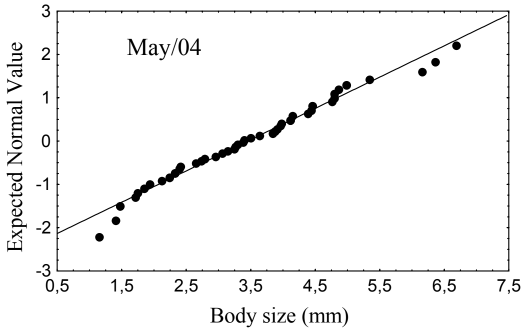
Table I. Taxa list and body size measure of the Fazzari stream chironomid assemblage collected from April/2004 to March/2005.

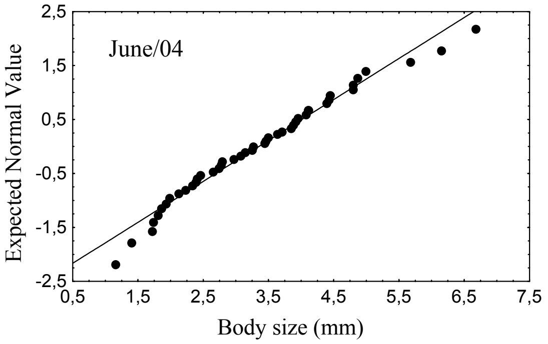
	Body size (mm)		Body size (mm)
Chironominae			
Beardius sp. 1	4.86	*Tanytarsus* sp. 1	3.46
Chironomus sp. 1	6.50	*Tanytarsus* sp. 2	2.40
Chironomus sp. 2	9.00	*Tanytarsus* sp. 3	3.95
Chironimini Gên. A sp. 1	3.29	*Tanytarsus* sp. 4	4.43
Chironimini Gên. B sp. 1	3.06	*Tanytarsus* sp. 5	2.64
Cryptochironomus sp. 1	5.24	*Tanytarsus* sp. 6	3.26
Endotribelos sp. 1	4.44	*Tanytarsus* sp. 7	3.14
Endotribelos sp. 2	6.67	*Tanytarsus* sp. 8	2.32
Endotribelos sp. 3	3.90	*Tanytarsus* sp. 9	4.08
Endotribelos sp. 4	3.88	*Virgatanytarsus* sp. 1	3.18
Endotribelos sp. 5	3.85	*Virgatanytarsus* sp. 2	2.12
Fissimentum sp. 2	4.98	**Orthocladiinae**	
Oukuriella sp. 1	4.11	*Corynoneura* sp. 1	1.48
Oukuriella sp. 2	4.78	*Corynoneura* sp. 2	1.71
Parachironomus sp. 1	3.01	*Corynoneura* sp. 3	1.15
Paratendipes sp. 1	3.63	*Lopescladius* sp. 1	1.97
Cladopelma sp. 1	4.11	*Nanocladius* sp. 1	1.48
Polypedilum sp.1	3.38	*Thienemanniella* sp. 1	1.80
Polypedilum sp.2	3.40	*Parametriocnemus* sp. 1	3.44
Polypedilum sp.3	2.77	*Parakieffiriella* sp. 1	1.40
Polypedilum sp.4	3.95	Orthocladiinae sp. 1	2.11
Stenochironomus jubatus	8.34	**Tanypodinae**	
Stenochironomus sp. 1	6.35	*Ablabesmyia* sp. 1	4.80
Stenochironomus sp. 2	5.34	*Ablabesmyia* sp. 2	4.38
Stenochironomus sp. 3	5.68	*Ablabesmyia* sp. 3	6.15
Xestochironomus sp. 1	4.75	*Fittkauimyia* sp. 1	6.30
Xestochironomus sp. 2	3.63	*Guassutanypus oliverai*	9.23
Caladomyia sp. 1	2.95	*Labrundinia* sp. 1	2.32
Caladomyia sp. 2	2.74	*Labrundinia* sp. 2	2.38
Caladomyia sp. 3	2.23	*Larsia* sp. 1	3.49
Nandeva sp. 1	2.12	*Monopelopia caraguata*	2.46
Rheotanytarsus sp. 1	2.78	*Monopelopia* sp. 1	4.14
Stempellina sp. 1	1.92	*Parapentaneura* sp. 1	3.97
Stempellinella sp. 1	1.84	*Pentaneura* sp. 1	3.24
Stempellinella sp. 2	1.74	*Pentaneura* sp. 2	3.71
Tanytarsus magnus	4.72	*Procladius* sp. 1	4.44

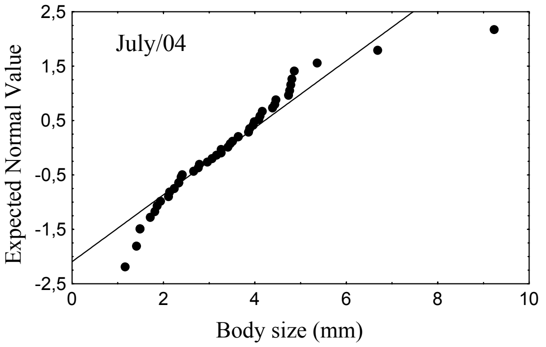

Annual
Expected Normal Value
3
2
1
0
-1
-2
-3
0
2
4
6
8
10
Body size (mm)

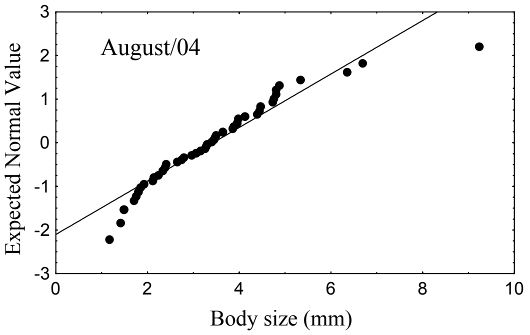

Annual
Expected Normal Value
3
2
1
0
-1
-2
-3
-0,1
0,1
0,3
0,5
0,7
0,9
1,1
Log Body size (mm)

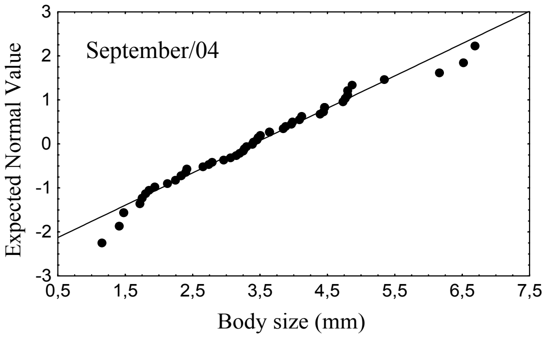

April/04
Expected Normal Value
3
2
1
0
-1
-2
-3
0
1
2
3
4
5
6
7
8
9
Body size (mm)


May/04
Expected Normal Value
3
2
1
0
-1
-2
-3
0,5
1,5
2,5
3,5
4,5
5,5
6,5
7,5
Body size (mm)


June/04
Expected Normal Value
2,5
1,5
0,5
-0,5
-1,5
-2,5
0,5
1,5
2,5
3,5
4,5
5,5
6,5
7,5
Body size (mm)


July/04
Expected Normal Value
2,5
1,5
0,5
-0,5
-1,5
-2,5
0
2
4
6
8
10
Body size (mm)


August/04
Expected Normal Value
3
2
1
0
-1
-2
-3
0
2
4
6
8
10
Body size (mm)


September/04
Expected Normal Value
3
2
1
0
-1
-2
-3
0,5
1,5
2,5
3,5
4,5
5,5
6,5
7,5
Body size (mm)

(continued)

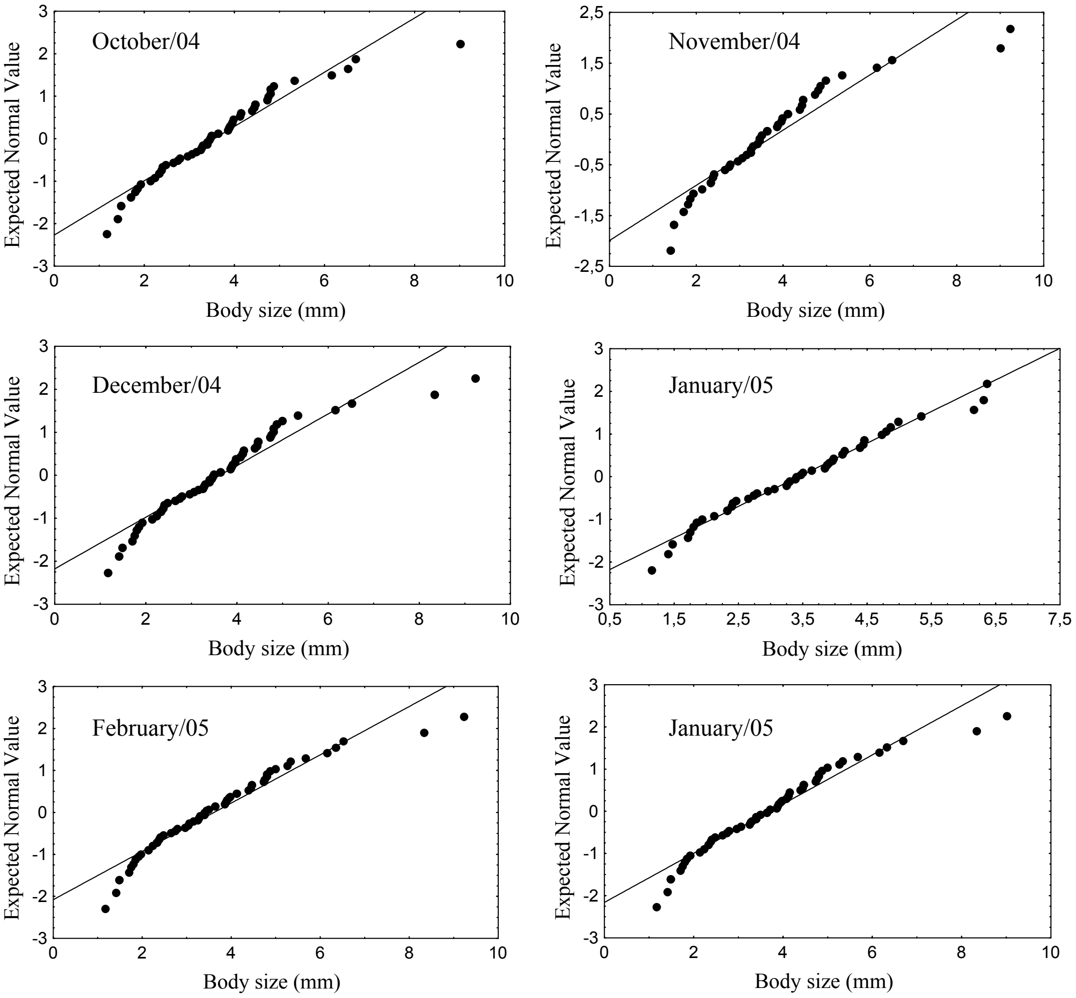


Figure 1. Probability plots of the Chironomidae species' body size distributions from Fazzari stream from April/2004 to March/2005.

Although the annual body size distribution were significantly right-skewed for the entire assemblage, when we broke down the data and performed the same analysis for each month separately we found a variable temporal pattern (Fig. 1), seven months (July/2004, August/2004, October/2004, November/2004, December/2004, February/2005 and March/2005) exhibit significantly right-skewed distributions whereas five (April/2004, May/2004, June/2004, September/2004 and January/2005) approach normality (Table II). The number of species peak in similar size (3-4 mm) for both summed and separated untransformed data, most of them belong to the tribes Chironomini and Tanytarsini. The log-transformed distributions do not deviate from normality for any of the 12 months.

Table II. Values of the Shapiro-Wilk tests of goodness of fit (W and *P*) and the one-sample t-test for skewness (ts and *P*) of the untransformed data for each month.

	W	***P***	**skew**	**SE**	**ts**	***P***
April/2004	0.957	0.114	-	-	-	-
May/2004	0.967	0.315	-	-	-	-
June/2004	0.968	0.384	-	-	-	-
July/2004	0.913	0.002	1.359	0.350	3.763	0.001
August/2004	0.921	0.002	1.270	0.336	3.666	0.001
September/2004	0.962	0.184	-	-	-	-
October/2004	0.940	0.013	1.075	0.324	3.225	0.01
November/2004	0.882	0.0001	1.480	0.350	4.098	0.001
December/2004	0.913	0.001	1.284	0.310	3.923	0.001
January2005	0.964	0.258	-	-	-	-
February2005	0.928	0.002	1.109	0.311	3.478	0.001
March/2005	0.938	0.009	0.955	0.316	2.944	0.01

The relationship between abundance and body size

The abundance-body size relationship for the entire year (Fig. 2 a) was significant (n = 70, $b = -1.67$, F = 14.83, $P = 0.001$). However, the coefficient of determination was low indicating a high level of scatter ($r^2 = 0.18$). Furthermore, the overall relationship shows a strong decrease in maximum abundance with increasing body size and peak abundance on intermediate-sized species.

The linear relationship of abundance and log body size was not significant for all months, when analyzed independently (Table II). In five months (April/2004, June/2004, July/2004, November/2004 and December/2004) there was no significant relationships between the variables, and the relations appear to correspond with the “polygonal” type reported by Brown and Maurer (1987) on which there is no marked increase in the minimum abundance of small-bodied species and, intermediate-sized taxa are most abundant (Leaper & Raffaelli 1999) and the linear regression is not significant (Fig 2 b-f).

The regression slopes of the seven months (May/2004, August/2004, September/2004, October/2004, January/2005, February/2005, March/2005) where a significant relationship was found were all negative, ranging from -1.62 to -1.17 (Table III).

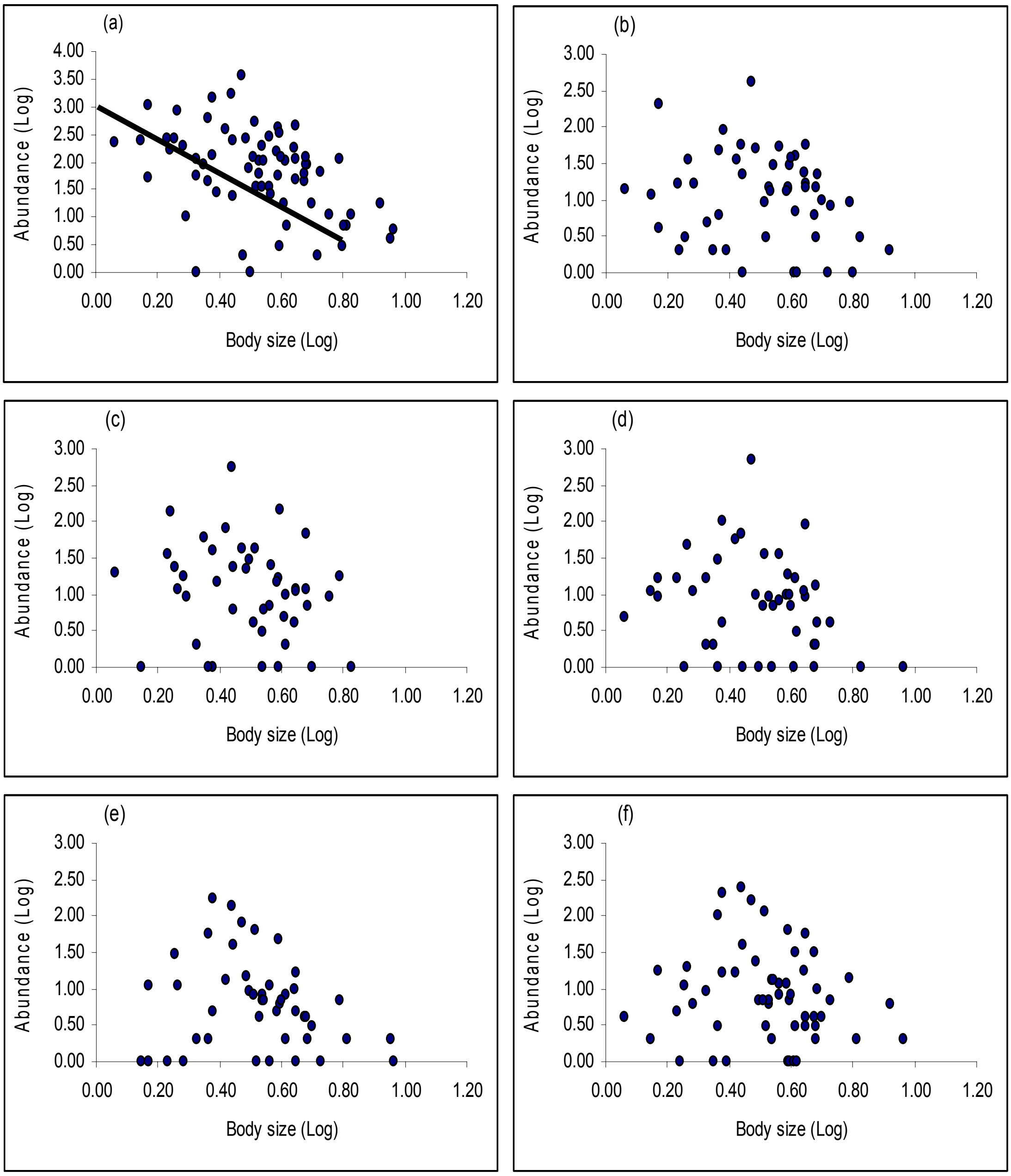


Figure 2. The abundance body size plots for the Fazzari stream Chironomidae assemblage, (a) entire year, (b) April/2004, (c) June/2004, (d) July/2004, (e) November/2004 and (f) December/2004.

Table III. Results of regressions on the relationships between population abundance and body size of the Fazzari stream Chironomidae assemblage data set from the entire year (All) and from each month independently, n – number of species, *b* – OLS slope, I*r*I – correlation coefficient, F and *P* values of the OLS test of significance.

Data	**n**	***b***	**I*r*I**	**F**	***P***
All	70	-1.67	0.42	14.83	0.001
April/2004	51	-0.64	0.20	2.14	0.147
May/2004	48	-1.37	0.42	9.80	0.003
June/2004	45	-0.66	0.17	1.34	0.252
July/2004	46	-0.78	0.23	2.36	0.128
August/2004	50	-1.62	0.41	11.77	0.002
September/2004	51	-1.24	0.37	7.82	0.007
October/2004	54	-1.51	0.39	9.42	0.004
November/2004	46	-0.54	0.17	1.26	0.267
December/2004	56	-0.37	0.11	0.66	0.575
January/2005	49	-1.28	0.46	12.74	0.001
February/2005	59	-1.17	0.33	6.85	0.011
March/2005	57	-1.37	0.41	12.56	0.001

2.4 Discussion

Species richness and body size distributions

Recent studies support the idea that most species tend to be of small to intermediate size, with the smallest and largest body species underrepresented (Gaston and Blackburn, 2000 for a review). This right-skewed distribution is retained even on logarithmic axes for larger geographic scale and higher taxonomic groups (Brown, 1995). Several hypotheses have been proposed to explain this pattern including: the way data are gathered, trade-offs between metabolic efficiency and reproductive success, differences in spatial scales, habitat heterogeneity, fractal distribution of resources, statistical artifacts and variation in taxonomic composition of the samples (Brown 1995; Blackburn & Gaston 1997; Storch & Gaston 2005).

Central tendencies in the relationship between chironomid species richness vs body size found here are likely to be influenced by habitat complexity and phylogenetic constraints related with the life-history of its subfamilies. Most small-sized chironomids belong to the Orthocladiinae subfamily, the largest ones belong to Tanypodinae and Chironominae, whereas intermediate sized individuals are from several species of Tanytarsini-Chironominae (the most speciose tribe in Neotropical region). According to Townsend *et al.* (1997) the relationship between biological traits (e.g. size) and habitat variables seems to be related to adaptation to physical constraints of the habitat. Furthermore, Schmid *et al.* (2002) have suggested that the body-size spectra of aquatic insects scale to habitat complexity (fractal Dimension). Adaptation to habitat characteristics in terms of resistance to drag and foraging strategies seems to be one of the most important evolutionary processes influencing the distribution of stream dwelling insects (Lamouroux *et al*., 2004). Small invertebrates with flexible and streamlined body shapes are more common in stressful conditions or relatively coarse substrate. The body shapes, morphology and feeding strategies help to reduce drag and enable organisms to use small interstices within the bed sediments or keep themselves attached to the substrate. This is probably the case of many small Orthocladiinae taxa**.** In contrast, predators/omnivores (tanypodines) and collectors (most chironomines) live on fine sediments deposited in slow-flowing habitats – the predominant habitats in Fazzari stream.

In the Fazzari stream chironomid assemblage, the body size distribution for the entire year was skewed to the right for untransformed data, whereas on the logarithmic scale the frequencies were normally distributed. Agosta and Janzen (2005) found very similar results describing the size distributions of a dry forest moth family in Costa Rica, which is not uncommon when local assemblages are analyzed (Gaston and Blackburn, 2000). According to Kozlowski and Gawelczyk (2002) skewness seems more variable in narrower systematic groups such as families and the distribution of a higher taxon may be the superposition of different distributions for lower taxa. Moreover, Brown and Nicoletto (1991) found that the body size distribution tends to assume a symmetrical or even a uniform distribution at small spatial scales such as a local patch. Therefore, different patterns may emerge depending on the spatial scale from which the observations were made (Blackburn and Gaston, 2002).

Many studies have shown that body size distributions vary spatially and taxonomically, but few have assessed if there are temporal changes in this relationship (Stead *et al.*, 2005). We observed consistent differences in the patterns of body size distribution at this intra-annual scale. In some months the distribution was right-skewed, but in others the data were normally distributed. These results do not allow causal inferences to be made, but add more evidence to a growing body of literature suggesting that no single mechanism structures the size distribution of communities (Kozlowski and Gawelczyk, 2002) and several mechanisms could influence them, specific to the life history of the organisms involved (Agosta and Janzen, 2005).

Abundance- body size relationships

In natural communities small organisms are more abundant than large ones, and the relationship between abundance and body size usually exhibits two major shapes: linear with negative slope and polygonal with no strong relationship between the variables (Gaston and Blackburn, 2000). We have observed both results in our data.

The significant relationships found for the entire data set parallels the results found in other studies on streams (Schmid *et al.*, 2000; Schmid *et al.*, 2002). However, the slope of -1.67 is clearly not in agreement with the energy equivalence hypothesis in which the regression is expected to be relatively constant across different communities, with a slope of −0.75 (Damuth, 1981; Brown *et al.*, 2004). This hypothesis states that since individual metabolic rates (R) scale with body mass (W) according to $R \infty W^{0.75}$ population abundance would be limited by energy requirements, so an approximately equal amount of energy would be available for each species in an assemblage. Recent studies of freshwater and terrestrial communities have rejected the energy equivalence hypothesis (Bini *et al.*, 2001 Schmid *et al.*, 2002; Stead *et al.*, 2005).

In contrast with the abundance-body size relationship found for the entire year, the monthly data showed that this relationship is temporally variable. While in some months the regression was significant with negative slopes, in others there was a polygonal pattern, suggesting that abundances of different chironomid species do not scale linearly and constantly with body size. Tokeshi (1990) studying a chironomid community associated with *Myriophyllum spicatum* L., already found that in some cases density was independent of body size. These polygonal plots are thought to be determined by ecological and evolutionary mechanisms (Lawton, 1989; Silva and Downing, 1995) and such a relationship has been termed a 'body-size constraint space', where maximum abundances declines with increasing body size across a community (Griffiths 1998) and where there is region where minimum abundances may be independent of body size (Brown, 1995). Our data agree with these patterns. Nevertheless, according to Warwick and Clark (1996), it is possible that the higher abundances of intermediated-sized animals in polygonal plots is a consequence of sampling artefacts. The present study used the same sampling procedure for all sampling occasions, so our results cannot be considered as a sampling artifact.

The relationships studied here are thought to be stable characteristics of the system, but they were variable when analyzed at smaller temporal scale like months. For example, if our data consisted of only one month of sampling, e.g. April/2004, the body size distribution would be normal and the abundance-body size relationship would not be significant. In contrast, if we considered only August/2004, the distribution would be skewed to the right and the relationship would be significant, with a negative slope. Other authors have already shown that body-size relationships seem to be non-stable properties of the communities spatially (Gaston and Blackburn, 2000) and temporally (Stead *et al.*, 2005). According to Schmid *et al.* (2002) this variability seems to be related to temporal variations in habitat structure (fractal D) and the regime of hydrological disturbances. In accordance with these studies, our results indicate that both abundance-body size and species richness-body size relationships in this chironomid assemblage do not show a single pattern at the intra-annual scale. However, the mechanisms behind this variation remain elusive and open to debate.

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Capítulo II

Padrões de emergência de uma diversa assembléia tropical de Chironomidae: existe apenas aleatoriedade?

3. EMERGENCE PATTERNS OF A DIVERSE NEOTROPICAL LOTIC CHIRONOMID ASSEMBLAGE: IS THERE ONLY RANDOMNESS?

Abstract

Fluctuations on animal communities are influenced by both biotic interactions and abiotic forcing. These characteristics may make communities dynamics complex when analyzing time series. We analyzed the emergence phenology of a high diverse chironomid assemblage. We used a time series of forty eight weekly samples from a tropical low order forested stream to describe how this assemblage vary in time and to test for association between emergence and some environmental variables believed to affect tropical insect phenology. Also, we used null model analysis to quantify temporal overlap on emergence among all species present. Emergence of the Chironomidae, subfamilies and of the commonest species was not associated with any environmental variables. The number of emerging individuals of two species was associated with photoperiod and of other two species with minimum air temperature. Taxonomic composition and species richness did not change over the series. Temporal overlap was greater than expected by chance, indicating that most species have similar emergence patterns and were emerging together throughout the year. The time series analysis indicated that there was a temporal structure in the emergence series which was not explained by any of the environmental variables. Biological interactions may be the major factor influencing tropical chironomid emergence.

Key words: Chironomidae, null models, phenology, time series, tropical streams

3.1 Introduction

Ecological communities are dynamic and vary in space and time (Rosenzweig, 1995; Wiens, 1986). Factors contributing to this variability operate at different scales, ranging from regional-level factors such as climate and geology (e.g. Lytle, 2001; Richards *et al.*, 1997), to habitat-level factors (e.g. Armitage *et al.* 1995; Peckarsky *et al.*, 2001) acting on individual taxa, particularly those related to an individual's requirements (Resh & Rosenberg, 1984).

Temporal variations in population abundance (seasonal, cyclic, or chaotic) may also depended on complex interactions between extrinsic forcing and intrinsic dynamics (Bjornstad *et al.*, 2004) and are very important in structuring the composition of ecological communities (Brown, 2003).

Phenology, the study of the relationship between temporal variation on biological phenomena (e.g. insect emergence, fruiting, pupation) and environmental factors, particularly climate (Scott & Epstein, 1986), is fundamental to understand community dynamics, since it determines the length of the growing season, which has major implications for breeding structure, habitat selection, quantity and quality of available resources (Stiles, 1977; Williams, 1999). Moreover, in the context of global climate change phenological studies have received an increased attention from biosphere modelers (Sellers, *et al.*, 1996; Chuine *et al.*, 2000) and conservation biologists (Terborgh, 1986), since there is a growing body of evidence showing that ecological and population processes are affected by climatic fluctuations (Stenseth *et al.*, 2002).

Several taxa of aquatic insects, manly in the temperate zone, show a characteristic emergence pattern, so their life cycles must be coupled with appropriate environmental conditions (Resh & Rosenberg, 1984). Among the Chironomidae (Diptera), which is by far the most diverse group of organisms in freshwater environments (Giller & Malmqvist, 1998), studies in temperate streams have shown that there is a seasonal shift in the adult emergence of tribes and subfamilies. The Chironomini and Tanypodinae dominate in the summer and the Orthocladiinae dominate in the winter and in the species richness, which is initially low, but increases during late spring (Coffman, 1973; Coffman & de la Rosa, 1998). These patterns depended on the temperature requirements of these subfamilies and tribes, and can vary with altitude and latitude (Ferrington *et al.*, 1993). Thus, if temperature limits the timing of chironomid emergence, the average duration of the emergence period should increase towards the tropics.

Coffman (1989) hypothesized that the lack of a clear seasonality of temperature and food types in tropical streams should result in an assemblage where chironomid species would be asynchronous in their life histories and consequently, each species would be represented at all times of the year by most larval instars and emergence should be continuous at all times of the year. In a more recent paper Coffman & de la Rosa (1998) compared Chironomidae phenology and faunal composition of temperate and tropical streams and postulated that the degree of change in taxonomic composition of tropical streams were largely independent of the interval between any two samples.

It is well established that even in thermally "aseasonal" tropical regions, natural environment exhibit some seasonality (Wolda, 1988). According to Armitage (1995) in areas where temperature changes are slight, other environmental fluctuations may be used as cues for timing of chironomid emergence. Among these, the following three can be considered important: photoperiod, rainfall and lunar periodicities. The first has been considered an informative signal to the species in streams where temperature does not vary seasonally (Resh & Rosenberg, 1984) due to its predictability and because insects respond to very low light levels (Saunders, 1976). Moreover, photoperiodic control of adult metamorphosis has been reported for some species of Chironomidae (see Danks, 1978). The second may cause hydrological changes during the wet season which often result in temporal variation in invertebrate communities of headwater streams (Townsend, Hildrew & Schofield, 1987; Miller & Golladay, 1996). Coffman & de la Rosa (1998) noticed that the streams in Costa Rica were not completely aseasonal, as shown by the dry and wet season patterns of lower and higher number of species emerging respectively. The influence of the moon on the emergence of some chironomids was noted, for example, in Lake George (Uganda), where no seasonality of emergence was noted for *Procladius brevipetiolatus* (Goetghebuer) but a clear lunar periodicity was observed, with greatest abundances in the first quarter of the lunar month and smallest in the third quarter (McGowan, 1975). Although lunar periodicities are thought to occur in several tropical chironomids (Armitage, 1995), to our knowledge, there have been no published investigations of this phenomenon in tropical streams.

Despite the ecological importance of chironomids (Cranston, 1995), phenological data for tropical lotic chironomids are scarce and according to Coffman & de la Rosa (1998) this is one of the reasons why our knowledge about patterns of species richness and phenology of the group is still obscure.

In this paper we use a time series of 48 weekly samples collected through one year to examine the community structure and the emergence phenology of the Chironomidae of a tropical, forested, headwater stream in Brazil. We attempt to answer the following questions: (*i*) is there any non-random patterns in the chironomid emergence time series; (*ii*) are there any relationships between emergence and environmental factors; (*iii*) does the taxonomic composition of the emerging species vary in time and (*iv*) do the Tanypodinae, Chironominae and Orthocladiinae subfamilies emerge uniformly throughout the year? In light of the results obtained, possible processes and mechanisms behind chironomid emergence phenology are discussed.

3.2 Materials and Methods

Study area

We carried out this study from April 2004 to March 2005, in three segments of the Fazzari Stream (within the Monjolinho River catchment, State of São Paulo, Southeastern Brazil, 21°59'S - 47°54'W, ~ 910 m a.s.l.). Regional climate is Cwa (Köppen classification), with wet summer and dry winter. The drier season goes from June to August and the wet season, from September to May. Annual average rainfall and mean atmospheric temperature lie around 1,595 mm and 21.7 °C, respectively.

The Fazzari stream is surrounded by native riparian vegetation on both sides, with tree canopy covering more than 70% of the channel, low deep (< 50 cm), absence of macrophytes, water with high level of oxygen dissolved, low electric conductivity, temperature ranging from 15-23°C and the streambed is characterized by predominance of organic material (wood and leaves). Our study segments were approximately 10–20 m long contained one riffle and one pool unit each, and were separated from each other by approximately 30 m. This is one of the most intensely chironomid sampled stream in southeastern Brazil (Roque *et al.* 2003) and many of the new chironomid species descriptions from Brazil in the last decade came from this site.

Sampling procedure

We carried out quantitative samples of floating chironomid pupal exuviae. According to Coffman and de La Rosa (1998) the advantages offered by the collection of pupal exuviae are well documented and include: all species emerge at the water surface, the exuviae remain floating for at least a day, large numbers of specimens can be rapidly collected, species from all microhabitats are included, and discrimination of species/morphoespecies is usually more readily made than with either larvae or adults. To these advantages may be added the ethical and non-destructive nature of the sampling of inanimate cast cuticles (Hardwick *et al*., 1995).

This method, moreover, avoids autocorrelation bias related to temporal field sampling without replacement of live individuals, causing no interference on population dynamics.

Two days after the beginning of each moon phase (new moon, first quarter, full moon and last quarter), we used hand nets (200 µm mesh size) to collect natural accumulations of floating pupal exuviae from behind stream flow blocks (e.g. logs) and drift nets (200 µm mesh size) to intercept exuviae that were possible induced to drift in the main flow by the disturbance caused by hand netting. Although Hardwick *et al*. (1995) have found diurnal variation in exuvial drift in second order streams of tropical Australia we believe that our samples included not only exuviae from immediate adult emergence but also those from at least two days before (Wilson & Bright, 1973). Moreover, since our study site is a small stream with a sinuous channel and low water flow, probably pupal exuviae accumulated near the place of adult emergence. We performed this procedure through 12 complete lunar cycles (each cycle comprehend all four moon phases), so our time series has 48 data points.

In the laboratory the material was sorted and the chironomids counted and identified to the lowest taxonomic level possible, using the keys of Borkent (1984), Coffman & Ferrington (1996) and Wiederholm (1986). In cases in which species identification was not possible, we separated individuals into morphotypes. The chironomid specimens are deposited in the collection of the Laboratório de Entomologia Aquática of Universidade Federal de São Carlos (SP).

Data of rainfall, photoperiod and maximum and minimum temperatures for the study period were obtained from the EMBRAPA Sudeste Meteorological Station, located approximately 5 km from the Fazzari Stream.

Data analysis

We used multiple regression (Sokal & Rohlf, 1995) to test the prediction that environmental factors constrains the emergence of Chironomidae. We used five environmental factors as independent variables: total rainfall (mm) of the period between sampling dates, maximum and minimum air temperatures (C°), moon phases and photoperiod (given as the mean number of hours of light between sampling dates). As moon phase is a multistate qualitative variable, it was recorded into a set of binary dummy variables (Legendre & Legendre, 1998). The dependent variables regressed were: Chironomidae species richness, abundance of Chironomidae, Chironominae, Orthocladiinae and Tanypodinae. We also used the abundance of species that were present in all collections and the most abundant species of each subfamily. Abundance was log transformed for this analysis.

After these procedures we constructed correlograms, using the autocorrelation function (Legendre & Legendre, 1998), with the residuals of each multiple regression. Our aim was to detect if there was any information in the data that was not explained by the multiple regression. All series used as response variables in the multiple regression were tested for the presence of trends before constructing the correlograms. This is because the correlograms are only meaningful for stationary time series (Chatfield, 1989). We used a sing test (Sokal & Rohlf, 1995) to check for the presence of trends.

Mantel statistics were used to detect and test for temporal variability in the taxonomic composition of emerging species. This type of analysis is computed from a matrix of similarities between pairs of observations in the temporal series. The matrix was constructed using Jaccard's coefficient of similarity and was compared to a model matrix, which was constructed using the smallest temporal distances between each weekly sample. The statistics were tested for significance using 999 permutations. The normalized Mantel-test statistic is that given in Legendre and Legendre (1998). Mantel test was carried out using NTSYS 2.1 software (Rohlf, 2000).

We analyzed the temporal overlap of emerging species using null models analyses (Gotelli & Graves, 1996). We used the randomization procedures in EcoSim software v. 7.0

(Gotelli & Entsminger, 2001) to test the null hypothesis of no temporal overlap in emergence. For this analysis, each row of the data matrix represented a species and each column represented a week of the year. The entries in the matrix consisted of the number of individuals of each species that emerged at that date. The Czechanowski index (Feinsinger, *et al.*, 1981) was used to measure the temporal overlap between a given pair of species, this index ranges from 0 for species that share no resource (time in this study) to 1.0 for species pairs that have identical resource utilization distributions. To characterize the temporal overlap patterns of the entire assemblage, the mean and variance of niche overlap among all unique pairs of species in the assemblage was calculated.

There are several options for the EcoSim model, based on assumed ecological interactions. For our test, we used the randomization algorithm RA3 for 1,000 interactions. From these 1,000 simulated data sets, the mean temporal overlap of all possible species pairs was calculated and compared to the distribution of simulated means. RA3 then examines all species simultaneously and tests for overlaps. If all species have similar emergence patterns, the observed overlap would be greater than expected (Albrecht & Gotelli, 2001). Therefore, if temporal overlap was detected we interpreted it as if most species were emerging together throughout the year.

In addition, we calculated the variance of temporal overlap. According to Inger & Colwell (1977) if there is guild organization within the species assemblage, the variance in overlap will be greater than expected: species pairs within a guild will have unusually low niche overlap, whereas species pairs in different guilds will have unusually high niche overlap, leading to a large variance in temporal overlap.

3.3 Results

Temporal patterns in number of emerging species and individuals of subfamilies

We recorded a total of 16,438 individuals distributed among 71 chironomid species in the 48 collections carried out over the entire study period (Table I). From these, 48 species belonged to the subfamily Chironominae (12,210 specimens), 08 species to Orthocladiinae (2,132 specimens) and 14 species to the Tanypodinae (1,597 specimens). Four species of the tribe Tanytarsini (*Caladomyia* sp.1, *C.* sp. 2, *Tanytarsus* sp. 9 and *Stempellinella* sp. 1) and one of the Corynoneurini (*Corynoneura* sp. 1) represented together more than 50% of all emerging specimens. Only six species (*Cryptochironomus* sp. 1, *Parachironomus* sp. 1, *Polypedilum* sp. 4, *Virgatanytarsus* sp. 1, *V.* sp. 2 and *Pentaneura* sp. 2) emerged less than four times throughout the year and three species (*Endotribelos* sp. 4, *Caladomyia* sp.1, *C.* sp. 2) were caught emerging in all of the 48 sampling occasions.

Table I. Summary of the time series total catches for all Chironomidae species at the Fazzri stream, São Carlos, Brazil

Taxa	Max.	Min.	Mean	Std.Dev.	Frequency of occurrence (%)
Beardius sp. 1	9	0	1.85	2.11	66.67
Chironomus sp. 1	2	0	0.15	0.41	12.50
Chironomus sp. 2	1	0	0.08	0.28	8.33
Chironimini Gên. A sp. 1	5	0	0.73	1.16	43.75
Chironimini Gên. B sp. 1	17	0	5.56	5.74	89.58
Cryptochironomus sp. 1	1	0	0.04	0.20	4.17
Endotribelos sp. 1	11	0	2.35	2.70	79.17
Endotribelos sp. 2	2	0	0.23	0.47	20.83
Endotribelos sp. 3	7	0	1.13	2.42	33.33
Endotribelos sp. 4	47	1	8.73	9.86	100.00
Endotribelos sp. 5	13	0	3.21	2.97	83.33
Fissimentum sp. 1	3	0	0.38	0.70	27.08
Oukuriella sp. 1	6	0	2.19	2.47	66.67
Oukuriella sp. 2	7	0	1.83	2.47	58.33
Parachironomus sp. 1	1	0	0.04	0.20	4.17
Paratendipes sp. 1	5	0	0.75	1.18	39.58
Cladopelma sp. 1	14	0	2.15	3.41	47.92
Polypedilum sp. 1	10	0	1.31	2.46	39.58
Polypedilum sp. 2	11	0	2.23	3.73	54.17
Polypedilum sp. 3	9	0	0.50	1.81	10.42
Polypedilum sp. 4	1	0	0.06	0.24	6.25
Stenochironomus jubatus	4	0	0.38	0.87	18.75
Stenochironomus sp. 1	2	0	0.15	0.41	12.50
Stenochironomus sp. 2	6	0	1.35	1.99	54.17
Stenochironomus sp. 3	8	0	0.23	1.17	8.33
Xestochironomus sp. 1	8	0	0.96	1.82	35.42
Xestochironomus sp. 2	24	0	5.92	5.94	85.42
Caladomyia sp. 1	259	2	77.65	70.69	100.00
Caladomyia sp. 2	220	1	33.85	42.75	100.00
Caladomyia sp. 3	22	0	1.83	4.47	43.75
Nandeva sp. 1	5	0	1.17	1.26	64.58
Rheotanytarsus sp. 1	31	0	5.23	5.86	85.42
Stempellina sp. 1	24	0	4.04	4.68	81.25
Stempellinella sp. 1	124	0	17.85	22.52	89.58
Stempellinella sp. 2	59	0	3.38	11.62	31.25
Tanytarsus impar	23	0	0.77	3.33	25.00
Tanytarsus magnus	21	0	1.27	3.50	35.42
Tanytarsus sp. 1	113	0	4.15	16.64	31.25
Tanytarsus sp. 2	133	0	31.27	29.57	91.67
Tanytarsus sp. 3	61	0	6.75	11.33	79.17
Tanytarsus sp. 4	41	0	9.13	9.05	91.67
Tanytarsus sp. 5	34	0	8.23	8.46	87.50
Tanytarsus sp. 6	69	0	10.79	12.30	93.75
Tanytarsus sp. 7	12	0	1.56	2.62	43.75
Tanytarsus sp. 8	5	0	0.92	1.15	56.25
Tanytarsus sp. 9	5	0	0.38	0.94	20.83
Virgatanytarsus sp. 1	1	0	0.02	0.14	2.08
Virgatanytarsus sp. 2	1	0	0.02	0.14	2.08

Taxa	Max.	Min.	Mean	Std.Dev.	Frequency of occurrence (%)
Corynoneura sp. 1	175	0	21.71	33.18	87.50
Corynoneura sp. 2	21	0	5.69	5.83	83.33
Corynoneura sp. 3	35	0	4.63	6.42	81.25
Lopescladius sp. 1	6	0	0.21	0.90	10.42
Nanocladius sp. 1	6	0	1.04	1.66	45.83
Thienemanniella sp. 1	51	0	5.48	10.18	66.67
Parametriocnemus sp. 1	6	0	0.75	1.34	37.50
Parakieffiriella sp. 1	35	0	4.92	7.29	68.75
Ablabesmyia sp. 1	24	0	2.54	5.45	60.42
Ablabesmyia sp. 2	10	0	3.60	3.43	85.42
Ablabesmyia sp. 3	12	0	2.33	2.97	58.33
Fittkauimyia sp. 1	1	0	0.06	0.24	93.75
Guassutanypus oliverai	1	0	0.13	0.33	12.50
Labrundinia sp. 1	41	0	12.52	11.94	85.42
Labrundinia sp. 2	19	0	2.79	3.72	72.92
Larsia sp. 1	13	0	2.13	2.49	68.75
Monopelopia caraguata	5	0	0.56	1.32	22.92
Monopelopia sp. 1	1	0	0.15	0.36	14.58
Parapentaneura sp. 1	14	0	2.50	3.00	68.75
Pentaneura sp. 1	8	0	2.46	2.26	79.17
Pentaneura sp. 2	11	0	0.52	2.10	6.25
Procladius sp. 1	8	0	0.98	1.78	39.58

On a monthly time scale, the number of emerging species ranged from 46 taxa in November/2004 to 60 in February/2005 (Fig. 1) while the number of individuals recorded varied by an order of magnitude (431-2343; Fig. 2). The relative proportion of emerging species belonging to each of the subfamilies remained constant.

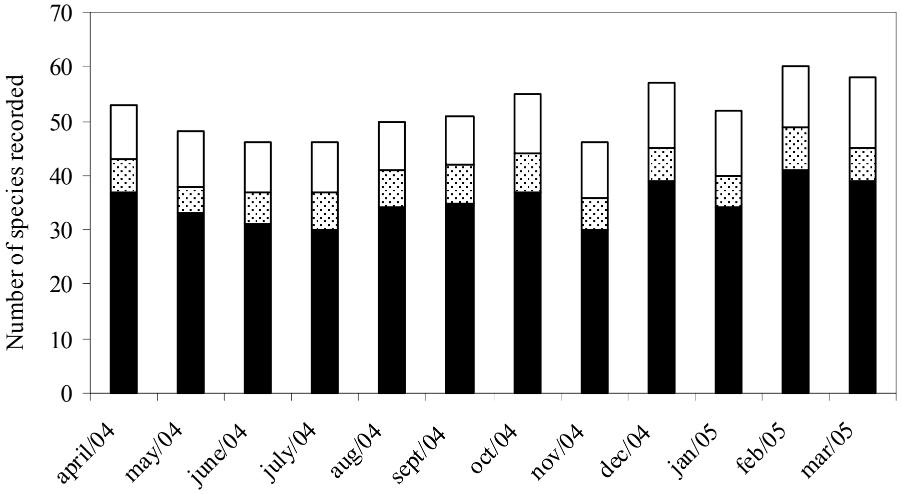


Figure 1. Number of emerging species recorded per month in Fazzari stream, São Carlos, Brazil. Filling of bars: solid – species of Chironominae; stippled – Orthocladiinae; empty – Tanypodinae.

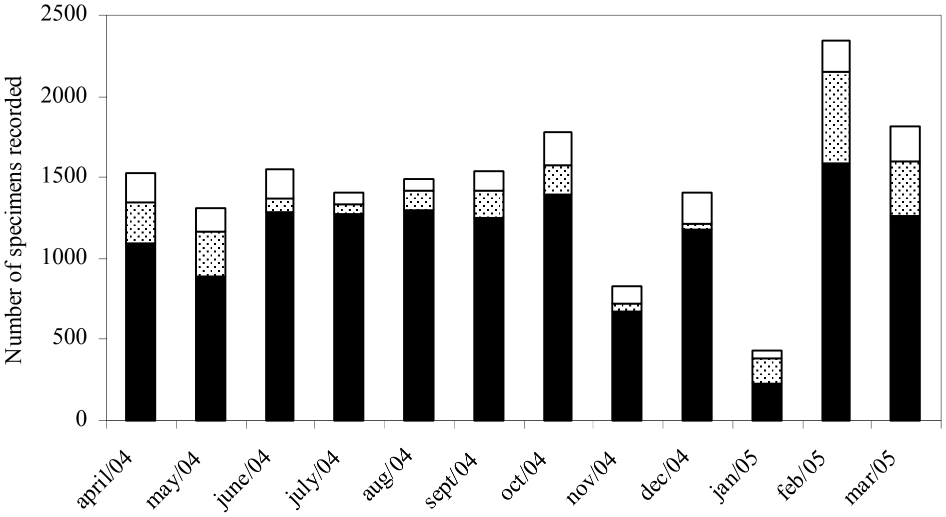


Figure 2. Number of individuals recorded per month in Fazzari stream, São Carlos, Brazil. Filling of bars: solid – species of Chironominae; stippled – Orthocladiinae; empty – Tanypodinae.

Relationship with environmental variables

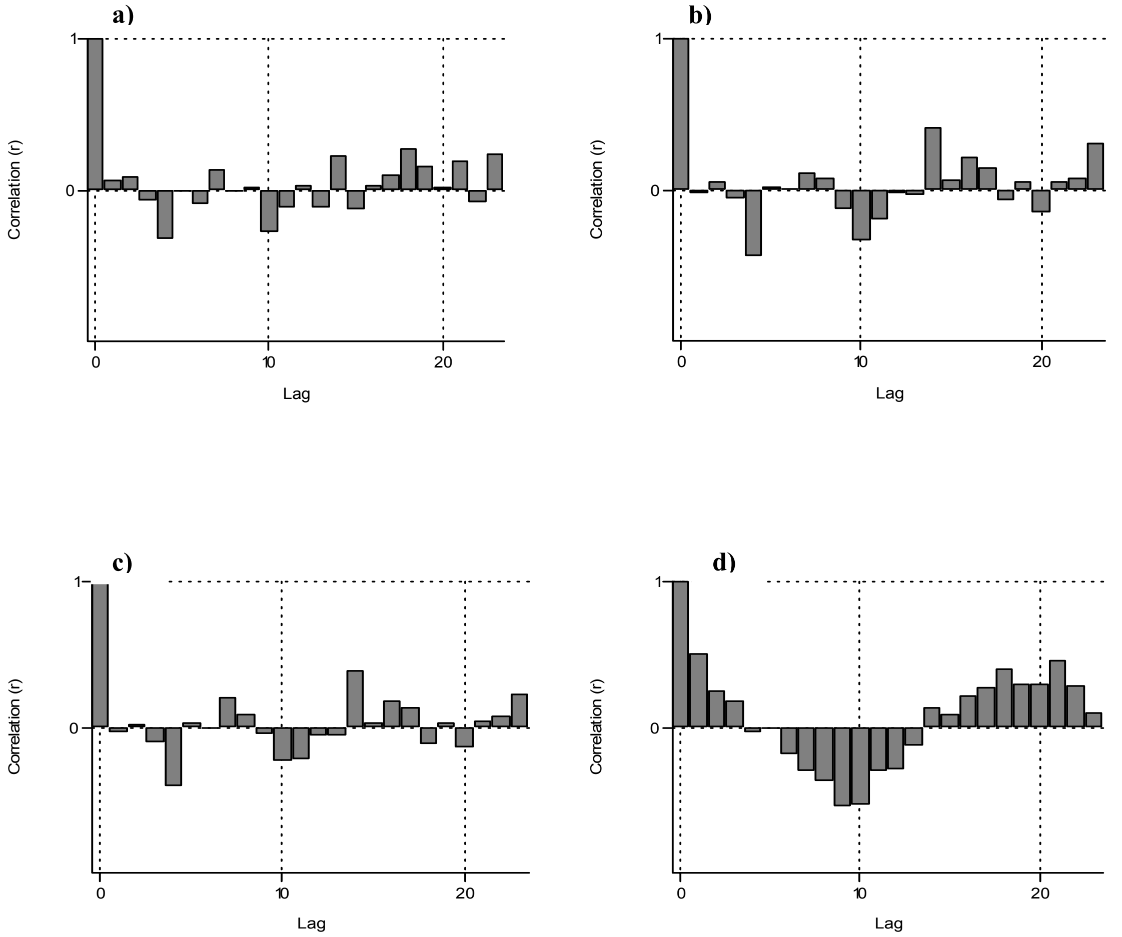
The summed rainfall of the days between each sampling date varied from zero to 120 mm. Both maximum and minimum air temperature varied from 16.0 to 33.0 °C and from 7.0 to 21.0 °C respectively. A complete view of the variation of these measures is given on Appendix 1.

The response variables, Chironomidae species richness, abundance of Chironomidae, Chironominae, Orthocladiinae, Tanypodinae and *Labrundinia* sp.1, were not related to any environmental variables (Table II). Individual taxa varied in the way their emergence was constrained by environmental variables. The abundance of emerging individuals of *Caladomyia* sp.1 and *Endotribelos* sp.4 were related with photoperiod ($p < 0.05$) and the abundance of emerging individuals of *Caladomyia* sp. 2 and *Corynoneura* sp. 1 were related with minimum air temperature ($p < 0.05$). Refer to Appendix 2 for the temporal variation of the number of emerging specimens of each taxa considered in multiple regression analysis.

Table II. Statistics of the multiple regressions. Separate F and *p* values are given for each dependent variable selected in this study.

Dependent variable	Independent variable	F	*p*	Dependent variable	Independent variable	F	*p*
Species richness	Max. temperature	2.423	0.127	*Caladomyia* sp. 1 abundance	Max. temperature	1.641	0.208
	Min. temperature	0.007	0.936		Min. temperature	0.694	0.410
	Photoperiod	0.428	0.517		Photoperiod	**4.533**	**0.039**
	Rainfall	0.049	0.825		Rainfall	0.422	0.520
	Moon phase	1.913	0.143		Moon phase	0.911	0.444
Chironomidae Abundance	Max. temperature	2.441	0.126	*Caladomyia* sp. 2 abundance	Max. temperature	0.274	0.603
	Min. temperature	0.311	0.580		Min. temperature	**4.887**	**0.033**
	Photoperiod	2.062	0.159		Photoperiod	0.644	0.427
	Rainfall	0.069	0.794		Rainfall	0.006	0.941
	Moon phase	1.155	0.339		Moon phase	0.428	0.734
Chironominae Abundance	Max. temperature	2.628	0.113	*Endotribelos* sp. 4 abundance	Max. temperature	0.659	0.422
	Min. temperature	1.178	0.284		Min. temperature	1.787	0.189
	Photoperiod	1.466	0.233		Photoperiod	**5.534**	**0.024**
	Rainfall	0.005	0.942		Rainfall	0.000	0.992
	Moon phase	1.242	0.307		Moon phase	1.016	0.396
Orthocladiinae Abundance	Max. temperature	1.371	0.248	*Labrundinia* sp.1 abundance	Max. temperature	2.151	0.150
	Min. temperature	3.058	0.088		Min. temperature	0.221	0.641
	Photoperiod	3.673	0.062		Photoperiod	0.833	0.367
	Rainfall	0.141	0.709		Rainfall	0.021	0.885
	Moon phase	0.802	0.500		Moon phase	0.464	0.709
Tanypodinae Abundance	Max. temperature	1.500	0.228	*Corynoneura* sp. 1 abundance	Max. temperature	1.280	0.265
	Min. temperature	0.231	0.633		Min. temperature	**5.467**	**0.024**
	Photoperiod	0.077	0.782		Photoperiod	2.201	0.146
	Rainfall	0.210	0.650		Rainfall	0.231	0.634
	Moon phase	0.541	0.657		Moon phase	0.608	0.614

No trend was detected in any of the analyzed series. The correlograms constructed with multiple regression residuals (Figure 3) shows that most autocorrelation coefficients of all series are different from zero for all non-zero values of k (Lag). This result indicates that these series are not random (Chatfield, 1989) and probably it exist a temporal structure on the emergence time series data, that is not explained by any of the environmental variables considered.



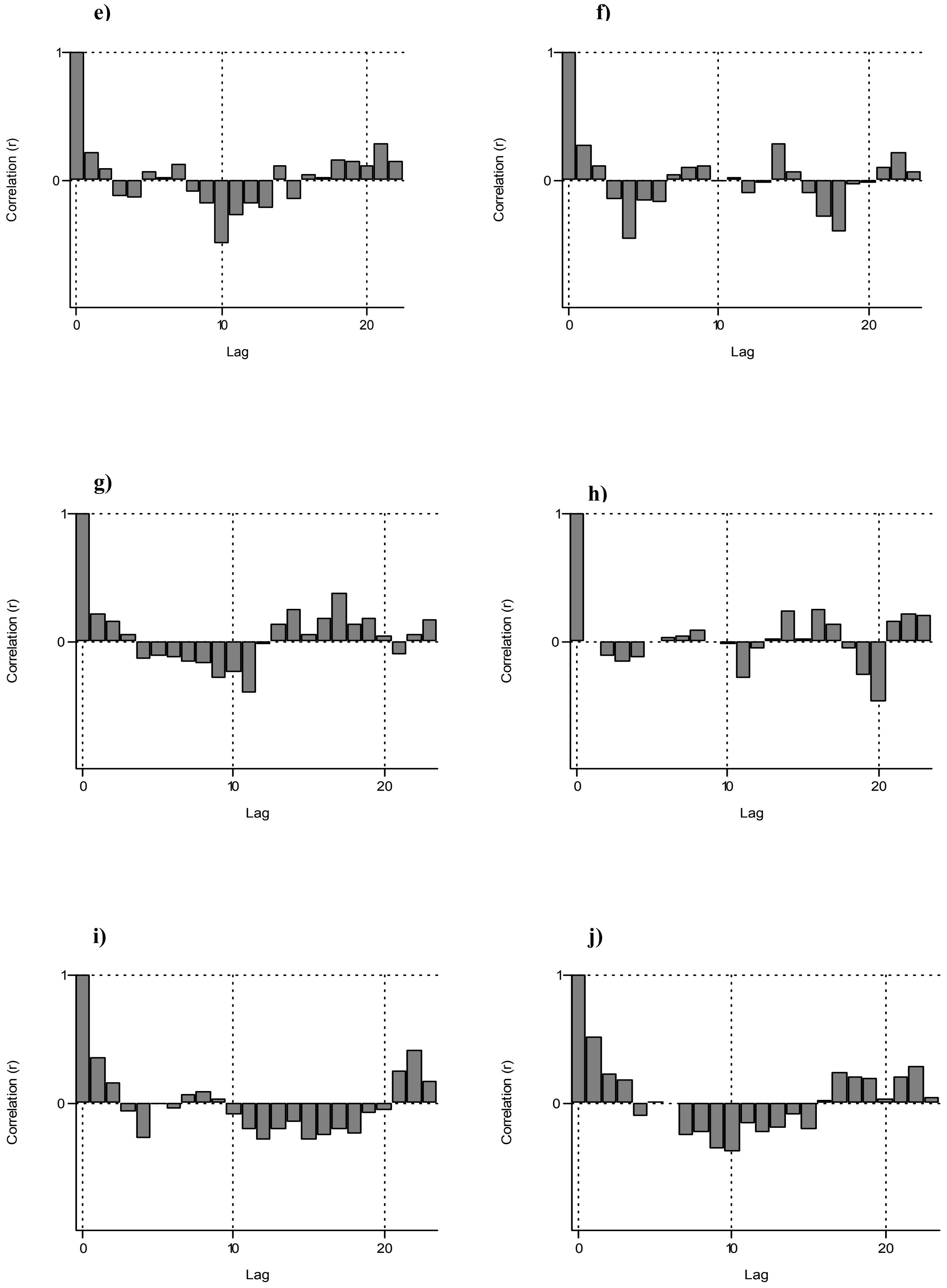


Figure 3. Correlograms constructed with multiple regression residuals a- Species richness, b- Chironomidae, c- Chironominae, d- Orthocladiinae, e- Tanypodinae, f- *Caladomiya* sp. 1, g- *Caladomiya* sp. 2, h- *Endotribelos* sp. 4, i- *Labrundinia* sp. 1, j- *Corynoneura* sp. 1.

Temporal patterns in taxonomic composition and temporal overlap

Taxonomic composition similarity matrix compared with the temporal structure matrix revealed significant mean association ($p< 0.0001$ for 999 simulations), but with a low value of correlation ($r = -0.182$), which indicates a weak relationship between the taxonomic composition and time.

Temporal overlap of emerging species was significantly greater than expected by chance. Both observed mean temporal overlap (0.269) and observed temporal overlap variance (0.035) differ significantly ($p< 0.05$) from the expected ($\text{mean}_{\text{exp.}} = 0.215$ and $\text{variance}_{\text{exp.}} = 0.023$). These values revealed that many species of this assemblage were emerging together throughout the year.

3.4 Discussion

Patterns of temporal variation in animal communities and the factors that control them are complex and still under debate (Bjørnstad & Grenfell, 2001). According to Wolda (1988) the timing and duration of the activity period in insects, and the shape of the abundance distributions, depend on the life history characteristics of the species concerned, and this information is scarce for the southern hemisphere. The only studies on emergence phenology of tropical lotic chironomids were those of Lehmann (1979, 1981) in Zaire, Ferrington *et al.* (1993) in Puerto Rico, Coffman & de la Rosa (1998) in Costa Rica and Boothroyd (2000) in New Zealand.

Our data combined with these cited above suggest that the length of lotic chironomid emergence period increases towards the tropics. Most species in this study emerged continuously throughout the year and three were present in all 48 weekly samples. Since it is unlikely that these three species have a one week life cycle, their populations should be represented at all times of the year by most, if not all, larval instars (Coffman & de la Rosa, 1998).

Some studies have indicated that temporal cues for tropical insect emergence are most likely to be rainfall related, with the beginning or end of the activity season associated with an alternation of rainy and dry periods (Wolda, 1981; Kaspari *et al.*, 2001). In this study, for the highest level of organization (entire assemblage) and for each subfamily separately none of the environmental variables (rainfall, maximum and minimum air temperature, moon phase and photoperiod) were important as a constraint factor for their emergence phenology.

On the other hand, some individual taxa appeared to use environmental cues for emergence. The abundance of emerging individuals of *Caladomyia* sp.1 and *Endotribelos* sp.4 were related with photoperiod while *Caladomyia* sp. 2 and *Corynoneura* sp. 1 were related with minimum air temperature.

Photoperiod can provide a reliable and informative signal to certain life-history stages of some aquatic insects (Sweeney, 1984). This undescribed species of *Endotribelos* live inside fallen-fruits (Roque *et al.*, 2005), probably in complete darkness, unable to sense photoperiod. However, photoperiod could be felt though its effects on the plants that produce these fruits. Changes in photoperiod are known to affect the fruiting period of Atlantic Forest trees (Morellato *et al.*, 2000), therefore, the temporal variation of the input of theses fruits may be factor behind the population dynamics of *Endotribelos* sp. 4.

Wolda & Flowers (1985) showed that in many species of Ephemeroptera from Panama the number of emerging individuals varied with the phases of the moon. Others also speculated on the existence of a relationship between lunar periodicity and emergence rhythm in some freshwater chironomids (e.g. Armitage, 1995). We expected that moon phase was a good predictor of tropical lotic Chironomidae emergence. It was not, neither for individual species. According to Corbet (1964), whatever the controlling time-cue may be, it is likely that some insect groups in non-tidal waters probably use endogenous variants, because there are so few discernable environmental changes that they could respond.

We found changes in taxonomic composition as a function of the time distance between samples. However, since the degree of association between them was very low we believe that these changes tend to be minimal. Coffman & de la Rosa (1998) had already pointed out that the rate of change of the taxonomic composition in tropical streams was, on average, about the same throughout the year. It has been argued that species richness influences temporal variability (Schläpfer *et al.* 1999), communities with many interacting species would be less prone to large fluctuations than communities with fewer species (MacArthur, 1955). So, as this chironomid assemblage is very species rich, we could not assert that this result will be true for poor assemblages.

There was no evidence of synchrony of emergence for the entire assemblage. The temporal overlap measured across the entire year was significantly greater than expected by chance, and most species were emerging together at each sample date, so they have similar patterns of emergence. These results indicate that there is no temporal sequencing of chironomid species in low order forested tropical streams. Moreover, this assemblage is not constrained on the time axis at this scale, although our analyses do not exclude the possibility of a temporal chaotic organization.

Also, the variance in temporal overlap was greater than expected by chance. According to Inger & Colwell (1977) this may be a consequence of a guild organization within the species assemblage. Our results are consistent with the view that temporal partitioning is not the most important mechanism allowing the coexistence of tropical stream chironomids (Coffman & de la Rosa, 1998) and other kinds of niche partitioning or ecological mechanisms may permit it. Although it is difficult to untangle the mechanism behind the coexistence of chironomids, food and spatial partitioning may account partially for this. There are evidences that chironomid larvae distribution on Brazilian streams is related to habitats, for example larvae of the genus *Rheotanystarsus* to riffle, *Stenochironomus, Xestochironomus, Oukuriella* to woods, most tanypodines to pools (Sanseverino & Nessimian, 2001; Henrique-Oliveira *et al.*, 2003; Roque, 2005). However in tropical streams, like Fazzari, most speciose genera as *Tanytarsus, Caladomyia* and *Polypedilum* have many morphological similar species that occupy similar habitats (Roque, 2005). In these cases, stochastic patch dynamics (Tokeshi & Townsend, 1987) may be a potential mechanism underlying the local coexistence of the species. In this hypothesis, eggs and larvae colonization driven by stochastic water transport, together with pacth formation reduce the potential impact of interspecific competition, helping to maintain the species richness of morphologically and ecologically similar species (Tokeshi, 1999).

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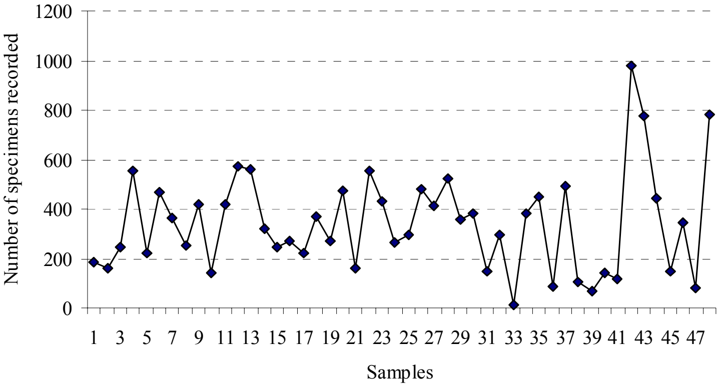
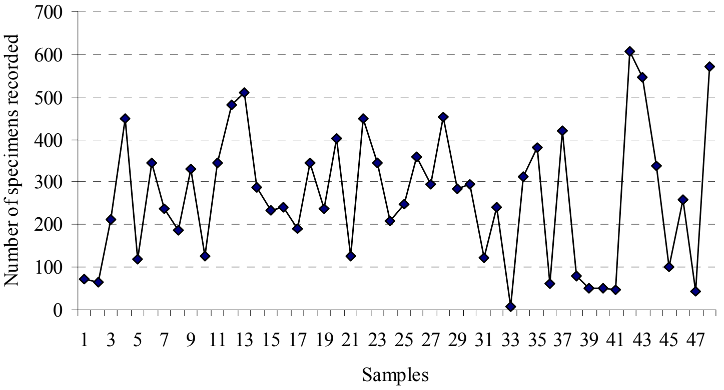
Appendix

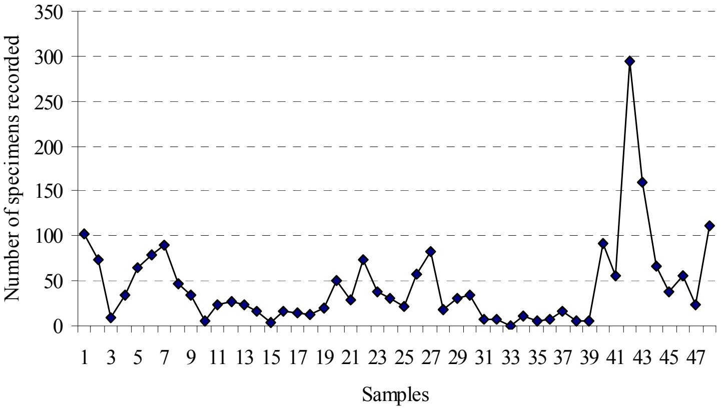
Appendix 1. Complete list of the selected environmental variables of the Fazzari stream, São Carlos, SP, Brazil.

Sample	Rainfall (mm)	Max. air temperature (°C)	Min. air temperature (°C)	Photoperiod (hrs)	Moon phase
7/4/2004	17	31	16	11.7	Full moon
15/4/2004	27	26	15	11.55	Last quarter
22/4/2004	12	28	19	11.4	New moon
29/4/2004	1	26	14	11.27	First quarter
7/5/2004	28	19	17	11.13	Full moon
14/5/2004	2	21	10	11.01	Last quarter
21/5/2004	32	25	13	10.9	New moon
31/5/2004	37	23	14	10.81	First quarter
6/6/2004	3	24	9	10.73	Full moon
13/6/2004	0	18	7	10.68	Last quarter
20/6/2004	12	25	12	10.66	New moon
28/6/2004	0	26	15	10.66	First quarter
5/7/2004	0	27	16	10.68	Full moon
12/7/2004	11	24	12	10.72	Last quarter
20/7/2004	28	16	13	10.79	New moon
28/7/2004	0	24	11	10.88	First quarter
3/8/2004	0	29	15	10.98	Full moon
10/8/2004	0	24	7	11.08	Last quarter
18/8/2004	0	29	11	11.21	New moon
25/8/2004	0	32	15	11.35	First quarter
31/8/2004	0	31	17	11.47	Full moon
8/9/2004	0	33	16	11.61	Last quarter
16/9/2004	0	28	13	11.77	New moon
23/9/2004	6	33	16	11.92	First quarter
30/9/2004	0	26	17	12.07	Full moon
8/10/2004	22	29	9	12.22	Last quarter
15/10/2004	38	21	17	12.38	New moon
22/10/2004	22	25	14	12.52	First quarter
30/10/2004	6	32	17	12.66	Full moon
7/11/2004	2	24	17	12.81	Last quarter
14/11/2004	36	29	13	12.94	New moon
21/11/2004	83	28	15	13.05	First quarter
28/11/2004	28	26	18	13.15	Full moon
6/12/2004	17	29	18	13.23	Last quarter
13/12/2004	94	27	15	13.29	New moon
20/12/2004	52	28	17	13.33	First quarter
28/12/2004	46	29	16	13.34	Full moon
5/1/2005	120	23	18	13.32	Last quarter
12/1/2005	49	28	20	13.27	New moon
20/1/2005	81	23	20	13.19	First quarter
28/1/2005	76	25	19	13.09	Full moon
3/2/2005	69	28	20	12.98	Last quarter
10/2/2005	3	28	16	12.87	New moon
17/2/2005	0	31	19	12.74	First quarter
28/2/2005	24	28	19	12.55	Full moon
7/3/2005	0	31	18	12.37	Last quarter
14/3/2005	40	27	21	12.36	New moon
21/3/2005	120	26	19	12.07	First quarter

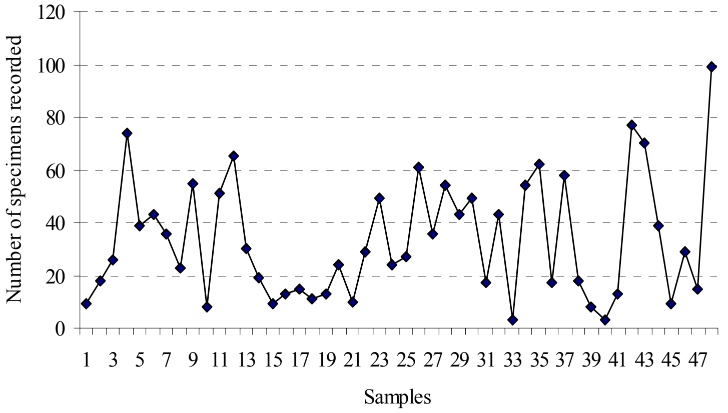
Appendix 2. Temporal variation of the number of specimens recorded for each taxa separately (considered in the multiple regression analysis) for the entire study period in Fazzari stream, São Carlos, Brazil. The samples are in chronological order, with sample 1 corresponding to 7/4/2004 and sample 48 to 21/3/2005.


Chironomidae

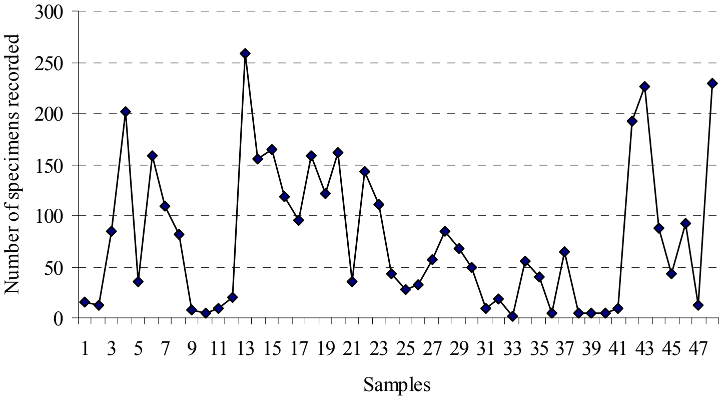

Chironominae


Orthocladiinae

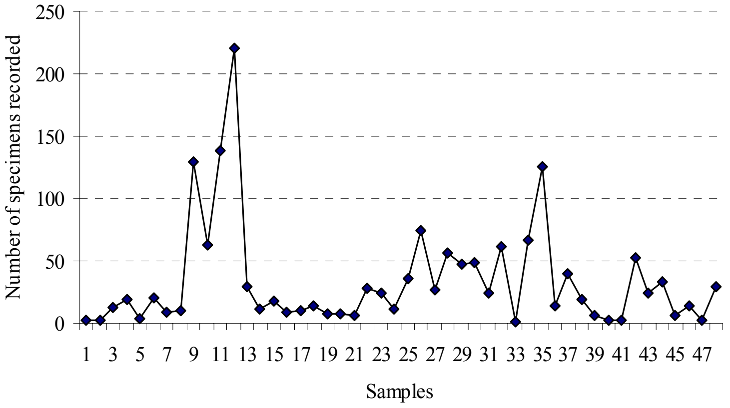
Tanypodinae



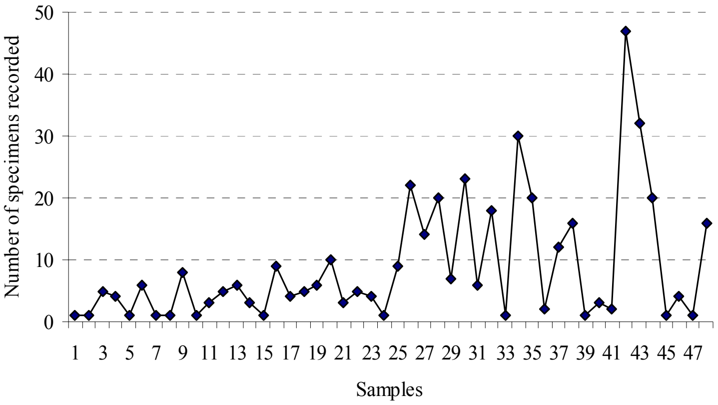
Caladomyia sp. 1



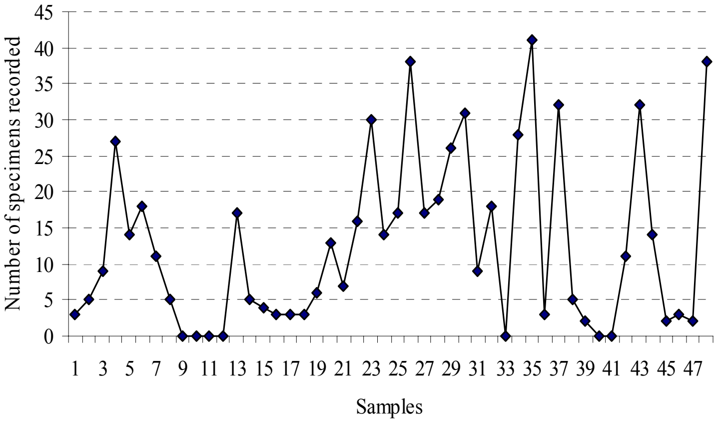
Caladomyia sp. 2



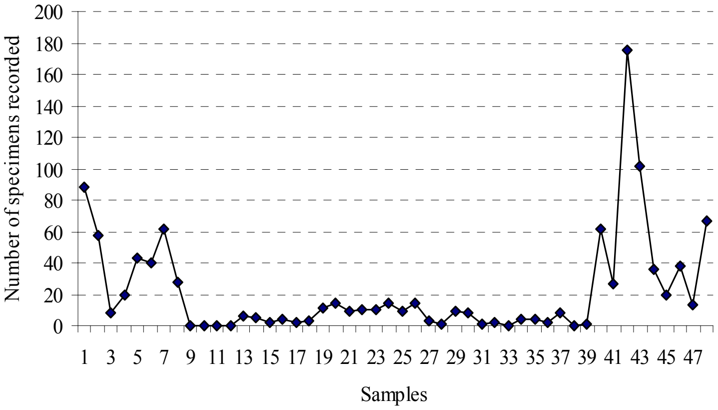
Endotribelos sp. 4



Labrundinia sp. 1



Corynoneura sp. 1



4. CONSIDERAÇÕES FINAIS

Este estudo representa a primeira fonte de dados clara sobre fenologia da emergência de Chironomidae em córregos brasileiros. Apesar de representar apenas um ano de amostragem, eles trazem consigo estimativas importantes. Nossa série temporal pode ser considerada longa para a escala semanal, além disso, a emergência de insetos tropicais parece não mudar muito de ano para ano (Wolda, 1992).

Embora cada capítulo desta dissertação tenha suas próprias conclusões, o que podemos dizer sobre os padrões de diversidade e organização temporal de Chironomidae em córregos brasileiros de baixa ordem e florestados é: o maior número de espécies, assim como o número de indivíduos é encontrado nas classes de tamanho menores e intermediárias e que estas relações, tidas como uma característica estável das comunidades terrestres, mudam ao longo do tempo; a composição taxonômica e a riqueza de espécies não mudam ao longo do ano; já o número de indivíduos que emerge apresenta uma estrutura temporal que não está associada a nenhuma variável ambiental aqui avaliada, porém esta estrutura depende da escala taxonômica considerada; interações bióticas podem ser as responsáveis por modular a dinâmica de emergência das espécies de Chironomidae.

De maneira geral, o que nos parece muito importante, principalmente para estudos futuros, é que não existe estacionalidade na emergência de Chironomidae no córrego do Fazzari e provavelmente em córregos com características similares. Portanto, acreditamos que uma coleta feita em qualquer época do ano em córregos deste tipo (desde que não seja depois de algum distúrbio forte) tem grandes chances de abranger boa parte da diversidade do local.

Reflexões pessoais

Parece que ainda estamos longe de obter séries temporais longas e suficientemente adequadas, sobre Chironomidae tropicais, para realizarmos análises mais robustas. Quando tivermos esses dados talvez sejamos capazes de fazer previsões (o que no meu ponto de vista é o objetivo último dos estudos de séries temporais) e entender os mecanismos que geram e mantém os padrões de diversidade deste rico grupo de insetos aquáticos. Programas de monitoramento contínuo da fenologia de diversos grupos como "Butterfly Monitoring Schemes", que é um programa que opera em diversos países da Europa e já detém 20 anos de observações semanais sobre a atividade de borboletas, deveriam ser adotados aqui no Brasil. Além de oferecerem uma excelente fonte de dados para compreensão de processos e mecanismos da dinâmica de comunidades animais; nos tempos atuais em que a preocupação com as mudanças climáticas globais ocupa lugar de destaque, essas séries de dados longas sobre fenologia têm sido usadas com sucesso para avaliação das conseqüências de mudanças no clima.

Finalmente, o surgimento de modernas abordagens estatísticas acopladas com interpretação biológica tem trazido avanços ao entendimento da dinâmica complexa dos sistemas ecológicos. A junção de estudos de série temporais com a teoria ecológica nos traz um interessante dilema: para entender qualquer sistema, nós precisamos analisar suas particularidades; para gerar padrões amplos, nós necessitamos extrair generalidades; portanto, o grande desafio para os estudos ecológicos de séries temporais é acomodar e simultaneamente transcender os detalhes da história natural (Bjørnstad & Grenfell, 2001).

4.1 Referências bibliográficas

Bjørnstad, O. N., Grenfell, B. T. 2001. Noisy clockwork: Time series analysis of population fluctuations in animals. *Science* 293: 638-643.

Wolda, H. 1992. Trends in abundance of tropical forest insects. *Oecologia* 89: 47-52.