



Diel variation of aquatic insect drift in streams of Southern Brazil

Ramiro de Campos^{1*}, Jonathan Rosa¹, Janet Higuti¹, Tayane Cristina Buggenhagen² and Ana Carolina de Deus Bueno Krawczyk²

¹Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais, Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura, Universidade Estadual de Maringá. Av. Colombo, 5790, 87020-900. Maringá, Paraná, Brazil. ²Universidade Estadual do Paraná, *Campus* de União da Vitória, União da Vitória, Paraná, Brazil. *Author for correspondence. E-mail: rami_campos@hotmail.com

ABSTRACT. Some organisms, such as aquatic insects, are transported from the upstream to downstream region of streams through a process called drift. This process occurs in passive and active ways and can be variable throughout the day, mainly between the nocturnal and diurnal periods. Here, we evaluate the periodicity of the drift of aquatic insects in two streams of the Middle Iguaçu basin, southern region of Brazil. We predicted that the drift of aquatic insects brings the highest richness, diversity and abundance during the nocturnal period, compared to the diurnal period. In addition, we expected that the composition of species is different between these periods. In each stream, aquatic insect sampling was carried out 10 times, for 24 hours, using drift nets. A total of 2,114 aquatic insect specimens were recorded, distributed in 26 families. Of these families, 20 were recorded during the diurnal period and 24 during the nocturnal period. Our results showed an increase in the diversity and abundance of aquatic insect drift in the nocturnal period. However, only abundance was significantly different between the periods. We attribute the higher abundance in nocturnal drift possibly to biological interactions. Thus, nocturnal drift can be a strategy of some aquatic insects to avoid visual predation by other invertebrates and/or vertebrates, in Neotropical streams. We highlight the importance of our study, because it can be used for comparison in surveys of lotic environments that have been impacted by human activity (e.g. by dam construction), which can alter the water flow, and consequently the pattern of insect drift.

Keyword: Lotic environment; entomological fauna; downstream movement; composition; ecological relationship.

Received on August 13, 2020.

Accepted on April 29, 2021.

Introduction

Lotic environments are characterized by having a unidirectional and continuous flow of water movement, and high heterogeneity in physical, chemical and geomorphological aspects along their route (Vannote, Minshall, Cummins, Sedell, & Cushing, 1980; Covino, 2017). In these environments, fluvial continuity plays an important role in the spread of aquatic organisms, such as immature stages of invertebrates, allowing the colonization of downstream regions (Callisto & Goulart, 2005), besides the spread of allochthonous organic matter (Hay, Franti, Marx, Peters, & Hesse, 2008; Tank, Rosi-Marshall, Griffiths, Entekin, & Stephen, 2010).

The movement of organisms through the water column, in the downstream direction, also called drift (Flecker, 1992), may happen in two ways: (1) passively, when there are physical disorders in the environments (e.g. discharge changes in rainy periods), and (2) actively, when the release of organisms into the water column is behaviourally determined. Several factors trigger behavioral drift, such as the need to maximize the most advantageous conditions for survival in the environment and increase efficiency in the search for food (Flecker, 1992), predatory pressure (Huhta, Muotka, & Tikkanen, 2000; McIntosh, Peckarsky, & Taylor, 2002) and competitive pressure (Brittain & Eikeland, 1988).

The intensity of organisms drifting in the water column can vary throughout the day, mainly between the nocturnal and diurnal periods, owing to the availability of hours with the presence or absence of light (Elliott, 1969; Mendonza, Montoya, & Perez, 2018). In this way, the periodicity (luminosity) influences the chemical and physical conditions of water and the biotic interactions between the communities (Douglas, Forrester, & Cooper, 1994; Guasch, Armengol, Martí, & Sabater, 1998; Kayombo, Mbvette, Mayo, Katima, & Jørgensen, 2002).

Benthic invertebrate communities are the most abundant in lotic ecosystems, and they participate in the nutrient cycle, by transforming the organic matter, making it available to lower trophic levels, and by serving as a food source for higher organisms (Moulton, Magalhaes-Fraga, Brito, & Barbosa, 2010). Given the importance of these communities, understanding their daily patterns of drift and distribution in the environment is very important. Several taxa have been recorded in drift, especially aquatic invertebrates (e.g. insect larvae, molluscs and crustaceans, Boyero & Bosch, 2002). Besides, studies have found that some taxa are dominant in drift, for example insects, such as Chironomidae larvae and Ephemeroptera nymphs (mainly Baetidae genera), which are frequently recorded in both tropical and temperate regions (Cowell & Carew, 1976; Callisto & Goulart, 2005; Gimenez, Lansac-Tôha, & Higuti, 2015).

The study of aquatic invertebrates in drift has been widely carried out in rivers of temperate regions. However, in tropical rivers, this process remains poorly studied (see Callisto & Goulart, 2005; Lobón-Cerviá, Rezende, & Castellanos, 2012). Thus, this study aimed to analyze the diel behavioral drift of aquatic insects using the attributes (richness, diversity, abundance and composition) of this community. We predicted that the drift of aquatic insects brings the highest richness, diversity and abundance during the night period. In addition, we expected the composition of species would be different between these periods.

Material and methods

Study sites

The Iguaçu River presents the biggest hydrographic basin in Paraná State, Brazil and, adding the affluents of Santa Catarina State, has a catchment area of approximately 70,800 Km² and covers an extension of 1,200 Km (Maack, 1968). This study was carried out in a region called Middle Iguaçu, in two second-order streams of the Iguaçu basin: Papuã, located in the south of Paraná State (26°07'04.1"S; 51°09'58.5"W) and Pintado, in the north of Santa Catarina State (26°20'32.4"S; 51°03'12.0"W) (Figure 1). The climate in the region is subtropical/mesothermal humid, according to the Köppen classification, with rainfall in all months of the year and average annual temperature of 17.9°C. The streams are located in a rural region and the landscape features extensive agriculture areas. There is extensive plant cover of Mixed Araucaria Forest on both banks of the streams, mainly along Papuã stream.



Figure 1. Location of the sampling sites. P1= Papuã stream, Paraná State, P2 = Pintado stream, Santa Catarina State.

Aquatic insect sampling

The aquatic insects were sampled in July 2012 in Papuã stream and August 2012 in Pintado stream. In each stream, one sampling site was selected, and samples were taken 10 times over 24 hours: every 3 hours in the diurnal period (08-11h, 11-14h and 14-17h) and every 2 hours in the nocturnal period (17-19h, 19-21h, 21-23h, 23-1h, 01-03h, 03-05h and 05-07h). For that, we used three drift nets (0.16 m² area and mesh size 250 µm), which were placed in different regions of the selected sampling sites (center and left and right banks) in each sampling time. The three drift nets were considered pseudoreplicas, and the material collected by them was later joined, forming one sample for each sampling time. In total, 20 samples (2 streams x 10 times of intervals) were considered in the present study.

The biological material was stored in plastic bags in the field. In the laboratory, samples were sorted on the light box, and the organisms were identified at the family level using Trivinho-Strixino & Strixino (1995); Merritt & Cummins (1996); Mugnai, Nessimian, and Baptista (2010). Only mayflies of the Baetidae family were identified at the genus level (Salles, Da-Silva, Serrão, & Francischetti, 2004; Falcão, Salles, & Hamada, 2011). The aquatic insects were fixed in alcohol 70° GL. The variables, nitrate, nitrite, ammonia, dissolved oxygen and pH, were measured in the field using the kit for water quality analysis (ALFAKIT). Water and air temperatures were measured using a mercury thermometer and the discharge using the float method (Palhares et al., 2007).

Data analysis

We assessed the variation of drifting aquatic insects between the diurnal and nocturnal periods, using richness, Shannon-Wiener diversity and abundance (number of individuals). We analyzed the possible significant differences in community attributes, between the diurnal and nocturnal periods, applying a generalized linear mixed model (GLMM; Logan, 2011) using a Gaussian or Poisson distribution. The GLMM was made using the richness, Shannon-Wiener diversity and abundance as the response variable, and the period (diurnal and nocturnal) as the explanatory variable (fixed effect). We removed the spatial effect by adding the streams as random variable (random effect). The data were checked for normality and homogeneity of variance to meet the conditions of multiple regressions.

We performed the Principal Coordinate Analysis (PCoA) to visualize the (dis)similarity of the species composition of aquatic insects, between the periods (diurnal and nocturnal) (Legendre & Legendre, 1998), using a presence/absence matrix and the Jaccard index. A multivariate Permutational Variance Analysis (PERMANOVA) was performed to evaluate changes in species composition of aquatic insects between diurnal and nocturnal periods (Anderson, 2006). A total of 999 permutations were performed to assess the significance. Finally, rarefaction analysis, considering the number of individuals, was performed to compare aquatic insects' richness during diurnal and nocturnal periods.

The statistical analyses were performed with the environment R version 3.3.1 (R Development Core Team, 2019), using function "biodiversity" in the vegan package for Shannon-Wiener diversity, and "nlme" packages for GLMM analyses (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2007). The PERMANOVA was performed according to the function "ADONIS", using the vegan (Oksanen et al., 2018) and permute packages (Simpson, 2018). Only the rarefaction curves were performed using the BioDiversity Pro Programme (McAleece, Gage, Lambshead, & Patterson, 1997).

Results

Limnological variables

The pH was neutral to slightly acid, with high oxygen concentrations in the streams, and nitrite and ammonia were also similar between the environments. Only nitrate was higher in Papuã stream (Table 1). The air and water temperatures, discharge and width were higher in Pintado stream (Table 1).

Aquatic insect community

A total of 2,114 aquatic insect specimens were found, distributed in 26 families. Of these families, 20 were found during the diurnal period and 24 during the nocturnal period (Table 2). The most abundant family was Baetidae, followed by Chironomidae and Simuliidae. These families represented 72.78% of the total number of organisms. The Baetidae family was represented by seven genera and the most abundant were *Americabaetis* sp. and *Baetodes* sp.

Table 1. Abiotic variables of Pintado and Papuã streams.

Variables	Pintado	Papuã
Water temperature (°C)	18.5	14
Air temperature (°C)	21	18.6
Discharge (m ³ s ⁻¹)	1.14	0.27
Ammonia (mg L ⁻¹)	0	0.12
Nitrate (mg L ⁻¹)	1.33	3.10
Nitrite (mg L ⁻¹)	0.03	0.03
Dissolved oxygen (mg L ⁻¹)	9	8
pH	7	6.5
Width (m)	23	7
Depth (cm)	30	21

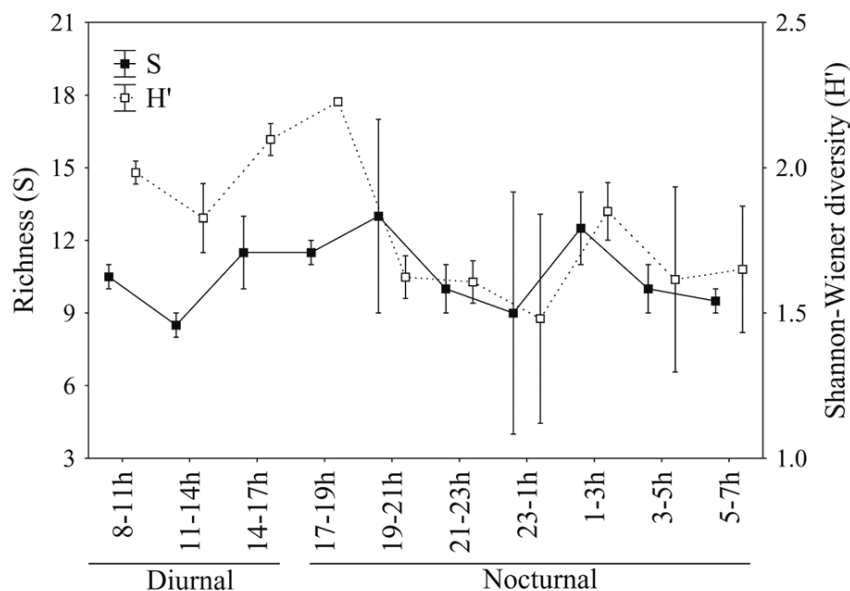
Table 2. Occurrence of aquatic insects in the different periods.

	Sampling period									
	Diurnal					Nocturnal				
	8-11h	11-14h	14-17h	17-19h	19-21h	21-23h	23-1h	1-3h	3-5h	5-7h
Ephemeroptera										
Baetidae										
<i>Americabaetis</i> sp.	X	X	X	X	X	X	X	X	X	X
<i>Cleodes</i> sp.					X	X		X	X	X
<i>Camelobaetidium</i> sp.	X			X	X	X		X	X	X
<i>Zelus</i> sp.					X	X		X	X	X
<i>Baetodes</i> sp.	X	X	X	X	X	X	X	X	X	X
<i>Moribaetis</i> sp.	X	X	X	X	X	X	X	X	X	X
<i>Tupia</i> sp.	X		X	X	X	X		X	X	
Leptophlebiidae	X	X	X	X	X	X	X	X	X	X
Leptohyphidae			X	X	X	X	X	X	X	X
Caenidae		X	X	X		X		X	X	X
Odonata										
Calopterygidae				X					X	
Plecoptera										
Perlidae	X		X	X	X	X	X	X	X	X
Gripopterygidae	X	X	X	X	X	X	X	X	X	X
Hemiptera										
Veliidae				X						
Coleoptera										
Elmidae	X	X	X	X	X	X	X	X	X	X
Psephenidae	X	X	X	X	X	X	X	X	X	
Haliplidae				X	X					
Dryopidae	X									
Megaloptera										
Corydalidae					X					
Trichoptera										
Hydropsychidae	X	X	X	X	X		X	X	X	X
Helichopsychidae		X	X				X			
Leptoceridae	X			X	X			X		X
Polycentropodidae									X	
Hydrobiosidae			X		X		X		X	
Hydroptilidae			X		X	X	X			
Diptera										
Simuliidae	X	X	X	X	X	X	X	X	X	X
Dixidae					X	X	X	X		
Empididae	X			X						
Ceratopogonidae	X				X					
Tipulidae			X							
Chironomidae	X	X	X	X	X	X	X	X	X	X
Lepidoptera										
Pyralidae			X				X	X		

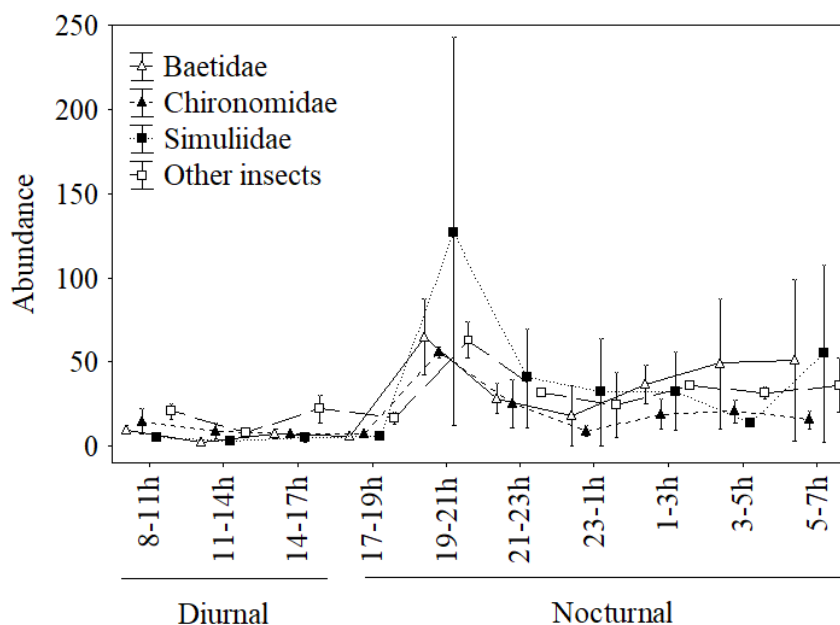
The richness ($p = 0.334$) and Shannon-Wiener diversity attributes ($p = 0.301$) were similar between diurnal and nocturnal periods (Table 3). Higher values of richness were recorded in the nocturnal period (19-21 and 1-3 hours), and Shannon-Wiener diversity in diurnal (14-17 hour) and nocturnal periods (17-19 hour) (Figure 2).

Table 3. Generalized linear mixed model (GLMM) results for the relationship between the richness, Shannon-Wiener diversity and abundance of aquatic insects with the periods (diurnal and nocturnal). Significant values are in bold.

Response variable	Effects	Estimate	Standard error	Z-value	P-value
Richness	Richness * Period	0.131	0.136	0.967	0.334
Shannon-Wiener diversity	Diversity * Period	-0.205	0.199	1.896	0.301
Abundance	Abundance * Period	1.285	0.070	18.230	<0.001

**Figure 2.** Mean values and standard error of richness (S) and Shannon-Wiener diversity (H') in different periods.

The abundance was significantly different between periods ($p < 0.001$), and its values were higher in the nocturnal period than in the diurnal period, especially in the first hours after nightfall. The Baetidae, Chironomidae and Simuliidae families showed this pattern, mainly at 19-21 hours, as well as other families (Figure 3).

**Figure 3.** Mean values and standard error of abundance of Baetidae, Chironomidae, Simuliidae and other aquatic insects in diurnal and nocturnal periods.

Aquatic insects' composition was very similar between the diurnal and nocturnal periods (Figure 4), and there were no significant differences for this attribute between the periods (PERMANOVA: $p = 0.156$).

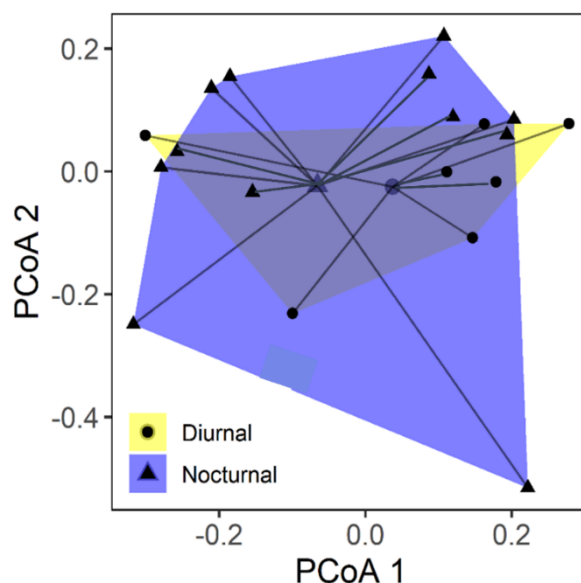


Figure 4. Dissimilarity of aquatic insect composition between diurnal and nocturnal periods.

Rarefaction curves showed higher richness in the nocturnal period and a tendency to reach an asymptote. On the other hand, an increase in richness was observed in the diurnal period (Figure 5), i.e., higher richness would be found with a higher number of individuals collected.

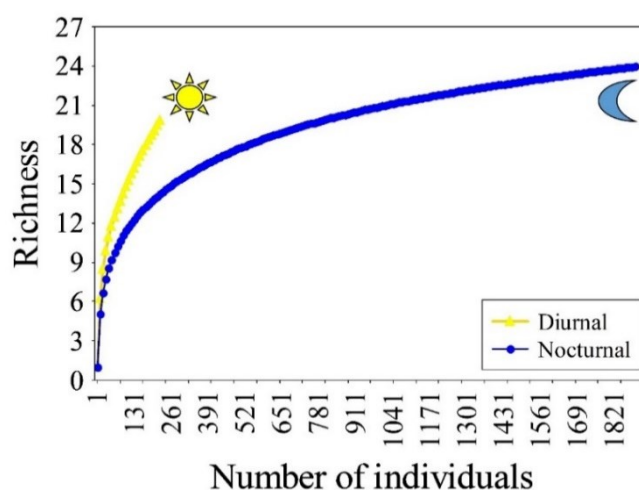


Figure 5. Rarefaction curves of aquatic insects' richness in diurnal and nocturnal periods.

Discussion

In lotic environments, the drift of larvae, nymphs or adults of organisms is an important mechanism for regulating populations, because it reduces their abundance in upstream regions, increasing this abundance in downstream regions (Baxter, Kennedy, Miller, Muehlbauer, & Smock, 2017). In the streams evaluated in the present study, some groups, such as Baetidae, Simuliidae and Chironomidae, may be using this mechanism to control their populations, since they were the most abundant in the drift. Some studies have shown that these groups are very abundant in the drift of lotic environments (Boyero & Bosch, 2002; Callisto & Goulart, 2005; Lobón-Cerviá et al., 2012; Mendoza et al., 2018). For example, Brittain & Eikeland (1988) found that Ephemeroptera, Simuliidae, Plecoptera and Trichoptera were the most abundant aquatic insects in a diel drift evaluation. Likewise, Schulz, Rosa, & Klein-Stolz (2019) found that Chironomidae comprised 70% of the total macroinvertebrates drifting in a Neotropical River in Southern Brazil.

The periodicity of drift of invertebrates in streams has been examined by numerous studies, which have found different diel patterns in the drift, mainly with maximum drift rates in nocturnal periods or those with low light (Hansen & Closs, 2007; Lobón-Cerviá et al., 2012). Aquatic invertebrates generally perform drift as

a strategy to escape from unfavorable physical, chemical and biological conditions and to colonize new environments (Brittain & Eikeland, 1988; Naman, Rosenfeld, & Richardson, 2016). Here, as predicted, aquatic insect attributes (richness, Shannon-Wiener diversity and abundance) showed the same pattern, with the highest drift during the nocturnal period. However, since only the abundance was significantly different, we consider that our prediction was partially supported. Our results are in agreement with Mendoza et al. (2018), in a study that found higher drift density values of aquatic macroinvertebrates at night in Neotropical streams in Venezuela. The fact that the species composition was similar between the diurnal and nocturnal periods might be because some invertebrates have constant drift in both periods (e.g. Coleoptera and some species of Chironomidae), as showed by Brittain & Eikeland (1988).

The high drift in the nocturnal period seems to be related to active rather than passive drift, since there were no extreme environmental changes during the sampling period (e.g. discharge changes). It might be caused by other adverse situations, such as the presence of predators, which lead these organisms to detach rapidly from the substrate and enter the water column (McIntosh et al., 2002). For example, we found some invertebrate predators, such as Megaloptera and Hemiptera. Thus, the high nocturnal drift activity might be related to an evolutionary response to minimize the risk of predation by invertebrate predators (or even fish, not assessed here, similarly showed by Allan, 1982; Ramirez & Pringle, 1998). Likewise, Flecker (1992) observed the highest drift of invertebrates during the nocturnal period in the presence of predator fish. The exploration of different habitats by fish, whether for shelter, food, or reproduction, occurs by actively moving to a downstream region or vice versa (here called vertical migration) or from one margin to another (here called horizontal migration), movements which affect the structure of the food web and the composition of prey (e.g. aquatic invertebrates) (Armstrong et al., 2013). Besides, in an experimental study, the genus *Baetis* (Baetidae) was also frequent in the drift, when the organisms were exposed to predation (Lancaster, 1990). On the other hand, Huhta et al. (2000) showed that in fishless rivers of northern Finland, the drift of Baetidae was aperiodic, while in the presence of fish predators the drift was nocturnal.

We can also infer that other factors might be responsible for the higher nocturnal drift, compared to diurnal drift in the present survey. The first one is phototaxis, and changes in light intensity can act as a trigger for active drift behavior (Naman et al., 2016; Baxter et al., 2017). Some dipterans and mayflies have negative phototaxis, which leads them to hide under pebbles during the day and drift during the night (Bishop, 1969). Second, active drift can be used to avoid adverse conditions, aiming to find a favorable site downstream in the river (Mazzucco, Van Nguyen, Kim, Chon, & Dieckmann, 2015). Finally, the nocturnal drift habit is also related to the life-cycle stage, and it is frequent in mature nymphs (Corkum & Pointing, 1979). For example, late-stage invertebrates are more prone to drift during the nocturnal period, when compared to the younger stages of development, owing to the fact that these organisms have a high risk of predation (Allan, 1982). The nocturnal peaks of drifting invertebrates might be associated with good diurnal vision in fish. However, the absence of light decreases the vision of fish, making difficult to capture prey in this period; thus, they present less predation activity during the night (Mazur & Beauchamp, 2003).

We highlight that the rarefaction curves showed that the richness of aquatic insects did not reach an asymptote in the diurnal period, which could increase the drift during the day, if more specimens were taken in future studies. However, since the insects seemed to have nocturnal preferences for drifting, even if we had collected more samples in the diurnal period, the richness would not have increased significantly. We point out that there is a gap in the information about aquatic invertebrates in Neotropical streams, e.g. the Middle Iguaçu River (Brazil), evidencing the importance of this study in ecological and biodiversity surveys. Only Camargo, Lahun, Rosa, & Deus Bueno-Krawczyk (2019) and Delonzek, Lahun & Krawczyk (2020) evaluated the invertebrate communities in this region and found a high abundance and richness of these organisms.

Conclusion

We conclude that the diel drift of aquatic insects in Neotropical streams can be periodic (with peaks in the nocturnal period), which is related to behavioral strategies for survival, e.g. biological interactions, in order to avoid predation. The present study is important because it brings information about insect drift in low-impacted streams in the Neotropical region. Therefore, our results can be used for comparison in other studies assessing the drift patterns of impacted streams or rivers in the same region (e.g. lotic environments in the Iguaçu River basin that suffer from land use and dam construction), which can present different results.

Acknowledgements

We thank Eliezer de Oliveira da Conceição for the production of the map. We thank Luci Fátima Pereira, Nelson J. Grob Junior and Alexandre Empinotti for the sampling support. We also thank Luci Fátima Pereira for helping in insect identification.

References

- Allan, J. D. (1982). The effects of reduction in trout density on the invertebrate community of a mountain stream. *Ecology*, 63(5), 1444-1455. DOI: <https://dx.doi.org/10.2307/1938871>
- Anderson, M. J. 2006. Distance-Based tests for homogeneity of multivariate dispersions. *Biometrics*, 62(1), 245-253. DOI: <https://dx.doi.org/10.1111/j.1541-0420.2005.00440.x>
- Armstrong, J. B., Schindler, D. E., Ruff, C. P., Brooks, G. T., Bentley, K. E., & Torgersen, C. E. (2013). Diel horizontal migration in streams: juvenile fish exploit spatial heterogeneity in thermal and trophic resources. *Ecology*, 94(9), 2066-2075. DOI: <https://dx.doi.org/10.1890/12-1200.1>
- Baxter, C. V., Kennedy, T. A., Miller, S. W., Muehlbauer, J. D., & Smock, L. A. (2017). Macroinvertebrate drift, adult insect emergence and oviposition. In F. R. Hauer & G. A. Lamberti (Eds.), *Methods in Stream Ecology* (p. 435-456). Academic Press. DOI: <https://dx.doi.org/10.1016/B978-0-12-416558-8.00021-4>
- Bishop, J. E. (1969). Light control of aquatic insect activity and drift. *Ecology*, 50(3), 371-380. DOI: <https://dx.doi.org/10.2307/1933885>
- Boyer, L., & Bosch, J. (2002). Spatial and temporal variation of macroinvertebrate drift in two neotropical streams. *Biotropica*, 34(4), 567-574. DOI: <https://dx.doi.org/10.1111/j.1744-7429.2002.tb00575.x>
- Brittain, J. E., & Eikeland, T. J. (1988). Invertebrate drift—a review. *Hydrobiologia*, 166(1), 77-93. DOI: <https://dx.doi.org/10.1007/BF00017485>
- Callisto, M., & Goulart, M. (2005). Invertebrate drift along a longitudinal gradient in a Neotropical stream in Serra do Cipó National Park, Brazil. *Hydrobiologia*, 539(1), 47-56. DOI: <https://dx.doi.org/10.1007/s10750-004-3245-4>
- Camargo, N. S. J., Lahun, A. L., Rosa, J., & Bueno-Krawczyk, A. C. D. (2019). Colonization of benthic invertebrates on artificial and natural substrate in a Neotropical lotic environment in Southern Brazil. *Acta Scientiarum. Biological Sciences*, 41(1), e45872. DOI: <https://dx.doi.org/10.4025/actasciobiolsci.v41i1.45872>
- Corkum, L. D., & Pointing, P. J. (1979). Nymphal development of *Baetis vagans* McDunnough (Ephemeroptera: Baetidae) and drift habits of large nymphs. *Canadian Journal of Zoology*, 57(12), 2348-2354. DOI: <https://dx.doi.org/10.1139/z79-305>
- Covino, T. (2017). Hydrologic connectivity as a framework for understanding biogeochemical flux through watersheds and along fluvial networks. *Geomorphology*, 277, 133-144. DOI: <https://dx.doi.org/10.1016/j.geomorph.2016.09.030>
- Cowell, B.C., & Carew, W.C. (1976). Seasonal and diel periodicity in the drift of aquatic insects in a subtropical Florida stream. *Freshwater Biology*, 6(6), 587-594. DOI: <https://dx.doi.org/10.1111/j.1365-2427.1976.tb01648.x>
- Delonzek, E. C., Lahun, A. L., & Bueno-Krawczyk, A. C. D. (2020). Colonization of benthic invertebrates in a stony river in Southern Brazil. *Luminária, União da Vitória*, 22(1), 17-26.
- Douglas, P. L., Forrester, G. E., & Cooper, S. D. (1994). Effects of trout on the diel periodicity of drifting in baetid mayflies. *Oecologia*, 98(1), 48-56. DOI: <https://dx.doi.org/10.1007/BF00326089>
- Elliott, J. M. (1969). Diel periodicity in invertebrate drift and the effect of different sampling periods. *Oikos*, 20(2), 524-528. DOI: <https://dx.doi.org/10.2307/3543213>
- Falcão, J. N., Salles, F. F., & Hamada, N. (2011). Baetidae (Insecta, Ephemeroptera) ocorrentes em Roraima, Brasil: novos registros e chaves para gêneros e espécies no estágio ninfal. *Revista Brasileira de Entomologia*, 55(4), 516-548. DOI: <https://dx.doi.org/10.1590/S0085-56262011005000048>
- Flecker, A. S. (1992). Fish predation and the evolution of invertebrate drift periodicity: evidence from neotropical streams. *Ecology*, 73(2), 438-448. DOI: <https://dx.doi.org/10.2307/1940751>
- Gimenez, B. C. G., Lansac-Tôha, F. A., & Higuti, J. (2015). Effect of land use on the composition, diversity and abundance of insects drifting in neotropical streams. *Brazilian Journal of Biology*, 75(4 Suppl 1), 52-59. DOI: <https://dx.doi.org/10.1590/1519-6984.03914>

- Guasch, H., Armengol, J., Martí, E., & Sabater, S. (1998). Diurnal variation in dissolved oxygen and carbon dioxide in two low-order streams. *Water Research*, 32(4), 1067-1074.
DOI: [https://dx.doi.org/10.1016/S0043-1354\(97\)00330-8](https://dx.doi.org/10.1016/S0043-1354(97)00330-8)
- Hansen, E. A., & Closs, G. P. (2007). Temporal consistency in the long-term spatial distribution of macroinvertebrate drift along a stream reach. *Hydrobiologia*, 575(1), 361-371.
DOI: <https://dx.doi.org/10.1007/s10750-006-0384-9>
- Hay, C. H., Franti, T. G., Marx, D. B., Peters, E. J., & Hesse, L.W. (2008). Macroinvertebrate drift density in relation to abiotic factors in the Missouri River. *Hydrobiologia*, 598(1), 175-189.
DOI: <https://dx.doi.org/10.1007/s10750-007-9149-3>
- Huhta, A., Muotka, T., & Tikkanen, P. (2000). Nocturnal drift of mayfly nymphs as a post-contact antipredator mechanism. *Freshwater Biology*, 45(1), 33-42. DOI: <https://dx.doi.org/10.1046/j.1365-2427.2000.00615.x>
- Kayombo, S., Mbwette, T. S. A., Mayo, A. W., Katima, J. H. Y., & Jørgensen, S. E. (2002). Diurnal cycles of variation of physical-chemical parameters in waste stabilization ponds. *Ecological Engineering*, 18(3), 287-291. DOI: [https://dx.doi.org/10.1016/S0925-8574\(01\)00086-6](https://dx.doi.org/10.1016/S0925-8574(01)00086-6)
- Lancaster, J. (1990). Predation and drift of lotic macroinvertebrates during colonization. *Oecologia*, 85(1), 48-56. DOI: <https://dx.doi.org/10.1007/BF00317342>
- Legendre, P., & Legendre L. 1998. *Numerical ecology*. Amsterdam: Elsevier Science.
- Lobón-Cerviá, J., Rezende, C. F., & Castellanos, C. (2012). High species diversity and low density typify drift and benthos composition in Neotropical streams. *Fundamental and Applied Limnology*, 181(2), 129-142.
DOI: <https://dx.doi.org/10.1127/1863-9135/2012/0242>
- Logan, M. (2011). *Biostatistical design and analysis using R: a practical guide*. John Wiley & Sons.
- Maack, R. (1968). *Geografia física do Estado do Paraná*. Curitiba: Livraria José Olympio.
- Mazur, M. M., & Beauchamp, D. A. (2003). A comparison of visual prey detection among species of piscivorous salmonids: effects of light and low turbidities. *Environmental Biology of Fishes*, 67(4), 397-405.
DOI: <https://dx.doi.org/10.1023/A:1025807711512>
- Mazzucco, R., Van Nguyen, T., Kim, D. H., Chon, T. S., & Dieckmann, U. (2015). Adaptation of aquatic insects to the current flow in streams. *Ecological Modelling*, 309-310(143-152), 143-152.
DOI: <https://dx.doi.org/10.1016/j.ecolmodel.2015.04.019>
- McAleece, N., Gage, J.D.G., Lambshead, P.J.D., Paterson, G.L.J. (1997) BioDiversity Professional statistics analysis software. Jointly developed by the Scottish Association for Marine Science and the Natural History Museum London.
- McIntosh, A. R., Peckarsky, B. L., & Taylor, B. W. (2002). The influence of predatory fish on mayfly drift: extrapolating from experiments to nature. *Freshwater Biology*, 47(8), 1497-1513.
DOI: <https://dx.doi.org/10.1046/j.1365-2427.2002.00889.x>
- Mendoza, M. D., Montoya, J. V., & Perez, B. Y. (2018). Diel periodicity of aquatic macroinvertebrate drift in a coastal stream in northern Venezuela. *Neotropical Biodiversity*, 4(1), 45-54.
DOI: <https://dx.doi.org/10.1080/23766808.2018.1450056>
- Merrit, R. W., & Cummins, K. W. (1996). *An introduction to the aquatic insects of North America*. Dubuque, IA: Kendall/Hunt Publishing Company.
- Moulton, T. P., Magalhães-Fraga, S. A., Brito, E. F., & Barbosa, F. A. (2010). Macroconsumers are more important than specialist macroinvertebrate shredders in leaf processing in urban forest streams of Rio de Janeiro, Brazil. *Hydrobiologia*, 638(1), 55-66. DOI: <https://dx.doi.org/10.1007/s10750-009-0009-1>
- Mugnai, R., Nessimian, J. L., & Baptista, D. F. (2010). *Manual de identificação de Macroinvertebrados aquáticos do Estado do Rio de Janeiro*. Rio de Janeiro: Technical Books.
- Naman, S. M., Rosenfeld, J. S., & Richardson, J. S. (2016). Causes and consequences of invertebrate drift in running waters: from individuals to populations and trophic fluxes. *Canadian Journal of Fisheries and Aquatic Sciences*, 73(8), 1292-1305. DOI: <https://dx.doi.org/10.1139/cjfas-2015-0363>
- Oksanen, J., Blanchet, G. F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., ... Wagner, H. (2018). *Vegan: community ecology package. R package version 2.4-0*. Recovered from: <https://CRAN.R-project.org/package=vegan>

- Palhares, J. C. P., Ramos, C., Klein, J. B., LIMA, J. C. M. M., Muller, S., & Cestonaro, T. (2007). Medição da vazão em rios pelo método do flutuador. *Embrapa Suínos e Aves-Comunicado Técnico (INFOTECA-E)*, 1-4. Recovered from: <http://www.infoteca.cnptia.embrapa.br/infoteca/handle/doc/443939>
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & Team, R. C. (2007). Linear and nonlinear mixed effects models. *R package version*, 3(57), 1-89.
- R development core team. (2013). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
- Ramírez, A., & Pringle, C. M. (1998). Invertebrate drift and benthic community dynamics in a lowland neotropical stream, Costa Rica. *Hydrobiologia*, 386(1), 19-26. DOI: <https://dx.doi.org/10.1023/A:1003409927131>
- Salles, F. F., Da-Silva, E. R., Serrão, J. E., & Francischetti, C. N. (2004). Baetidae (Ephemeroptera) na região sudeste do Brasil: novos registros e chave para os gêneros no estágio ninfal. *Neotropical Entomology*, 33(6), 725-735. DOI: <https://dx.doi.org/10.1590/S1519-566X2004000600010>
- Schulz, U. H., Rosa, M. F., & Klein-Stolz, G. F. (2019). Drift and emergence patterns of nonbiting midges (Chironomidae, Diptera, Insecta) in a subtropical river. *Ecological Research*, 34(6), 835-841. DOI: <https://dx.doi.org/10.1111/1440-1703.12061>
- Simpson, G. L. (2018). *Permute: functions for generating restricted permutations of data*. R Package 0.9-4. Recovered from: <https://cran.r-project.org/package=permute>.
- Tank, J. L., Rosi-Marshall, E. J., Griffiths, N. A., Entekin S. A., & Stephen, M. L. (2010). A review of allochthonous organic matter dynamics and metabolism in streams. *Journal of the North American Benthological Society*, 29(1), 118-146. DOI: <https://dx.doi.org/10.1899/08-170.1>
- Trivinho-Strixino, S., & Strixino, G. (1995). *Larvas de Chironomidae (Diptera) do Estado de São Paulo: Guia de identificação e diagnose dos gêneros*. São Carlos, SP: PPG-ERN/Ufscar.
- Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37(1), 130-137. DOI: <https://dx.doi.org/10.1139/f80-017>