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Desiccation and recovery of periphyton biomass and density in a subtropical lentic ecosystem

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ABSTRACT. This study assessed the desiccation effects on biomass and algal density of periphyton in a subtropical lentic ecosystem. This experiment was conducted with only one *in situ* experimental desiccation event for 15 hours in a mature periphytic community. The periphyton after desiccation was distinct in density and biomass estimators (dry weight and chlorophyll *a*) when compared to the control periphyton. After the tenth day of desiccation, the community presented similar values for biomass estimators when compared to the control periphyton. The density and biomass estimators of the periphyton community was affected by the desiccation event and required about ten days to recover to pre-disturbance conditions.

Keywords: chlorophyll *a,* disturbance, dry weight, resilience, floodplain.

Dessecamento e recuperação da biomassa e densidade do perifíton em ecossistema lêntico subtropical

RESUMO. Este estudo avaliou os efeitos do dessecamento sobre a biomassa e a densidade algal do perifíton em ecossistema lêntico subtropical. Neste experimento foi realizado um evento *in situ* de 15h de emersão sobre a comunidade perifítica em estágio maduro de desenvolvimento. O perifíton sujeito ao dessecamento foi distinto na densidade e nos estimadores de biomassa (peso seco e clorofila) em relação ao perifíton controle. Após do décimo dia de dessecamento, a comunidade apresentou valores similares dos estimadores de biomassa quando comparado com o perifíton controle. A densidade e os estimadores de biomassa da comunidade perifítica foram afetadas pelo evento de dessecamento e requereu dez dias para retornar as condições de pré-distúrbio.

Palavras-chave: clorofila *a*, distúrbio, peso seco, resiliência, planície de inundação.

Introduction

A disturbance is any process that reduces or removes biomass and changes the community structure (HUSTON, 1991). In aquatic ecosystems, disturbances are generally recurrent, caused by pulses, which interfere with the stability of the system. They can vary greatly in length, range and predictability. Both floods and droughts may disarrange habitats and create new ones, which can then be colonized and inhabited under stable flow conditions (LAKE, 2000).

In a floodplain system, the pulse regime affects the aquatic terrestrial transition zone and the littoral zone, modifying the habitat quality and its biota and impacting the river-floodplain system as a whole (WANTZEN et al., 2008), and thereby influencing the community stability. The stability of the community determines its capability to resist to disturbances and can be evaluated by measuring the system's resistance and resilience. Resistance is defined as the community's ability to maintain the initial equilibrium, whereas resilience is the system's ability to return to the equilibrium state after an alteration (WETZEL, 1999). In the littoral regions of floodplains, diverse microhabitats associated with the surfaces of submerged macrophytes, detritus and sediments (WETZEL; LIKENS, 2000) ease the prolific development of the periphytic community. Disturbance events are the greatest creators of spatial and temporal heterogeneity in the structure and dynamics of these communities.

The seasonality of pulse effects on periphytic algal communities in aquatic environments has been investigated by limnologists; however, the impacts of drought have been little explored for floodplain systems (LAKE, 2000; ROBSON; MATTHEWS, 2004; STANLEY et al., 2004; CARAMUJO et al., 2008; ROBSON et al., 2008). One of the most significant human threats to aquatic ecosystems is the hydrologic change, such as reservoir construction (POFF et al., 1997). Alteration of the hydrological system leads to loss of habitats and changes in water quality (McCORMICK et al., 1996). In subtropical systems, there is a lack of knowledge about the effects of induced desiccation on systems with artificial control over the hydrological regime, in which the dam operation produces daily variations in water level, temporarily exposing the community in the littoral region (SOUZA-FILHO et al., 2004; AGOSTINHO et al., 2009).

The presence of 26 large reservoirs in the upper Paraná river causes a high level of regulation on the hydrological regime, and this control influences the nutrient cycling and the structure and composition of several assemblages (AGOSTINHO et al., 2000, 2009; STEVAUX et al., 2009); but so far, knowledge of how these changes affect the periphytic community is limited (AGOSTINHO et al., 2009), especially in relation to desiccation of littoral regions as a consequence of low hydrometric levels. This study describes the effects of an experimental desiccation disturbance on the periphyton community and the dynamic response of this community after the event. The aims of this study were: a) to verify if the density and biomass of a periphytic algal community have been affected by the exposure to desiccation, b) to evaluate if the physiological status of the periphyton community has been altered after desiccation and c) to examine if the desiccated periphyton community has recovered to pre-desiccated community conditions.

Material and methods

The upper and middle Paraná river are located within Brazil and drain an area of 891 km^2. This river covered an extensive floodplain (480 km length and 20 km width), which was reduced in 1998 by the construction of the Porto Primavera dam in the intermediate region of this stretch. Currently, the section between the Porto Primavera and Itaipu reservoirs is the last free flowing stretch (AGOSTINHO et al., 2000; STEVAUX et al., 2009). Due to the lower demand for electricity at night, the Porto Primavera dam restricts downstream water flow during this period. These daily fluctuations in the water level affect all regions downstream including the upper Paraná river floodplain.

The experiment was conducted in the littoral region of Garças lake (22°43'S; 53°14'W) (Figure 1), from February 26^{th} to April 10^{th}, 2007 during the potamophase (high water period), totaling 42 experimental days. This lake is strongly affected by water level fluctuations due to the direct connection with the Paraná river.

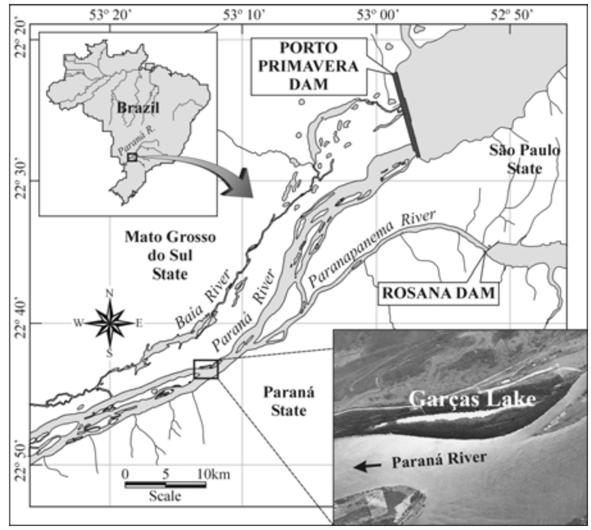

Figure 1. Map of Garças lake, upper Paraná river floodplain.

Glass slides (7.5 cm long and 2.5 cm wide) were kept in two wood supports, destined for different treatments for the colonization of the periphytic community. Each support had eight drawers, distributed in such a way to allow light to reach all the slides (15 glass slides). The supports were attached to macrophytes (*Eichhornia azurea* (Sw.) Kunth) floating in the water column, and the slides remained completely submerged.

The glass slides were colonized by the periphytic community for 21 days, thus reaching a climax (RODRIGUES; BICUDO, 2004). After this period, slides were removed from the water at night for 15 hours of desiccation. For this, the support with slides for periphyton treatment was placed on the lake banks. After 15 hours, the support with slides was slowly re-immersed in the lake to minimize the detachment of algae. The removal of periphyton from the water followed by its re-immersion in the lake was an attempt to simulate the effects of upstream dam operations on the organisms. The support with slides for control periphyton remained in the littoral region throughout the study for further comparison.

To estimate the state of the periphytic community before and after the desiccation event, we held a sampling before the desiccation event. The other samplings occurred simultaneously in treatment and control supports on the days 1, 3, 5, 10, 15 and 20, after the desiccation event.

The substrates (control and treatment) were randomly sampled with previous sortition among the support drawers and slides. We collected slides in replicates to estimate density and triplicates to estimate dry weight and chlorophyll *a*. These slides were carefully maintained in humid glass flasks of

150 mL inside a cooler with ice and taken to the laboratory in the Base de Pesquisa Avançada/Universidade Estadual de Maringá in Porto Rico town (Paraná State). In the laboratory, the periphytic material was removed using razor blades and distilled water and conditioned in glass flasks.

Taxa quantification was undertaken using an inverted Olympus® CK2 microscope and sedimentation chambers, following the method proposed by Utermöhl (1958) with random fields (BICUDO, 1990). The quantification was carried out until counting at least 100 individuals of the most abundant taxon and achieved the stabilization of the species accumulation curve. The equation used to calculate the density followed Ros (1979) adapted to substratum area, with results expressed in area units (individuals cm^{-2}).

The methods employed for the determination of dry weight were performed according to Schwarzbold (1990). Glass-fiber filters (Whatman GF/C), pre-combusted at 550°C in a muffle furnace for two hours and pre-weighed, were used to filter the periphytic material in a low-pressure vacuum pump. Afterwards, these filters were oven dried at 65°C for 48 hours and weighed to determine the dry weight (DW). Later, they were transferred to a muffle furnace at 550°C for two hours and weighed again to determine the ash weight (AW). The ash-free dry weight (AFDW) was obtained by calculating the difference between the DW and AW.

To extract the pigments, for chlorophyll we used 90% acetone as solvent. The filters without pre-calcinations and with periphytic material were macerated in darkness and centrifuged. The supernatant was then analyzed using a spectrophotometer at 663 and 750 nm wavelengths, corrected for phaeophytin (NUSCH; PALME, 1975). The calculation was made using the formula described in Wetzel and Likens (2000).

The ratio of chlorophyll *a* to phaeophytin was calculated from ln-transformed data to avoid the use of unrepresentative ratio that occur when the phaeophytin concentrations are below 1.0 (PETERSON et al., 1990). We used the formula chl *a* / phaeo = ln (chl *a* + 1) - ln (phaeo + 1), which estimates the physiological status of the community, once the phaeophytin is a product of chlorophyll *a* degradation.

The Mann-Whitney U-test, with normal approximation of 'Z', was used to compare possible differences between materials (treatment and control) for density and biomass estimators. The Kruskal-Wallis test (H) was applied to evaluate possible differences between periods of successional treatments. When the significance level of 0.05 was reached, a *Bonferroni* post hoc test was performed (ZAR, 1996).

Results

Before the desiccation event, the periphytic matrix in both materials showed similar patterns of colonization and color. After the experimental desiccation, the periphytic matrix on the treatment substratum appeared yellowish-brown and had a higher amount of inorganic material attached.

After the disturbance, the density of treatment periphyton dropped to 29.76%; however, the treatment periphyton showed higher density values than the control on days 3, 5 and 20 after desiccation (Figure 2). The density of the control and treatment periphyton on the days subsequent to the experimental desiccation was not significantly different (H = 19.06; p = 0.06).

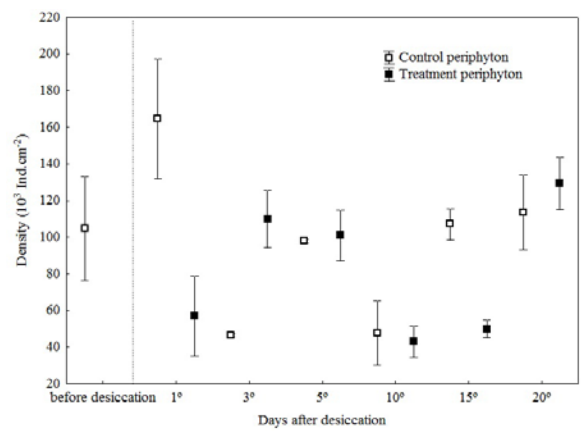

Figure 2. Density of periphytic community from control and treatment material. Dotted line set apart the community before desiccation from that after desiccation disturbance period. Values of mean (□) and Std error (I).

During the experimental phase, for the control periphyton, we detected the predominance of the organic fraction (AFDW) over the inorganic (AW). DW mean values ranged from 69 to 269 $\mu g\ cm^{-2}$, on days 3 and 20 after desiccation, respectively. A reduction of 147 $\mu g\ cm^{-2}$ was found in the DW mean values before the desiccation event and on the 3rd day after desiccation. From day 3 to the end of the experiment (day 20), there was an upward trend in DW values until the peak was reached. The mean values of AFDW ranged from 57 to 112 $\mu g\ cm^{-2}$ and of AW from 12 to 157 $\mu g\ cm^{-2}$. The mean values of AW exceeded those of AFDW only on the day 20 after desiccation (Figure 3).

Treatment periphyton showed a 17.6% decrease in DW concentration after the desiccation (day 1) with respect to the community at equilibrium (before desiccation), with 5.7% represented by AW and 11.9% by AFDW. After this period, there was a sharp increase of 149 μg cm^{-2} in DW until day 5. The DW mean concentration ranged from 129 to 327 μg cm^{-2} on days 20 and 5, respectively. The inorganic fraction was higher than the organic throughout most of the study and indicated a mean variation from 57 to 243 μg cm^{-2} on days 1 and 5, respectively. Over the same time period, the AFDW varied between 63 and 121 μg cm^{-2}, surpassing the AW only on days 1 and 3. The AW presented the same general variation pattern verified for DW (Figure 3).

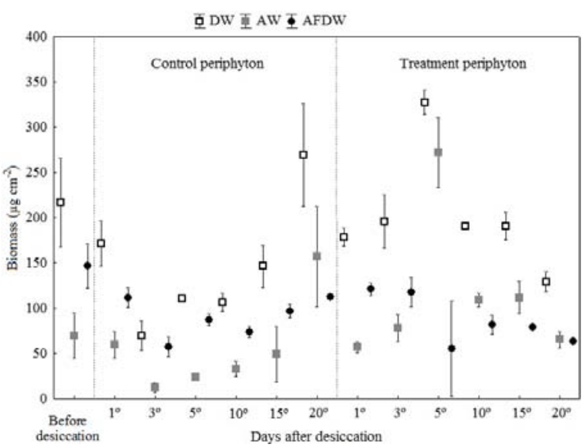

Figure 3. Biomass of periphytic community from control and treatment. Dry weight (DW), ash weight (AW) and ash-free dry weight (AFDW). Dotted line sets apart the community before desiccation from that after the disturbance period in control and treatment periphyton. Values of mean (□) and Std error (I).

When comparing the control and treatment, DW total concentrations were significantly different (Z (U) = -2.69; $p < 0.01$) and usually higher in the treatment, e.g., 3120 μg cm^{-2} for treatment compared to 2206 μg cm^{-2} for control, and with an inverse trend of DW fluctuation between the materials (Figure 3). Comparing periphyton materials for the days after desiccation, a significant difference between control and treatment samples was verified (H = 28.08; $p < 0.01$). The post hoc test revealed differences between day 5 of the treatment ($p < 0.03$) and all other days after experimental desiccation, except for the material before desiccation and day 20.

Considering the inorganic fraction (AW), we detected a significant difference between the treatment and control (Z(U) = -3.11; $p < 0.01$). Significant differences between the days after the desiccation were also verified (H = 26.49; $p < 0.01$), and the post hoc test also revealed a difference between day 5 of the treatment periphyton ($p < 0.01$) and all other days after the desiccation event for the control periphyton, except for day 20. Regarding the organic fraction (AFDW), no difference between the treatment and control periphyton was verified (Z(U) = 0.55; p = 0.58). Otherwise, a difference was observed during the period after the desiccation event (H = 26.66; $p < 0.01$) only between days 5 and 20 and the periphyton before the desiccation event (p = 0.04 for both days).

The photosynthetic biomass in the control periphyton presented mean concentration values ranging from 2.15 to 5.77 μg cm^{-2} on days 10 and 1 after the desiccation event, respectively (Figure 4). For the treatment periphyton, mean values of the photosynthetic biomass varied between 2.97 and 5.30 μg cm^{-2} on days 20 and 5, respectively. One day after the desiccation event (1st day), we could not verify expressive oscillations in the chlorophyll *a* concentration of the treatment sample when compared to the community at equilibrium (before desiccation). We registered a decrease from day 5 to day 10 of 2.15 μg cm^{-2}, followed by a tendency of closeness between the mean value of the materials (Figure 4).

Comparing the treatment and control periphyton, the treatment sample presented superior values of photosynthetic biomass from days 1 to 10. Among them, we did not verify a significant difference in chlorophyll *a* (Z(U) = -0.59; p = 0.55).

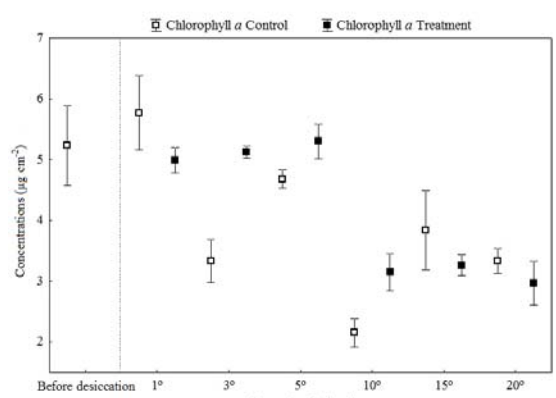

Figure 4. Photosynthetic biomass of periphytic algal community. Concentration of chlorophyll *a* and phaeophytin in control and treatment periphyton. Dotted line sets apart the community before desiccation from that after the desiccation disturbance period. Values of mean (□) and Std error (I).

On the 1st day, the ratio of chlorophyll *a*/phaeophytin increased in the control periphyton and decreased in the treatment periphyton. After this, we observed reversed patterns of oscillation between the periphytic materials until day 5, and on day 15th, the pattern in the ratio returned to normal (Figure 5). The ratio of the periphytic materials was the same (Z(U) = -0.45; p = 0.65).

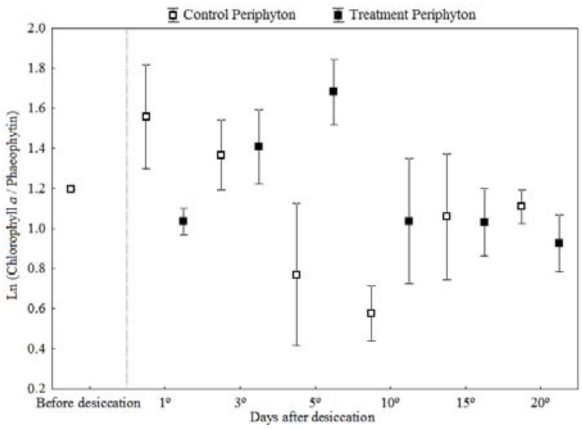

Figure 5. Physiological status of the periphytic algal community in control and treatment periphyton. Dotted line sets apart the community before desiccation from that after the desiccation disturbance period. Values of mean (□) and Std error (I).

Discussion

Anthropogenic disturbances differ from natural disturbances in frequency and intensity and may cause distinct responses from the communities. The present study indicated that periphytic communities can respond to a single event with 15 hours of desiccation. There was a remarkable difference between the periphyton communities of the treatment and control after desiccation. The community subjected to desiccation appeared yellowish-brown and had a higher amount of attached material, probably due to inorganic and organic particles displaced from the sediment. According to Allison (2003), the mucilage in the matrix may adsorb inorganic and organic sediments, and its content can be indirectly measured as a percentage of ash (HOAGLAND, 1983).

The density and biomass estimators of periphytic algae also pointed out a change after the desiccation event, indicating a response of this community to the disturbance. Removal of algal cells affected by the event following re-immersion in the lake possibly contributed to decrease density values. However, this community response did not differ significantly from the control, probably due to the low severity of the conditions under which the event was held, i.e., slow drying at night and the lake under a high-water period. Differences between daytime and nighttime conditions—such as light (solar radiation), temperature, and humidity during desiccation events—can affect algal survival and growth (USHER; BLINN, 1990; BLINN et al., 1995; ROBSON; MATTHEWS, 2004; ROBSON et al., 2008; BERGEY et al., 2010).

The dry weight of the treatment periphyton significantly differed only in relation to the total values and not between the first days after desiccation. There was a decrease in this estimator, primarily due to organic fraction and increase in the ratio ln (chlorophyll *a* / phaeophytin), indicating a matrix disruption and degradation of the periphytic algal community. Wetzel (1990) argued that under conditions of water shrinkage, the nutrient flow decay rate, plant metabolism, and interaction between communities are outstandingly changed. Structural and physiological changes within the periphytic matrix may generate higher spatial and temporal heterogeneity than in habitats that are more sensitive to disturbances (PETERSON et al., 1990). For the control community, the decrease in the analyzed attributes reflected the continuity in the successional natural processes of this community, which are noticed by means of the senescence after the third week of colonization, as shown by Rodrigues and Bicudo (2004).

The recolonization process of the matrix exposed to the desiccation disturbance possibly started with the increase in the density values, dry weight, and chlorophyll *a* observed up to day 5 after desiccation. Thus, our results suggested that a loss in density and biomass opens space for new colonizers, since the disturbance may interrupt the normal trend of community development, allowing a higher heterogeneity of microhabitats and greater nutrient input and cycling. This, in turn, favors the invasion of propagules and new individuals and creates opportunities for growth, survival, and reproduction (PETERSON et al., 1990; LAKE, 2003), mainly in the littoral region where the periphyton is abundant and the availability of space may limit and restrict the community's development (LOWE, 1996). The increases in AW values in the days after desiccation also indicate the recovery of the periphytic community, since this matrix development promotes upload of particulate matter from the water column, resulting in a rapid rise in the inorganic component of the biofilm (ALLISON, 2003; RYDER, 2004).

From the tenth day after desiccation until the end of the study, we verified similar values for density and chlorophyll in control and treatment periphyton; however, with a variable pathway between them along the days. Although without a clear pattern of convergence between the two materials, a recovery in the values of the parameters for the treatment sample was observed. The control and treatment communities probably exhibited different behaviors because the treatment was taken to an earlier stage of development distinct from the natural course of successional development, as already observed (RODRIGUÉZ, 1994; RODRIGUES; BICUDO, 2004). So, the recurrence time between these events is crucial for the reestablishment of the community, influencing its successional process and changing the community structure and functioning. Imposing physical disturbances, whose recurrence time surpasses the natural ones, may limit a community/ecosystem to the initial conditions of the development stage, i.e., immature in stability (ABUGOV, 1982). As this community is primarily autotrophic and works as a basis for the food chain and as a link between physical and chemical components of the environment, the reduction in periphytic productivity associated with changes in biomass has significant implications for the energy flow, nutrient cycling, and other processes in flooding areas (McCORMICK et al., 1998).

According to Agostinho et al. (2000), the high-water period (potamophase) on this floodplain coincide with higher temperature and precipitation, so the desiccation event during the nocturnal period in this study may have been slower due to the high humidity favored by precipitation and mild temperatures at night. These factors potentially influenced the results, confirming the non-significant values compared to control after the event. Some studies have shown that the incidence of solar radiation for extended and continuous periods is responsible for significant reductions in periphytic biomass as well as the degradation of photosynthetic material (USHER; BLINN, 1990; HANSSON, 1992; ANGRADI; KUBLY, 1993); however, less severe environmental conditions may allow a physiological response and provide a more rapid recovery (SHEPARD, 1987; HAWES et al., 1992).

Under nighttime conditions when the event was held, the results of this study suggested that the initial time required for recovery of the desiccated community is approximately ten days after the disturbance. According to Peterson (1996), the conditions in which a disturbance is processed should be considered because they may influence the community recovery. Some studies have shown that when desiccation occurs rapidly, it alters the process of recolonization and regrowth of dry algal biofilm (BENENATI et al., 1998; MOSISCH, 2001) and when desiccation occurs naturally, the regrowth in this biofilm is apparent (ROBSON; MATTHEWS, 2004). Furthermore, the time required to begin the recovery of community structure can be considered relatively short, despite the high reproductive rates and short life cycle of the algae, which could facilitate a rapid reestablishment. This result suggests that the biofilm residual and the short exposure time also may have contributed to the recovery of the community, since the algae may present mechanisms to resist against a short emersion time (EVANS, 1959; HOSTETTER; HOSHAW, 1970; MORISON; SHEATH, 1985; HAWES et al., 1992) and ease the colonization of other algal cells.

Despite the algal estimator values from the treatment periphyton had not pointed out a trend of convergence with the control periphyton, the recovery of the desiccated community was evident, suggesting its resilience; the community structure showed a trend towards recovery on a week after the event, around the day 10. This fact may be related to periphyton traits; for example, the community presents spatially inter-related organisms enclosed in a mucilage matrix, with the structure and functioning of each organism depending on the others. According to Pimm (1984), the more closely related the organisms, the more resilient the community. Still, the floodplain functioning, which shows a high level of daily variation, may have prompted an increased resilience in this community. Furthermore, the disturbance history influences algal microdistribution more often than the habitat parameters—substratum size, near-bed current velocity, and water depth—combined (MATTHAEI et al., 2003).

Conclusion

The desiccation caused changes in the density of the community and in certain biomass estimators. Also affects the community structure and functioning of periphytic algae, the variations in hydrometric levels, which may occur as a result of dam operation upstream of the upper Paraná river floodplain. However, the community showed resilience, by reestablishing the attribute values estimated after the event, and for this, the community required about ten days, thus water level variations shorter than this period may interfere with the dynamics of the community, affecting colonization and succession and influencing processes and organisms that are interconnected.

Acknowledgements

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References

ABUGOV, R. Species diversity and phasing of disturbance. **Ecology**, v. 63, n. 2, p. 289-293, 1982.

AGOSTINHO, A. A.; THOMAZ, S. M.; MINTE-VERA, C. V.; WINEMILLER, K. O. Biodiversity in the high Paraná river floodplain. In: GOPAL, B.; JUNK, W. J.; DAVIS, J. A. (Ed.). **Biodiversity in wetlands**: assessment, function and conservation. Leiden: Backhuys Publishers, 2000. p. 89-118.

AGOSTINHO, A. A.; BONECKER, C. C.; GOMES, L. C. Effects of water quantity on connectivity: the case of the upper Paraná river floodplain. **Ecohydrology and Hydrobiology**, v. 9, n. 1, p. 99-113, 2009.

ALLISON, D. G. The biofilm matrix. **Biofouling**, v. 19, n. 2, p. 139-150, 2003.

ANGRADI, T. R.; KUBLY, D. M. Effects of atmospheric exposure on chlorophyll 'a', biomass and productivity of the epilithon of a tailwater river. **Regulated Rivers: Research and Management**, v. 8, n. 4, p. 345-358, 1993.

BENENATI, P. L.; SHANNON, J. P.; BLINN, D. W. Desiccation and recolonization of phytobenthos in a regulated desert river: Colorado river at Lees Ferry Arizona, USA. **Regulated Rivers: Research and Management**, v. 14, n. 6, p. 519-532, 1998.

BERGEY, E. A.; BUNLUE, P.; SILALOM, S.; THAPANYA, D.; CHANTARAMONGKOL, P. Environmental and biological factors affect desiccation tolerance of algae from two rivers (Thailand and New Zealand) with fluctuating flow. **Journal of North American Benthological Society**, v. 29, n. 2, p. 725-736, 2010.

BICUDO, D. C. Considerações sobre metodologias de contagem de algas do perifíton. **Acta Limnologica Brasiliensia**, v. 3, n. 1, p. 459-475, 1990.

BLINN, D. W.; SHANNON, J. P.; STEVENS, L. E.; CARDER, J. P. Consequences of fluctuating discharge for lotic communities. **Journal of the North American Benthological Society**, v. 14, n. 2, p. 233-248, 1995.

CARAMUJO, M. J.; MENDES, C. R. B.; CARTAXANA, P.; BROTAS, V.; BOAVIDA, M. J. Influences of drought on algal biofilms and meiofaunal assemblages of temperate reservoirs and rivers. **Hydrobiologia**, v. 598, n. 1, p. 77-94, 2008.

EVANS, J. H. The survival of Freshwater algae during dry periods: part II. Drying experiments: part III. Stratification of algae in pond margin litter and mud. **The Journal of Ecology**, v. 47, n. 1, p. 55-81, 1959.

HANSSON, L. A. Factors regulating periphytic algal biomass. **Limnology and Oceanography**, v. 37, n. 2, p. 322-328, 1992.

HAWES, I.; HOWARD-WILLIAMS, C.; VINCENT, W. F. Desiccation and recovery of antartic cyanobacterial mats. **Polar Biology**, v. 12, n. 6-7, p. 587-594, 1992.

HOAGLAND, K. D. Short-term standing crop and diversity of periphytic diatoms in a eutrophic reservoir. **Journal of Phycology**, v. 19, n. 1, p. 30-38, 1983.

HOSTETTER, H. P.; HOSHAW, R. W. Environmental factors affecting resistance to desiccation in the diatom *Stauroneis anceps*. **American Journal of Botany**, v. 57, n. 5, p. 512-518, 1970.

HUSTON, M. A. **Biological diversity**: the coexistence of species on changing landscapes. Albany: Cambridge University Press, 1991.

LAKE, P. S. Disturbance, patchiness, and diversity in streams. **Journal of North American Benthological Society**, v. 19, n. 4, p. 573-592, 2000.

LAKE, P. S. Ecological effects of perturbation by drought in flowing waters. **Freshwater Biology**, v. 48, n. 7, p. 1161-1172, 2003.

LOWE, R. L. Periphyton patterns in lakes. In: STEVENSON, R. J.; BOTHWELL, M. L.; LOWE, R. L. (Ed.). **Algal ecology**: freshwater benthic ecosystems. San Diego: Academic Press, 1996. p. 57-76.

MATTHAEI, C. D.; GUGGELBEGER, C.; HUBBER, H. Local disturbance history affects patchiness of benthic river algae. **Freshwater Biology**, v. 48, n. 9, p. 1514-1526, 2003.

McCORMICK, P. V.; RAWLIK, P. S.; LURDING, K.; SMITH, E. P.; SKLAR, F. H. Periphyton-water quality relationship along a nutrient gradient in the northern Florida Everglades. **Journal of North American Benthological Society**, v. 15, n. 3, p. 433-449, 1996.

McCORMICK, P. V.; SHUFORD III, R. B. E.; BACKUS, J. G.; KENNEDY, W. C. Spatial and seasonal patterns of periphyton biomass and productivity in the northern Everglades, Florida, U.S.A. **Hydrobiologia**, v. 362, n. 1-3, p. 185-208, 1998.

MORISON, M. O.; SHEATH, R. G. Responses to desiccation stress by *Klebsormidium rivulare* (Ulotrichales, Chlorophyta) from a Rhode Island stream. **Phycologia**, v. 24, n. 2, p. 129-145, 1985.

MOSISCH, T. D. Effects of desiccation on stream epilithic algae. **New Zealand Journal of Marine and Freshwater Research**, v. 35, n. 1, p. 173-179, 2001.

NUSCH, E. A.; PALME, G. Biologische methoden für die praxis der gewässeruntersuchung. Bestimmung des Chlorophyll *a* und phaeopigmentgehaltes in oberflächenwasser. **GWF-Wasser Abwasser**, v. 116, n. 12, p. 562-565, 1975.

PETERSON, C. G. Response of benthic algal communities to natural physical disturbance. In: STEVENSON, R. J.; BOTHWELL, M. L.; LOWE, R. L. (Ed.). **Algal ecology**: freshwater benthic ecosystems. San Diego: Academic Press, 1996. p. 375-402.

PETERSON, C. G.; HOAGLAND, K. D.; STEVENSON, R. J. Timing of wave disturbance and the resistance and recovery of a freshwater epilithic microalgal community. **Journal of North American Benthological Society**, v. 9, n. 1, p. 54-67, 1990.

PIMM, S. L. The complexity and stability of ecosystems. **Nature**, v. 307, n. 26, p. 321-326, 1984.

POFF, N. L.; ALLAN, J. D.; BAIN, M. B.; KARR, J. R.; PRESTEGAARD, K. L.; RICHTER, B. D.; SPARKS, R. E.; STROMBERG, J. C. The natural flow regime: a paradigm for river conservation and restoration. **BioScience**, v. 47, n. 11, p. 769-784, 1997.

RYDER, D. S. Response of epixylic biofilm metabolism to water level variability in a regulated floodplain river. **Journal of the North American Benthological Society**, v. 23, n. 2, p. 214-223, 2004.

ROBSON, B. J.; MATTHEWS, T. G. Drought refuges affect algal recolonization in intermittent streams. **River Research and Applications**, v. 20, n. 7, p. 753-763, 2004.

ROBSON, B. J.; MATTHEWS, T. G.; LIND, P. R.; THOMAS, N. A. Pathways for algal recolonization in seasonally-flowing streams. **Freshwater Biology**, v. 53, n. 12, p. 2385-2401, 2008.

RODRIGUES, L.; BICUDO, D. C. Periphytic algae. In: THOMAZ, S. M.; AGOSTINHO, A. A.; HAHN, N. S. (Ed.). **The upper Paraná river and its floodplain**: physical aspects, ecology and conservation. Leiden: Backhuys Publishers, 2004. p. 125-143.

RODRIGUÉZ, M. A. Succession, environmental fluctuations, and stability in experimentally manipulated microalgal communities. **Oikos**, v. 70, n. 1, p. 107-120, 1994.

ROS, J. **Práticas de ecologia**. Barcelona: Omega, 1979.

SHEPARD, K. L. Evaporation of water from the mucilage of a gelatinous algal community. **British Phycological Journal**, v. 22, n. 2, p. 181-185, 1987.

SCHWARZBOLD, A. Métodos ecológicos aplicados ao estudo do perifíton. **Acta Limnologica Brasiliensia**, v. 3, n. 1, p. 545-592, 1990.

SOUZA-FILHO, E. E.; ROCHA, P. C.; COMUNELLO, E.; STEVAUX, J. C. Effects of the Porto Primavera dam on physical environment of the downstream floodplain. In: THOMAZ, S. M.; AGOSTINHO, A. A.; HAHN, N. S. (Ed.). **The upper Paraná river and its floodplain**: physical aspects, ecology and conservation. Leiden: Backhuys Publishers, 2004. p. 55-74.

STANLEY, E. H.; FISHER, S. G.; JONES JR., J. B. Effects of water loss on primary production: a landscape-scale model. **Aquatic Sciences**, v. 66, n. 1, p. 130-138, 2004.

STEVAUX, J. C.; MARTINS, D. P.; MEURER, M. Changes in regulated tropical rivers: the Paraná river downstream Porto Primavera Dam, Brazil. **Geomorphology**, v. 113, n. 3-4, p. 230-238, 2009.

USHER, H. D.; BLINN, D. W. Influence of various exposure periods on the biomass and chlorophyll 'a' of *Cladophora glomerata* (Chlorohyta). **Journal of Phycology**, v. 26, n. 2, p. 244-249, 1990.

UTERMÖHL, H. Zur Vervollkmmnung der quantitativen phytoplankton-methodik. **Mitteilungen Internationale Vereinigung Theoretische und Angewandte Limnologie**, v. 9, p. 1-38, 1958.

WANTZEN, K. M.; JUNK, W. J.; ROTHHAUPT, K. O. An extension of the floodpulse concept (FPC) for lakes. **Hydrobiologia**, v. 613, n. 1, p. 151-170, 2008.

WETZEL, R. G. Land-water interfaces: Metabolic and limnological regulators. **Internationale Vereinigung fur Theoretische und Angewandte Limnologie**, v. 24, n. 1, p. 6-24, 1990.

WETZEL, R. G. Biodiversity and shifting energetic stability within freshwater ecosystems. **Archiv für Hydrobiologie (Serie Advances in Limnology)**, v. 54, p. 19-32, 1999.

WETZEL, R. G.; LIKENS, G. E. **Limnological analyses**. New York: Springer Science/Business Media, 2000.

ZAR, J. H. **Bioestatistical Analysis**. New Jersey: Prentice Hall, 1996.

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