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Tese de Doutorado

Dinâmica e sucessão das algas epifíticas em lagoa rasa subtropical (Lagoa Mangueira, Rio Grande do Sul, Brasil)

Denise Matias de Faria

Porto Alegre

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Denise Matias de Faria

Tese de doutorado apresentada ao Curso de Pós-Graduação em Botânica, Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como requisito parcial para obtenção do título de Doutor em Ciências.

Orientadora: Dra. Luciana de Souza Cardoso

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Sumário

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Apresentação

A tese está composta por três capítulos apresentados em formato de manuscritos. Os mesmos abordam aspectos ecológicos da comunidade de algas aderidas em substrato natural na Lagoa Mangueira, localizada no Estado do Rio Grande do Sul, Brasil.

O Capítulo 1 apresenta um estudo que testou se as diatomáceas epifíticas respondem ao gradiente longitudinal da lagoa durante dois verões em três pontos distantes (Norte, Centro e Sul). As amostras utilizadas para este estudo fazem parte do monitoramento realizado pela equipe do Instituto de Pesquisas Hidráulicas (IPH-UFRGS), que fez parte do CNPq/PELD, sítio 7. Até aquele momento, além de levantamentos florísticos, apenas relatório entregue a instituição constava como único documento sobre o estudo do perifiton neste sistema. Realizou-se analise taxonômica das diatomáceas seguida de classificação em formas de vida e guildas, abordagem que se mostrou válida e com resultados consistentes, evidenciando que as diatomáceas e suas estratégias ecológicas respondem às particularidades do ambiente. Desta forma, utilizar as amostras históricas ajudou a prover dados que corroboraram com os demais estudos realizados para as demais comunidades bióticas (fitoplâncton, zooplâncton e peixes) que evidenciam o gradiente longitudinal da lagoa e a hidrodinâmica regida pelo vento. Este manuscrito foi publicado em 2015 no periódico Inland Waters 5(2): 117-124.

Os resultados obtidos no Capitulo 1 nos motivaram a ir à campo e conduzir um experimento *in situ* para avaliar a sucessão das algas epifíticas no Sul da lagoa, área mais propensa a ação dos ventos de direção NE. No Capítulo 2, foram apresentados os resultados desta expedição realizada durante 60 dias no verão de 2012. Na mesma oportunidade foram coletadas amostras de zooplâncton que foi considerado como potencial predador. Foram limpas

200 folhas de macrófitas para remover o biofilme preexistente objetivando "zerar" a colonização e acompanhar a sucessão das algas sob a intensa ação do vento que ocorre nos verões na costa do Rio Grande do Sul. O estudo evidenciou que a fase avançada da sucessão foi dominada por diatomáceas fortemente aderidas e adaptadas a estas altas médias da velocidade do vento (± 15 m s^{-1}). O epifíton mostrou-se uma grande fonte de produtividade primária para a teia-trófica e fortes correlações provaram que a comunidade sustentou o controle *bottom-up* da comunidade zooplanctônica. O Manuscrito será re-submetido ao periódico Hydrobiologia.

No Capítulo 3 foi testada a resposta do epifíton à dinâmica do vento durante frentes frias no inverno de 2013. Durante trinta dias o epifíton foi amostrado a cada três dias para verificar a ação da entrada das frentes frias, e as mudanças de velocidade e direção do vento. Três situações diferentes foram testadas: comunidade natural, sucessão em um banco de macrófitas e um mesocosmo construído para proteger o banco de macrófitas da ação do vento. No 12° dia de estudo ocorreu alta precipitação que resultou na inundação do mesocosmo pela água circundante. Desta forma, foram providenciadas amostras logo após o evento para verificar a interferência deste distúrbio no experimento controlado. Como resultado, comprovou-se que o mesocosmo diminuiu a ação do vento atrasando a deposição das células metafíticas para início da colonização e a sucessão só começou após o distúrbio que nivelou a água do mesocosmo e a água da lagoa. Dominância de diatomáceas fortemente aderidas ocorreu em todos os experimentos, sendo resistente ao distúrbio. As diversidades das comunidades responderam à dinâmica do vento, sendo mais baixas quando a velocidade do vento excedeu a média do período (5 m s $^{-1}$). O Manuscrito será submetido ao periódico Hydrobiologia. Por fim, na última seção são apresentadas as considerações finais.

Resumo

A Lagoa Mangueira é uma extensa lagoa rasa subtropical localizada no sul do estado do Rio Grande do Sul, Brasil. É um ambiente que varia de oligo à mesotrófico, com extensa área litoral colonizada por macrófitas aquáticas, fornecendo grande área de substrato para o desenvolvimento da comunidade aderida. A parte sul da lagoa é caracterizada pela alta transparência e alto pH, e a parte norte é mais rasa com alta concentração de ácidos húmicos devido a interação com banhado. Devido sua forma e posição geográfica a lagoa sofre constante ação dos ventos de direção NE, com mudanças para o quadrante SE-SO durante as frentes frias. O vento neste ambiente é um fator regulador da hidrodinâmica, afetando espacial e temporalmente as comunidades aquáticas (fitoplâncton, zooplâncton, e peixes), podendo ser considerado um distúrbio constante no ambiente. Entretanto, ainda há uma lacuna quanto à contribuição das algas epifíticas para a teia trófica, bem como a resposta dessa comunidade à hidrodinâmica. O Capítulo 1 apresenta um estudo que testou se as diatomáceas epifíticas respondem a heterogeneidade espacial da lagoa durante dois verões em três pontos distantes (Norte, Centro e Sul). Verificou-se que as diatomáceas exibem um gradiente longitudinal N→S e a área central assume características semelhantes aos pontos Norte e Sul dependendo da dinâmica do vento. No Capítulo 2, foi avaliada a sucessão das algas epifíticas no Sul da lagoa, durante 60 dias no verão de 2012, para investigar os fatores reguladores do desenvolvimento da comunidade *in situ*, considerando o zooplâncton como potencial predador. O estudo evidenciou que a fase avançada da sucessão foi dominada por diatomáceas fortemente aderidas e adaptadas às altas médias da velocidade do vento (± 15 m s^{-1}). O epifíton mostrou-se uma grande fonte de produtividade primária para a teia trófica e fortes correlações provaram que a comunidade

sustentou o controle *bottom-up* da comunidade zooplanctônica. O Capítulo 3 descreve o estudo que testou a resposta do epifíton à dinâmica do vento (velocidade e direção) durante frentes frias (inverno de 2013) em três situações diferentes: comunidade natural, sucessão em um banco de macrófitas e um mesocosmo (protegido da ação do vento). O epifíton revelou-se resiliente, uma vez que o vento favoreceu a colonização e estabilização, recuperando-se rapidamente após o distúrbio. O mesocosmo diminuiu a ação do vento atrasando a deposição das células metafíticas para início da colonização e a sucessão só começou após um grande distúrbio (vento 10 m s^{-1}) que nivelou a água do mesocosmo e a água circundante. Dominância de diatomáceas foi registrada em todos os experimentos. As diversidades das comunidades de todos os experimentos responderam à dinâmica do vento, sendo mais baixas quando a velocidade do vento excedeu a média encontrada para o período (5 m s^{-1}).

Palavras-chave: distúrbio, heterogeneidade espacial, predação, produtividade primária, sucessão ecológica

Abstract

Mangueira Lake is a large shallow subtropical lake located in the Southern Rio Grande do Sul State, Brazil. The lake ranges from oligo to -mesotrophic conditions and presents a large littoral zone covered by macrophytes, providing large area for attached community development. The southern area of the lake is characterized by high transparency and high pH and the northern area is shallower with high concentration of humic acids because of its interaction with the wetland. Due to its shape and geographic position, the lake undergoes constant wind action from NE direction and from SE–SW during cold-fronts. The wind regulates the hydrodynamics in this environment affecting spatial and temporally the aquatic communities (phytoplankton, zooplankton and fishes), and can be considered a constant disturbance. However, epiphytic algae contribution for food-web, as well as their responses to hydrodynamics, are still a lack. Chapter 1 presents a study in which we tested if epiphytic diatoms respond to the lake spatial heterogeneity during two summers in three distant sites (North, Center and South). As a result we noted that diatoms exhibited a longitudinal gradient from N→S whereas the center area assumes characteristics similar to both North and South areas depending on wind dynamics. In Chapter 2, we investigated epiphyton succession during 60 days in southern part of the lake in the summer of 2012, aiming to describe the driving factors of the community development *in situ*, considering zooplankton as a potential grazer. The study highlighted that the advanced phase of succession was dominated by tightly attached diatoms adapted to high wind mean velocity (± 15 m s^{-1}). We also showed that epiphyton was great source of primary production for the food-web and strong correlations proved that the community is handling zooplankton bottom-up control. Chapter 3 describes a study that tested the response of the epiphyton to the wind dynamics

(velocity and direction) during cold-fronts (2013 Winter) in three different situations: natural community, succession in a macrophyte bank and in an enclosure (protected from the wind). As a result, epiphyton revealed to be resilient once wind favored colonization and stabilization, rapidly recovering after disturbance. The enclosure acted buffering wind forces delaying succession derived by settlement of metaphytic cells and the succession only started after a huge disturbance (wind 10 m s^{-1}) which leveled the enclosure water and the lake water. Dominance of diatoms was registered in all experiments. The communities' diversities responded to wind dynamics, whereas all experiments showed lower diversities when wind velocity exceeded the system's means (5 m s^{-1}).

Capítulo I

Periphytic diatoms exhibit a longitudinal gradient in a large subtropical

shallow lake

Article

Periphytic diatoms exhibit a longitudinal gradient in a large subtropical shallow lake

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Abstract

Some limnological differences among 3 areas in Mangueira Lake, Brazil, a large shallow oligo-mesotrophic system under continuous wind influence, were related to the wind action and influenced diatom community structure. Our goal was to investigate if wind and precipitation influence the attached communities, producing a heterogeneous diatom distribution along the lake. Sampling was performed in summers 2006 and 2008 at the North, Center, and South points of the lake. Biofilms were scraped from natural substrata for quantitative analyses; 17 species were considered abundant. The South is characterized by high transparency and high pH and is influenced by continuous wind perturbation (NE direction), both in frequency and intensity. The diatom community was characterized by low-profile guild and pioneer life-forms, which are resistant to physical disturbances. The North is shallow with high humic acids because of its proximity and interaction with the wetland, and it was characterized by high-profile and motile guilds. Interannual spatial variation was registered due the influence of continuous precipitation before the 2008 sampling date, which made the lake more homogeneous than it was in 2006. The Center acted as a transition point, which was more similar to the North in 2006 and more similar to the South in 2008. The longitudinal gradient was generated due to abiotic characteristics of the North and the South. The diatom community exhibited a longitudinal gradient N—S, and the diatom life-forms and ecological guilds were a useful tool for examining spatial heterogeneity.

Key words: ecological guilds, freshwater, life-forms, water level, wind

Introduction

Algae assemblages are known to respond rapidly to environmental changes (Mattila and Räisänen 1998), and attached algae, unable to migrate away from adverse conditions, are a reliable proxy to analyze environmental conditions (Stevenson 1997). Diatoms are a diverse group of unicellular algae with complex taxonomy and structures by which cells can adhere to substrates (Round et al. 1990). Although identification at the species level can be sometimes difficult (Berthon et al. 2011), diatom growth forms with similar ecological characteristics can be used to determine ecological traits because they correspond to adaptations related to use resources (Passy 2007), and their associations to environmental gradients can be as strong as for species composition (DeNicola and Kelly 2014).

Life-forms and ecological guilds can elucidate the structure of the biofilm (Rimet and Bouchez 2011) and in running waters can adapt to resources (Passy 2007, Lange et al. 2011), organic pollution and trophic levels (Berthon et al. 2011), light (Lange et al. 2011), and pesticide contamination (Rimet and Bouchez 2011). Life-forms and their strategies are also useful for determining disturbance effects (Schneck and Melo 2012); however, the use of those metrics in lakes is still poorly understood (DeNicola and Kelly 2014). Diatom growth can be controlled by light, grazing, temperature, and water chemistry (Patrick and Reimer 1966, Round 1990). Resource availability and

both in macrophytes and filamentous algae but are also motile, we chose to classified them as prostrate (attached by mucilage pads and parallel to substrate) in the low-profile guild.

Data analyses

Principal components analysis (PCA) was performed to determine spatial and interannual (2006 and 2008) patterns of environmental conditions. Environmental data were also correlated with biotic data using the software Statistica 7.1 (StatSoft Inc. 2005) to select explanatory variables for multivariate analyses. A dendrogram of similarity (Euclidian distance) was used to verify species distribution. Canonical correspondence analysis (CCA) was used to investigate longitudinal and interannual gradients of environmental data, diatom life-forms, and ecological guilds. Data were transformed by log x+1. Ordination analysis was performed using the software PC-ORD v6.0 for Windows (McCune and Mefford 2011).

Results

Environmental data

Comparing data from 10 days before sampling date, wind mean velocities were higher in 2006 than in 2008 (1.2–2.2 ms^{-1}) until day 4, when they became higher in 2008 (2.8–5.2 ms^{-1}; Fig. 1). In 2006, the mean direction was SE, affecting the Center more than the other sites. Precipitation had a peak of 39.3 mm 4 days before the sampling in 2006; however, it was higher (15.2 mm) during the sampling date in 2008 (Fig. 1), increasing the water level (Table 1). In both years, the South point was characterized by higher pH and photic zone, whereas the North point presented higher humic acids and TP (Table 1). The Center point had higher availability of silica, but some interannual patterns were observed: TSS peaked in 2006, and COD, TS, and TN, and TN:TP ratios peaked in 2008 (Table 1). Comparing interannual variability, summer 2008 had higher temperatures, Z, and Secchi depth in all sample points than 2006 (Table 1).

Limnological variables measured in Mangueira Lake (Table 1) were used to perform a PCA, explaining 91.2% of the variance in the first 2 axes (Fig. 2). The first axis revealed interannual distribution (78.6%, p < 0.002), and the second axis explained the spatial distribution (12.6%). The variables that were higher in 2008 (Table 1) and correlated with first axis were conductivity (−0.99), alkalinity (−0.98), silica (−0.96), DOC (−0.95), Secchi depth (−0.95), TOC (−0.93), TN:TP (−0.91), temperature (−0.88), humic acids (−0.83), and TN (−0.70); 2006 was characterized by TIC (0.99), DO (0.94), TP (0.77), and

SRP (0.75). The second axis revealed that the South was distinct from the other areas due to high Z (−0.88) and pH (−0.65). A longitudinal gradient was observed in 2008 from N→S, whereas the North was marked by high humic acids, solids, carbon, and nutrients. NE wind caused displacement of these materials to the lake, and the Center point still had considerable concentrations. The South was deeper and showed higher pH than other points in both years. In 2006 the perfect longitudinal gradient was broken due a peak of TSS at the Center point (38.0 mg L^{-1}),
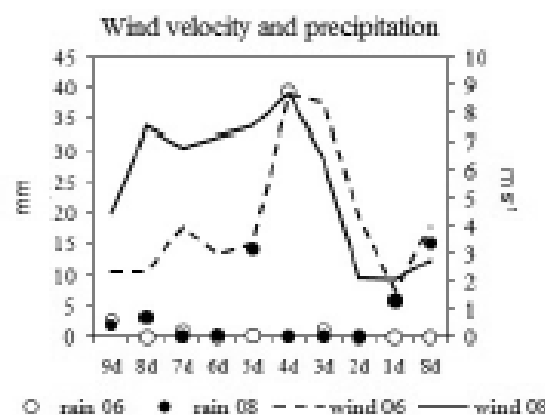
Fig. 1. Wind velocity and precipitation during the 10 days (d) before the sampling date (Sd) in summers 2006 and 2008.
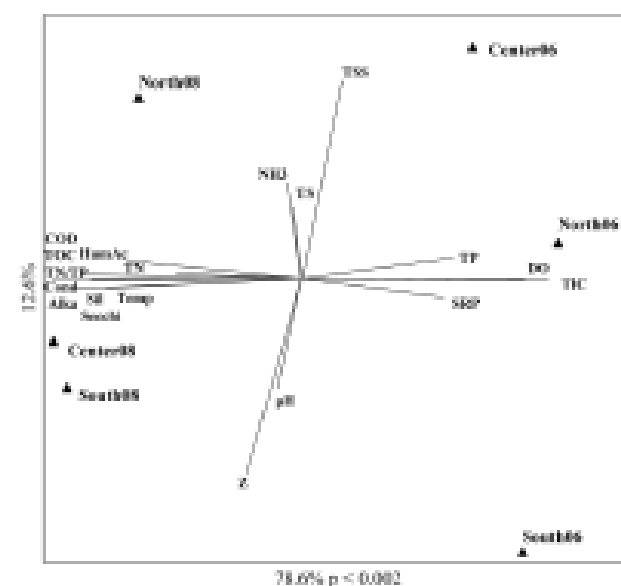
Fig. 2. Principal components analysis (PCA) showing spatial and temporal variation of limnological variables in Mangueira Lake: alkalinity (Alka), ammonia (NH$_3$), conductivity (Cond), chemical oxygen analysis (COD), dissolved oxygen (DO), humic acids (HumAc), pH, Secchi depth (Secchi), silica (Sil), soluble reactive phosphorus (SRP), temperature (Temp), total nitrogen (TN), total solids (TS), total suspended solids (TSS), total phosphorus (TP), total inorganic carbon (TIC), total organic carbon (TOC).

Table 1. Limnological variables measured in Mangueira Lake during the study period.

	Summer 2006			Summer 2008		
	North	Center	South	North	Center	South
Water temperature (°C)	22.91	23.68	23.67	24.51	24.77	26.14
Depth (m)	0.94	0.78	1.54	1.00	1.50	1.60
Secchi depth (m)	0.40	0.40	0.45	0.76	0.94	1.15
Conductivity (mS cm^{-1})	0.26	0.28	0.27	0.35	0.35	0.36
Alkalinity (mg L^{-1})	58.9	58.1	57	69.4	70.6	72.8
Dissolved oxygen (mg L^{-1})	7.66	8.6	8.85	5.81	5.85	5.68
pH	7.99	8.23	8.41	8.0	8.32	8.56
COD (O$_2$ L^{-1})	5.00	4.00	3.00	15.0	30.0	18.0
Humic acids (mg L^{-1})	0.032	0.017	0.010	0.071	0.051	0.053
Total solids (mg L^{-1})	211.0	194.0	159.0	186.0	206.0	187.0
Total suspended solids (mg L^{-1})	13.5	38.0	5.0	13.0	6.0	6.0
Silica (mg L^{-1})	1.40	1.90	1.80	2.49	2.74	2.66
Total nitrogen (mg L^{-1})	0.11	0.09	0.07	0.16	0.23	0.11
Ammonium (NH$_4$) (mg L^{-1})	0.07	0.07	0.03	0.1	0.1	0.02
Total phosphorus (mg L^{-1})	0.052	0.032	0.029	0.029	0.019	0.019
Soluble reactive phosphorus (mg L^{-1})	0.023	0.018	0.029	0.021	0.012	0.014
TN:TP	2.1	2.8	2.4	5.5	12.1	5.8
Total organic carbon (mg L^{-1})	0.01	2.45	0.63	5.46	6.18	9.19
Total inorganic carbon (mg L^{-1})	13.59	9.39	14.17	0.19	0.28	0.17

promoted by SE wind during that time. Thus, based on environmental and abiotic data, the Center can assume characteristics of both extremes of the lake, creating a transition point between the North in 2006 and South in 2008.

Biotic data

Of 59 diatom species identified, only 17 were abundant (Table 2). Richness (38 taxa) and densities were higher in the Center in 2006, and an increased gradient of richness and densities was established from the North to the South in 2008 (Fig. 3). A dendrogram of similarity (Euclidian distance) applied to diatom species (Fig. 4) showed that the South community was similar in both years due to *Achnanthidium minutissimum* dominance, which was responsible for 80.4% and 53.4% of the total density in 2006 and 2008, respectively. The Center and North presented a diatom community with >75% of similarity in 2006; in 2008, the Center diatom community was more heterogeneous (Fig. 4).

Four environmental variables (pH, Z, humic acids, and TSS) were strongly correlated with the biotic matrix and were responsible for ordination on the CCA. CCA using life-forms and ecological guilds (Fig. 5) explained 97%

($p < 0.05$) of the variance in the first 2 axes. On the first axis, humic acids (−0.65) characterized the North points both years; on the other side of ordination, pH (0.55) was more related with the South and Center in both years. In the second axis, Z (0.59) had more influence in the Center and South in 2008 during the rainy summer, whereas TSS (−0.56) separated the Center in 2006 from the other sampling units because of the peak (38.0 mg L^{-1}), which was a consequence of the SE wind direction.
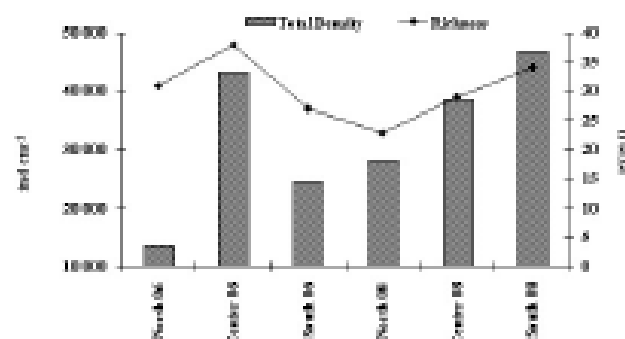

Fig. 3. Attributes of the diatom community in Mangueira Lake at each sample point (North, Center, and South) in summer (2006 and 2008).

Table 2. Classification of abundant species (>1% of total density) in life-forms and ecological guilds (EG) and their densities (ind cm⁻²) in Mangueira Lake during the study period.

		Summer 2006			Summer 2008		
Life-forms		North	Center	South	North	Center	South
Pioneer	*Achnanthidium minutissimum*	1783	8640	19 881	1829	3862	25 075
Pedunculate	*A. minutissimum, Ctenophora pulchella, Fragilaria* sp., *F. fragilarioides, Gomphonema* sp., *G. angustatum, G. capitatum, G. gracile, G. parvulum, Ulnaria ulna*	10 739	30 318	20 871	5487	8976	27 881
Prostrate	*Epithemia sorex, E. turgida*	608	4157	2140	0	25 197	10 732
Motile	*Navicula cryptocephala* complex, *Nitzschia acicularis*	696	2118	187	500	289	401
Planktonic	*Aulacoseira* sp.	217	0	0	3048	0	802
Colonial	*Aulacoseira* sp., *Fragilaria* spp., *Staurosirella* spp.	1042	1018	267	15 976	96	1805
EG		North	Center	South	North	Center	South
Low-profile	*A. minutissimum, Epithemia* spp.	2391	12 797	22 021	1829	29 059	35 807
High-profile	*Aulacoseira* sp., *C. pulchella, Fragilaria* spp., *Gomphonema* spp., *Staurosirella* spp., *U. ulna*	1042	1018	267	15 976	96	1805
Motile guild	*Navicula cryptocephala* complex, *N. acicularis*	696	2118	187	5000	289	401

For biotic data, the first axis showed that high-profile (−0.93) and motile guilds (−0.68) were characteristically related with the North due to high abundance of planktonic (−0.94), colonial (−0.93), and motile (−0.68) life-forms; the low-profile guild (0.76) was typically from the Center and South areas, with high abundance of prostrate (0.84), pedunculate (0.50), and pioneer (0.48) life-forms. The pioneer life-form was dominant in the South; therefore, an interannual difference for biotic data was noted in the Center due to high abundance of pedunculate life-forms in 2006 and prostrate life-forms in 2008.

Discussion

Some limnological differences among the 3 areas in Mangueira Lake were related to wind action. The South is markedly more transparent and deep and has higher pH than the North. The predominant NE wind can move surface water through the South and provide considerable energy to suspend sediment. Simultaneously, fine sediments and associated nutrients are transported to the North by contra-currents, resulting in a large photic zone in the South (Rodrigues 2009). Wind is the main factor responsible for transporting substances and phytoplankton in Mangueira Lake; if wind remains stable for a day or longer, horizontal and vertical water circulation occurs (Cardoso et al. 2012).

The increased gradient N→S in periphyton richness and densities in 2008 was related to the NE wind direction, and the highest TSS and richness and densities on the Center point in 2006 were due to the SE wind direction. Wind action could also prompt high pH in Mangueira Lake, especially in the South, by suspending salts associated with the sandy marine-derived sediments of this region (Tomazelli and Villwock 2005). Marine shells are found at the sediment surface, and thus the high conductivity and pH of Mangueira Lake could be explained by remineralization as well as by sedimentary–geological interactions. Diatom assemblages were dominated by taxa with alkaline and neutral pH preferences (Patrick and Reimer 1966, Van Dam et al. 1994). Periphytic algae are better developed for basic water with available nutrients, carbonates, and bicarbonates that can promote phosphorus absorption, although the rate at which specific taxa grow in tropical and subtropical environments is unknown (Domitrovic et al. 2013).

The South community was dominated by the low-profile guild and seemed better adapted to wind perturbation. The low-profile guild consists of species adapted to high disturbance, irrespective of nutrient supply (Passy 2007). *Achnanthidium minutissimum*, a pedunculate pioneer life-form, was dominant in diatom assemblages in both years studied. This species is known to live attached to substrata resistant to physical disturbances, such as
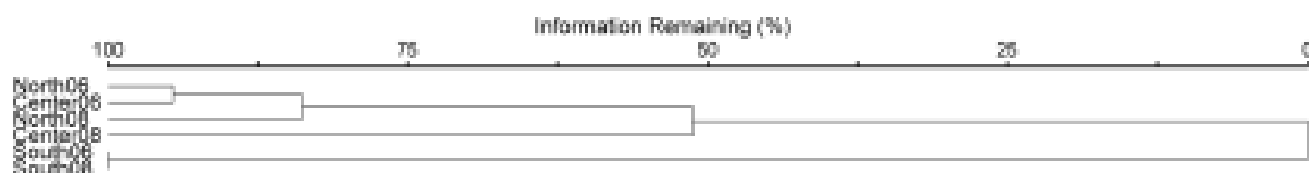
Fig. 4. Dendrogram of similarity (Euclidian distance) applied to diatom species (>1% of total density) of Mangueira Lake.
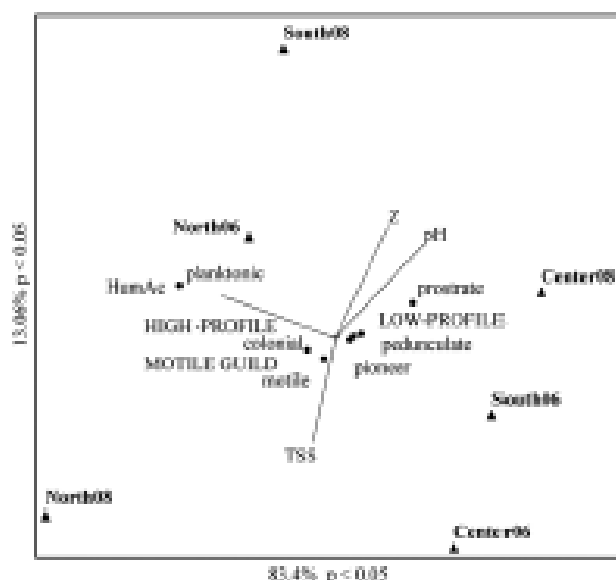

Fig. 5. Canonical correspondence analysis (CCA) showing spatial and temporal variation of the diatom life-forms and ecological guilds in Mangueira Lake (pH, humic acids [HumAc], total suspended solids [TSS], and depth [Z]).

water turbulence (Rimet and Bouchez 2012), and is adapted to current velocities (Passy 2007). Lowe (1996) observed that, once the communities undergo regular high-energy wave disturbance, epiphytic communities in the eulittoral zone are dominated by algae tightly attached to the substratum. Mucilage stalks of diatoms firmly attach to substrata while remaining flexible enough to tolerate wave action (Lowe 1996). Stressful conditions allow competitive advantages for a particular taxon, in this case *A. minutissimum*, which is widely recorded as an intermediary colonizer resistant to disturbances (Biggs and Thomsen 1995, Peterson 1996). Following Connell (1978), under intense disturbances, diversity is reduced because only some populations of pioneer species can establish themselves, as we observed in the South due to *A. minutissimum* dominance. Continuous perturbation can be understood as a steady condition that results in a steady-state community (Chorus and Schlag 1993), leading to monodominance in both years.

The North area of the lake is more susceptible to the effects of shallow water levels and is characterized by high TS and humic acids because of its proximity and interaction with the wetland. The North community was dominated by the high-profile and motile guild; the high-profile guild is predominant in low-disturbance and resource-rich habitats whereas the motile guild comprises tolerant species (e.g., tolerant to eutrophication and pollution; Passy 2007). The ecology of planktonic diatoms such as *Aulacoseira* spp. (Passy 2007) involves adaptations and strategies in which the growth peak occurs during turbulent periods. As these diatoms achieve high densities, their silicified cell walls shed and fall to the sediment, where they form resistant spores. Wind forces are an advantage to these spores because they can suspend cells from the sediment to the photic zone (Reynolds 1984). Motile diatoms recorded include species that tolerate turbidity and favor increased nutrients, such as *Navicula cryptocephala* complex (Van Dam et al. 1994), *Nitzschia* spp. (Lobo et al. 2010), and *Staurosirella* spp. (Michel et al. 2006). Similarly, heterogeneous spatial distributions due to wind action and the exchange between the lake and wetland in the extreme North were also reported by Rodrigues et al. (2011) during a fish community analysis and by Crossetti et al. (2013) in relation to phytoplankton community.

The Center is a transition point between the extremes of the lake. In the present study, the Center was characterized by pedunculate life-forms in 2006 and prostrate life-forms in 2008. In contrast to the South community, pedunculate life-forms from the high-profile guild, such as *Gomphonema* spp. and species of Fragilariales, were dominant in the Center in 2006 when conditions were similar to those in the North, marked by high TSS. These periphytic diatoms have specialized structures to attach to substrata and compete for resources such as light (Peterson 1996). *G. parvulum* was also recorded by Crossetti et al. (2013) in phytoplankton samples from the Center as a periphytic diatom that occasionally occurred in lake plankton because of wind suspension (Padisák et al. 2006).

In large shallow lakes with spatial heterogeneity, hydrodynamic factors of plankton distribution are determined by the irregular supply of resources (Cardoso et al. 2012), during which phytoplankton structure is influenced by water level variations and abiotic conditions such as light and nutrient availability (Crossetti et al. 2007). These driving factors were also important for the spatial distribution of the periphytic community in Mangueira Lake. In 2008, disturbance caused by precipitation favored prostrate diatoms, and the Center was better represented by an increase in *Epithemia* density. According to Potapova and Charles (2002), several species of *Epithemia* prefer fast-

flowing areas. *Epithemia* spp. are common N-fixing diatoms; these cyanobacteria-symbionts were also noted in a shallow lake in Hungary (Ács et al. 2005) during a summer with an unusually low water level. In our study, the TN:TP ratio in 2006 was uniform in the lake (2.1–2.8), whereas in 2008 this ratio was almost double of that of the North (5.5) and South (5.8) and much higher in the Center (12.1). Stancheva et al. (2013) showed the opposite in rivers, however, where relative abundance of *Epithemia* as well as the endosymbiont biovolume were reduced with increases in N concentrations and TN:TP ratios of 15:1, although *Epithemia* is favored by lower TN:TP ratios (Kelly 2003). There is little information about the nutrient requirements of individual species for tropical (Domitrovic et al. 2013) or subtropical environments. Macrophytes as host plants may increase phosphate availability to epiphytes, however, decreasing the local TN:TP ratio (Burkholder et al. 1990); therefore, the species of macrophytes where the periphyton community is attached can also control the TN:TP ratio. De Oliveira et al. (2010), studying a shallow hypereutrophic tropical reservoir, found that the TN:TP ratio was not a significant predictor, but that light was the factor responsible for the temporal variations of chlorophyll *a* in the periphyton.

Diatom life-forms and ecological guilds proved to be a reliable proxy to evaluate spatial heterogeneity in a shallow lake, based on the ecological state of the 3 sampling points of Mangueira Lake under different environmental conditions. The sampling points also revealed the existence of a longitudinal gradient in Mangueira Lake that varies with wind dynamics and precipitation (frequency and intensity), consistent with our hypothesis that spatial heterogeneity caused by environmental gradients are driven by wind and quantitatively and qualitatively influence the attached community. Wind force from the NE was demonstrated to be an agent acting to displace nutrients and algae and to model periphytic community structure on the South. Life-forms and ecological guilds both proved to be effective tools for making ecological inferences and were consistent with a limnological gradient occurring from the North to the South points in Mangueira Lake.

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Capítulo II

Epiphyton dynamics during succession experiment in a large shallow lake:

relations with disturbance and bottom-up zooplankton control

1   **Epiphyton dynamics during succession experiment in a large shallow lake: relations with disturbance and**

2   **bottom-up zooplankton control**

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8   **Abstract:** We investigated epiphyton summer succession during 60 days in a subtropical shallow lake, southern

9   Brazil, aiming to identify the driving factors for algae development under natural conditions, considering

10   zooplankton as potential grazers. Macrophytes were cleaned on the field with soft sponge, identified and randomly

11   sampled in short-term interval, as well as zooplankton for estimate their relations during succession process. Algae

12   were incubated immediately after sampling for primary production data. Early stage of succession was dominated by

13   loosely attached algae and advanced phase was characterized by increase and persistence of tightly attached diatoms

14   which showed to be well adapted to high mean's wind velocity (15 m s^{-1}). Summer storms (high precipitation 46.7

15   mm and wind 29.5 m s^{-1}) favored both prostrate diatoms biomass and TP input. Epiphyton was great source of

16   primary production for the food-web and maximum carbon uptake (8028.8 mg C m^{-2} h^{-1}) was coincident with

17   heterogeneous community following biomass variation and community structure. Strong correlations proved that

18   algal abundance was reduced with increases zooplankton richness, but diversity increased with predator's

19   abundance; Rotifera was favored with algal diversity and Copepods and Cladocerans raised in water when diatoms

20   biomass increased in biofilm handling zooplankton bottom-up control.

21   Keywords: ^{14}C uptake, life-forms, nutrient levels, periphyton, precipitation, wind, subtropical

22

23

24   **Introduction**

25   Attachment strategies and algae growth forms have been used to asses ecological traits in running waters,

26   great corresponding to adaptations to resources (Passy, 2007; Lange et al. 2011; Berthon et al. 2011; diatoms only)

27   and to physical disturbances (Schneck & Melo, 2012; whole attached community). During succession process,

28   temporal changes in dominant growth forms showed to be related to changes in community resources (Passy, 2007;

29   Kelly et al., 2009) and the use of life-forms can supply strong information about the structure of the biofilm (Rimet

30   & Bouchez, 2011); however, it is still poorly understood to lentic environments (DeNicola & Kelly, 2014).

31   Colonization of clean substrata involves the formation of an organic biofilm, followed by the passive

32   settlement of cells with subsequent increases in abundance arising via reproduction as r-strategists (Szlauer-

33   Łukaszewska, 2007); species growing is evidenced by a sequence defined on time and space until a complex

34   community in a mature state (Hoagland et al., 1982; Biggs, 1996; Stevenson, 1996). The successional sequence is

35   organized by a complex interaction of factors controlled by light, grazing, temperature and water chemistry (Patrick

36   & Reimer, 1966; Stevenson, 1996), habitat, substrate availability, reserve of propagules of species (Hutchinson,

37   1975; Peterson & Stevenson, 1992) and species efficiency in resources competition (Ferragut & Bicudo, 2010).

38   Successional phases vary with the environment, trophic states, substrata exposure times and disturbances that are

39   experienced during succession (Szlauer-Łukaszewska, 2007; Rodrigues dos Santos & Ferragut, 2013). Thus,

40   availability of resources, as light and nutrients, are regulatory factors that can redirect the successional trajectory on

41   a local scale (Ferragut & Bicudo, 2010).

42   Shallow lakes have a high potential to development for attached algae (Wetzel, 1990) presenting large areas

43   with sufficient light and a diverse variety of submerged substrates for algal growth (Lowe, 1996; Liboriussen &

44   Jeppensen, 2006) as sediment (epipelon), stones (epilithon), macrophytes (epiphyton) and others. The size, shape

45   (Wehr & Sheath, 2003) and hydrodynamics of coastal shallow lakes directly affect their physical and chemical

46   properties (Scheffer, 1998). In subtropical shallow lakes with wind driven hydrodynamics, the water column is not

47   stratified resulting in intense water circulation (Cardoso et al., 2012) and Cardoso & Motta Marques (2004)

48   indicated zooplankton species associated with the effects of fetch in the lake. Besides wind action, littoral zone at

49   shallow depths are exposed to water-level, wave action and high radiation (Cantonati & Lowe, 2014). Moreover,

50   littoral zones community suffers hardly changes responding to rain, watershed and river flows (Rimet et al., 2015).

51   Disturbance events are determinant of community structure (Peterson & Stevenson, 1992), and the presence,

52   frequency and intensity of them are more decisive than the origin (Sommer et al.,1993).The intensity of disturbance

53   affects community diversity (Ács & Kiss, 1993) and also emphasizes the importance of refuges for streams benthic

54   algae (Schneck & Mello, 2012). Refuges and propagules availability will determine community ability to recovering

55   (Lake, 2000). In a subtropical shallow lake, Cardoso & Motta Marques (2004, 2009) showed that phytoplankton and

56   zooplankton community changes were strictly related to wind action in pelagic zone. Wind action in littoral zone

57   also showed to model attached community selecting them by their adaptations (Faria et al., 2015; Rimet et al., 2015)

58   however, the effect of disturbances still remains poorly understood, particularly in terms of establishment of

59   equilibrium states and non-equilibrium theories (Lengyel et al., 2014).

60   Benthic algae are an important source to whole-lake primary production in shallow lakes (Vadeboncoeur et

61   al., 2008) and depend not only on light but also on the morphometry of the lake (Ask et al., 2009). As a quality food

62   resource for many consumers (McCormick et al., 2001), in Mangueira Lake, the food web showed to be sustained

63   by autochthonous carbon; in addition to macrophytes, epiphyton plays an important role in nutrient cycling and

64   storage, with effects on zooplankton and fishes (Rodrigues et al., 2014). During summers, phytoplankton growth

65   was limited by warming and low nutrient supplies as well as high grazing rates (Fragoso Jr. et al, 2011).

66   Zooplankton biomass in pelagic zone of South area showed temporal variability following the phytoplankton rates

67   (Rosa, 2015), so we assume that epiphyton could act as a principal community in carbon supply.

68   In this study our goal was to investigate epiphytic algae development and their autogenic process, as

69   nutrient levels and primary production, in natural environment to understand which main factors drive epiphytic

70   algae dynamics. We monitored epiphytic algae succession in natural substrate in Mangueira Lake over a 60-day

71   period in summer to determine (1) if nutrients and/or disturbances are the main factors driving epiphyton succession

72   on natural conditions in a macrophyte bank and (2) if epiphyton primary production sustains the carbon production

73   in littoral zone acting as bottom-up control for zooplankton.

74   **Materials and Methods**

75   Study area

76   Mangueira Lake is located in southern Brazil on a narrow strip of land between the Atlantic Ocean and

77   Mirim Lake (Crossetti et al., 2013). This coastal lake ranges from oligo to –mesotrophic conditions and covers

78   approximately 820 km^2. It is 90 km long and 3–10 km wide, and the average depth is 3 m (Zmax = 6 m) (Cardoso et

79   al., 2012). The lake is under continuous wind influence, with predominantly NE-SW winds during the summer.

80   Field and laboratory procedures

81   Wind (velocity and direction) and precipitation data were obtained from Santa Vitoria do Palmar

82   Meteorological Station (maintained by INMET, Meteorological National Institute) from January 13 to March 18 of

83   2012, three times per day (0 am, 12 pm and 6 pm) to describe the summer wind and precipitation patterns as well to

84   evaluate their disturbance potential.

85   We conducted the experiment *in situ* in the southern part of the lake (33°30'36.94"S; 53°7'0.64"W) over 60

86   days in summer 2012 (from January 18 to March 18). We chose two banks of the emergent macrophyte

87   *Schenoplectus californicus* L. in the littoral zone for study, distant each other 50 m. The macrophytes (n=240;

88   with120 leaves in each bank) were randomly chosen and carefully cleaned with a soft sponge to remove the

89   preexistent biofilm. On the top of the leaves were marked with adhesive tape for identification, marking 'day one' of

90   the experiment. Sampling were in replicates (n=2, one in each bank) on days 3, 6, 9, 12, 15, 20, 30, 45 and 60 of

91   succession, where leaves were randomly sampled and stored. Immediately after sampling, the biofilms were

92   removed from the substrate with toothbrushes, fixed in Lugol 5% for quantitative analysis (n=2, replicates) and

93   stored frozen for nutrient and pigments analyses (compound sample, n=2). On each sampling day, zooplankton

94   samples were taken using a suction pump filtering 100 L into nylon net of 25 μm mesh, concentrated in 250 mL of

95   polyethylene bottles and fixed with formaldehyde 4% (Wetzel & Likens, 2000). Water was sampled with plastic

96   bottles (n=2) that were stored frozen for nutrient analysis (nitrogen and phosphorus series) according to the method

97   further down.

98   Water depth and transparency were measured using a metered cable and Secchi disk, respectively.

99   Temperature, dissolved oxygen, pH and conductivity were measured *in situ* with an YSI 6920 probe. Water samples

100   were collected in littoral zone. The following nutrients were measured, including total nitrogen (TN), nitrate (NO_3),

101   ammonia (NH_3), total phosphorus (TP), and orthophosphate (PO_4) (Mackereth et al., 1989). Chlorophyll (Chl a) and

102   pheophytin (Pheo) were extracted from GF/F filters in 90% ethanol (Jespersen and Christoffersen, 1987) and

103   measured by spectrophotometry (APHA, 2005). In addition to measurements, TN and TP molar ratios were

104   calculated. We based on Kahlert (1998) optimum ratios for benthic algae (18 : 1).

105   Primary production

106   Immediately after sampling, epiphyton was incubated for estimation of carbon uptake. Attached algae were

107   removed and incubated with filtrate lake water. Surface area of plant was measured before scraping biofilm. Algae

108   primary production was estimated by the radiolabeled sodium bicarbonate (Na $H^{14}CO_3$) method (Wetzel & Likens,

109   2000). For each sample, 500 μL of radiolabeled bicarbonate (8.0 μCi mL^{-1} final concentration, PerkinElmer) was

110   added to glass bottles (50 mL) and filled with the water containing the sampled algae (1 dark, 2 light, 1 initial).

111   Incubation of the covered bottles was performed for 4h (12 pm until 4pm) inside a PVC box. A Photosynthetically

112   Active Radiation (PAR) sensor (Hobo weather station) was used to detect and record the incidence of PAR during

113   the experiment. The data, registered with the logger aid, provided a daily profile of light radiation. Interruption of

114   incubation activity in the initial and incubated bottles was achieved by adding 1 mL of formaldehyde (final

115   concentration 0.4%, 1:100). The bottles were stored and refrigerated in the dark until processing. Beta-particle

116   emission counts were performed in a Rack beta Liquid Scintillation Counter (LKB Wallac 1209). The results were

117   calculated in g C $m^{-2} h^{-1}$.

118   Biotic data

119   Algae were identified and counted according to Utermöhl's (1958) method which yields 90% counting

120   efficiency (Pappas & Stoermer, 1996). The data were converted into density (ind m^{-2}; APHA 2005) and biomass

121   ($10^5 μm^{-3} m^{-2}$; Hillebrand et al., 1999). Species diversity (H) was calculated as the Shannon-Wiener index. We

122   classified taxa (total density and biomass >1%, according to Lavoie et al., 2009) in to six categories of life-forms

123   (modified from Schneck & Melo, 2012; Rimet & Bouchez, 2012; Rimet et al., 2015) presented on Table 3. Life-

124   forms were sub-classified based on the largest linear dimension axis (GALD) (Lewis, 1976) in four categories: class

125   I (< 10 μm), class II (11-20 μm), class III (21-50 μm) and class IV (> 50 μm).

126   For Zooplankton, an aliquot of each sample unit was quantified in a Sedgwick - Rafter chamber (APHA,

127   2005) with a minimum of 80% efficiency (Papas & Stoermer, 1996), and the values expressed as density (ind m^{-3})

128   and biomass (mg L^{-1}) (adapted from Wetzel & Likens, 2000). Species diversity (H) was calculated as the Shannon-

129   Wiener index. The cell volume was calculated using geometric formulas of the specific forms or length-weight

130   regression (Bottrell et al., 1976; Dumont et al., 1975; Ruttner-Kolisko, 1977; Malley et al., 1989), which 10 to 20

131   individuals of each taxon were measured. Zooplankton species and groups were also classified related to the size of

132   particules that they are able to ingest, crossing data with algae GALD, aiming to understand the relations between

133   zooplankton feed behavior and epiphyton.

134   Data analyses

135   The succession rate of the community composition (σ) was calculated according to the method of the sum

136   of differences (Lewis, 1978). We conducted descriptive analyses for the biotic data and T-tests of dependent

137   samples between days (on successional sequence) to investigate the responses of the categories to disturbances using

138   Statistica 7.1 software (StatSoft, Inc., 2005). We also performed correlation analyses (*r*-Pearson p<0.05) between

139   the epiphyton community and environmental data (meteorological data and water data), biofilm nutritional states,

140   primary production, and zooplankton biomass to identify relationships among them and explanatory variables to

141   include in the subsequent multivariate analyses. Ordination analyses were performed using the software PC-ORD

142   version 6.08 for Windows (McCune and Mefford, 2011). PCA of water attributes was performed to reveal

143   environmental changes over the course of the experiment in littoral zone. CCA was used to identify relationships

144   among the algal life-forms and zooplankton groups (both with biomass data) with the associated water measures TP,

145   TN, Chla, Secchi depth and temperature as well as disturbances (precipitation and wind). The data were logx+1

146   transformed prior to multivariate analysis.

147   **Results**

148   Environmental data and water attributes

149   Wind direction was constant (N–NE), with a high mean velocity (15 ± 6 m s^{-1}) throughout the summer. The

150   peak of wind velocity was on day 20 (29.5 m s^{-1}, with a mean of 28 m s^{-1} three days before sampling) and remained

151   high until day 30 (7 m s^{-1}) and then stabilized at 16 m s^{-1} until the end of experiment. The range of precipitation was

152   low (3 ± 8 mm), with two peaks on days 20 (47 mm) and 36 (33 mm); subsequent precipitation was constant and

153   moderate until day 60 (2.5 mm). So, we considered the summer storm (day 20) as disturbance, the mean velocity for

154   the system (15 m s^{-1}) as wind steady condition and winds lower than that as a quiescence, driving epiphyton

155   succession process.

156   Ordination analysis (PCA) of the environmental data revealed the significance for the first axis (80.73%, P

157   < 0.01), identifying the influence of disturbance on the nutrients homogeneity in water column, as a result of the

158   high precipitation ($r = 0.99$) and wind velocity ($r = 0.82$) on day 20, increasing TP ($r = 0.63$) and PO4 ($r = 0.55$) and

159   reducing pH ($r = -0.90$) and conductivity ($r = -0.95$) (Fig. 1). Littoral zone water was under N-limiting conditions (N

160   : P molar ratio < 16 of Redfield ratio) and presented homogeneous distribution of nutrient concentrations (CV $<$

161   25%) during summer 2012 (Table 1). pH was alkaline (mean 8.7) and oligohaline (mean 0.42 mS cm^{-1}).

162   Epiphyton nutrient levels and primary production

163   Epiphyton was N limited (4 ± 1) (Table 2). Biofilm TP increased with time, whereas TN varied during

164   succession being correlated with pheophytin ($r = 0.80$, $P = 0.017$). No correlations were observed between nutrient

165   content and water chemistry in littoral zone.

166   The Chla values were high until day 12 decreasing thereafter followed by increases in pheophytin,

167   indicating community degradation (Fig. 2). Maximum carbon uptake was on day 15 (8028.8 mg C m^{-2} h^{-1}). Even in

168   low Chla (2.5 mg m^{-2}), high assimilation was detected (7917.0mg C m^{-2} h^{-1}) on day 6. PP : Chla ratio was negatively

169   correlated to pheophytin ($r = - 0.73$; $P = 0.041$) evidencing epiphyton productivity. No correlations were observed

170   among nutrients and carbon uptake. Lowest solar radiation favored production (PAR ranged from 243 to 1806 μmol

171   m^{-2} s^{-1}); however, production also happened under high light incidence (PAR > 1365 μmol m^{-2} s^{-1}). Besides high

172   value identified on day 6, was possible to observe that primary production followed epiphyton biomass variation

173   (Fig. 2).

174   Epiphyton and Zooplankton community structure and succession rate

175   During succession, 55 epiphytic taxa were counted (>1%), and the peak in richness and total density (11398 ind

176   m^{-2}) were registered on day 15, and characterized the end of the early succession stage, coincident to the

177   zooplankton biomass peak (Table 2, Fig.3). No correlations were observed among community attributes and water

178   chemistry. No significant changes on richness was observed after that ($P < 0.01$; T-test for dependent samples) and

179   density substantially decrease from day 15 to 20 ($P = 0.048$). Some important relations between producers and

180   predators were observed. Epiphyton density was inversely correlated with zooplankton richness ($r = -0.80$, $P =$

181   0.017) and diversity ($r = -0.81$, $P = 0.014$). On the other hand, algal diversity was intensified with zooplankton

182   density ($r = 0.74$, $P = 0.037$).

183   Epiphyton succession (Fig.3) began with Chlorophyceae (low biomass [0.01 10^{5}μm^{-3} cm^{-2}] but high density

184   [96.6±68.4ind m^{-2}]) mostly *Monoraphidium* spp. which was responsible for peak in Chla ($r = 0.94$, $P = 0.001$). Day

185   6 was marked by low biomass and peak of phytoflagellates. Zygnemaphyceae (*Cosmarium* spp.) dominated

186   community biomass until day 12. Diatoms stabilization was noted on day 15, dominating until advanced stage of

187   succession. Bacillariophyceae was correlated with increases in biomass ($r = 0.91$, $P= 0.001$) and responsible for

188   more than 70% of total biomass after day 20. Day 20 was marked by summer storm which favored diatoms attached

189   parallel to substrata (manly *Epithemia* spp.). Succession rate was high until day 9 due the small sized taxa that was

190   registered being able to colonize substrates faster than other species; the rate reduced after day 12-15 due diatoms

191   stabilization. NH$_3$ concentration in biofilm increased with the rate stabilization ($r = -0.73$, $P= 0.039$) as well as

192   pheophytin was correlated with biomass ($r = 0.90$, $P = 0.002$). Zooplankton community was dominated by Rotifera

193   and Protist (Tecamoeba and Ciliate) during the study time, therefore small size class of potential predators were

194   found, thus density and biomass were strongly correlated ($r =0.96$, $P< 0.001$) (Fig.3). Zooplankton biomass was

195   correlated with diatoms biomass ($r = 0.95$, $P< 0.001$). On day 20 (disturbance day), zooplankton substantially

196   decreased in density and biomass; biomass was recovered only on day 45. Copepod and Cladoceran were more

197   frequent when large motile diatoms appeared in biofilm, in direction to the end of the experiment. Succession rate

198   showed decline constantly after day 9 and epiphyton and zooplankton succession rates were correlated ($r = 0.97$, $P<$

199   0.001). Zooplankton individuals were also found in biofilm; Protist (mainly Ciliate) was found on epiphyton

200 samples during all study time. Tecamoeba peak occurred on day 45 as well Rotifera eggs reinforcing the bottom-up

201 relations between producers and predators.

202   For the algae taxa, six life-forms and four GALD (the largest linear dimension axis) were classified in this

203 study, whereas the zooplankton taxa were organized into the zooplankton groups and the GALD of particles that

204 they are able to ingest (Table 3). We do not use day 6 on ordination analysis because of the monodominance of

205 phytoflagellate acted as outlier. Gradient analysis (CCA) explained 73.0% of the variance for the first two axes ($P=$

206 0.02) clearly separating early phase of succession (until day 15) from succession advanced phase. Nutrients

207 available in water formed a gradient whereas TN was related to early phase ($r = 0.61$, axis 1) and TP ($r = -0.56$, axis

208 1; $r = -0.59$, axis 2) with the high precipitation on day 20 ($r = -0.40$, axis 1). Community answered to this gradient;

209 succession began with loosely attached algae (I-L, $r = 0.70$; axis 1 and III-L, $r = -0.65$; IV-L, $r = -0.77$ axis 2) and

210 small filamentous life-form (II-F, $r = 0.47$ axis 1); after day 12, prostrate diatoms increased in biomass (II-P, $r =$

211 0.46 axis 1 and III-P, $r = -0.81$ axis 2). Small ciliates was more abundant on day 12 (I-CIL, $r = -0.83$ axis 2). Large

212 prostrate diatoms (IV-P, $r = -0.79$ axis 1, $r = -0.55$ axis 2) were resistant and resilient to the disturbance which were

213 strongly correlated with precipitation ($r = 0.90$, $P = 0.002$) and wind ($r = 0.83$, $P = 0.011$). Small erect life-form (II-

214 E, $r = -0.80$ axis 1) and Tecamoeba (II-TECA, $r = -0.54$ axis 2) were also favored by disturbance. Day 30 was

215 characterized by dry weather, high temperature and moderate wind (< 7 ms^{-1}) causing loss in biomass favoring small

216 filamentous algae (trichomes of Cyanobacteria) and dominance of phytoflagellates. Advanced phase of succession

217 (wind, 15 ms^{-1} and low precipitation, 1.7 mm) was driven for high transparency ($r = -0.77$) and chlorophyll a ($r = -$

218 0.41) in axis 1 whereas motile diatoms increased in biomass (III-M, $r = -0.84$) on day 45 and 60 (IV-M, $r = -0.46$) as

219 well erect diatoms (IV-E, $r = -0.80$) and filamentous life-form (IV-F, $r = -0.86$) related to the biggest zooplankton

220 size class as Cladoceran (IV-CLADO, $r = 0.52$), Copepods (IV-COPE, $r =0.47$) and Rotifera (IV-ROTI, $r = 0.41$).

221   Large filamentous life-forms and small motile diatoms were favored with larger Secchi depth ($r = 0.77$, $P =$

222 0.024; $r = 0.085$, $P = 0.007$; respectively). Large motile diatoms were correlated to availability of TP in biofilm ($r =$

223 0.095, $P< 0.001$) also favoring zooplankton density ($r = 0.84$, $P = 0.008$). Moreover, Rotifera (III-ROTI) was

224 favored with increases with filamentous Cyanobacteria (II-F; $r = 0.78$, $P = 0.022$) and small loosely attached

225 Chlorophyceae (II-L; $r = 0.82$, $P = 0.011$). Ciliate (II-CIL) was also correlated to filamentous Cyanobacteria (II-F; r

226   = 0.89, P = 0.003). Erect life-form did not vary in time. Precipitation and wind were responsible TP inputs favoring

227   adnate and/or prostrate life-form (r = 0.72, P = 0.040) which rapidly increases in biomass (r = 0.72, P = 0.043). The

228   community composition subsequently changed, with an increase and persistence of diatoms on advanced phase,

229   dominated by tightly attached and motile diatoms, and also with increases in loosely attached and filamentous algae.

230   **Discussion**

231   Disturbance is the main factor driving epiphyton succession and stabilization

232   In Mangueira Lake, the early stage of succession was observed during the first two weeks and loosely

233   attached algae (unicellular green algae, desmids and flagellate algae) showed to be efficient pioneering colonizers,

234   which are commonly reported in tropical reservoirs during early colonization (Ferragut & Bicudo, 2012; Pellegrini

235   & Ferragut, 2012; Rodrigues dos Santos & Ferragut, 2013). Although for temperate environment, small adnate or

236   erect diatoms are known to start the colonization (Hoagland et al., 1982, Stevenson, 1996; Ács et al. 2007, in

237   laboratory conditions). Surface colonization always began with a nutrient 'conditioning film' (Ács et al., 2007) due

238   organic matter and bacterial activities (Carrias et al., 2002) and our explanatory hypothesis is that mucilaginous

239   biofilm could favor the adhesion of loosely attached algae after cells settlement. Together with the stabilization of

240   the water due macrophyte bank (Jeppesen et al., 1998) guarantee the success of this life-form as pioneers under

241   intense wind action in Mangueira Lake. The community composition subsequently changed, with an increase and

242   persistence of diatoms and filamentous algae on advanced phase, as expected (Hoagland et al., 1982; Biggs et al.,

243   1996; Szlauer-Łukaszewska, 2007).

244   In the present study, we recognized that summer storm, as on day 20, are natural disturbance that drove

245   epiphyton succession whereas tightly attached life-forms, as adnate and/or prostrate (*Epithemia* spp) and erect life-

246   form were resistant during disturbance. Schneck & Melo (2012) evaluating the resistance and resilience of

247   organisms in a lotic environment, also found that adnate and/or prostrate taxa (including *Epithemia*) were more

248   resistant to disturbance. These groups primary formed by diatoms have specialized structures for tightly adhering to

249   the substrate (Peterson & Stevenson, 1992) which are flexible enough to tolerate wave action (Lowe, 1996). The

250   ability of resistance to disturbances defines algal persistence (Stevenson, 1996). Community composition in

251 Mangueira Lake was consistent with Lowe's (1996) observation that epiphytic communities in the eulittoral zone are

252 dominated by tightly attached algae in the presence of regular high-energy. As observed by Ács & Kiss (1993) for

253 lotic environment, under constant disturbance algae showed to be accommodate to some disturbance levels. Effects

254 of disturbance was also observed to zooplankton, which during disturbances on day 20 community was substantially

255 reduced in biomass with dominance in small forms as tecamoebas, organisms suspended from sediment.

256   When wind disturbance was strongly reduced (as observed on days 6 and 30) in frequency and intensity (<

257 $7m\ s^{-1}$) together with high temperatures, community richness and diversity decreased. Once Mangueira Lake is

258 under strong wind forces during this summer, their reduction could act as intermediate quiescence, based on the

259 mean of the system ($15\ m\ s^{-1}$). Following Connell's (1978), the absence of disturbance causes competitive exclusion

260 and reduces diversity to minimal levels whereas decrease in biomass (phytoplankton). Diversity and richness

261 increased when wind velocities was under the mean for the system and epiphytic community became resilient 15

262 days after disturbance when species tended to return to pre-disturbance patterns of heterogeneity (Fraterrigo et al.,

263 2008). Wind velocity, lower and above the means found for the system, could be considered as disturbance for

264 attached community during succession process, once influenced community structure, richness and diversity.

265   Mangueira Lake was under N-limiting conditions and epiphyton was also identified as N limited

266 community. Nutrient limitation could be related to phytoplankton growing rates in spring induced by warming,

267 leading to nutrient limitation in summer (Fragoso Jr. et al, 2011). This conditions favored *Epithemia* a known N-

268 fixing diatom (Deyoe et al., 1992). Nitrogen limited environment is common to present N-fixing algal proliferations,

269 as *Epithemia* in temperate rivers (as well Cyanobacteria); moreover, when consumed by grazer or while decompose,

270 they can also become N source for the environment (Power et al., 2009). TP concentrations in water were high

271 consistent to eutrophic state contrasting with historical oligo-mesotrophic conditions. On the other hand, we found

272 that TP increases in water were strongly correlated with disturbance, once water TP can rapidly increases during

273 strong wind periods in shallow lake (Zhu et al., 2005). As a wind-exposed shallow lake, Mangueira Lake is under

274 complete vertical mixture and seiches can transport materials (Fragoso Jr. et al, 2011), so nutrient pool is common

275 for costal shallow lakes in southern Brazil due sediment suspension driven by wind hydrodynamics (Cardoso &

276 Motta Marques, 2009).

277   We found low correlations of littoral community with local water; however TP biofilm was strongly related

278   to TP inputs in water due disturbance caused by summer storm. TP in biofilm also increased with succession time;

279   the accumulation of TP in biofilm is well known (McCormick et al., 2001) and favored diatom biomass.

280   Allochthonous detritus can influence nutrient ratios due to terrestrial and atmospheric inputs (Hillebrand & Sommer,

281   1999), but diatom biomass is known to increase with TP (Liboriussen & Jeppesen, 2006).

282   As observed by Rimet et al (2015) in Lake Geneva, water chemistry in littoral zone change faster than

283   pelagic chemistry. Lake Geneva is a large lake but deeper than Mangueira Lake, although presented similar wind

284   dynamics dominated by north-east wind. As observed by them, littoral zone are exposed to wind and waves action

285   whereas chemical and biological compartments are created; those zones which are not protected from disturbance

286   was dominated by diatoms adapted to turbulent environment (pioneer life-form) masking the effects of nutrients

287   changes. In a previous study conducted during summers in Mangueira Lake, we also found that wind dynamics is a

288   main force that regulates littoral zone dynamics and their attached communities, and diatoms in South area are

289   dominated by pioneer life-form more related to wind disturbance than to wind-driven nutrient gradient (Faria et al.,

290   2015). On the present study, correlations showed that increases in biomass (adnate and/or prostrate life-form after

291   storm) were related both to wind and precipitation. So we noted that during succession process in a macrophyte bank

292   was possible to identify some life-forms responding to nutrient inputs in water chemistry due disturbance better than

293   a steady-state community, which was dominated by a pioneer and tolerant life-form adapted to disturbance

294   condition.

295   Epiphyton was a productive community and sustains bottom-up zooplankton control

296   Epiphyton revealed to be a productive community and our results are in agreement with studies showing

297   that the food-web in Mangueira Lake is sustained by autochthonous carbon from macrophytes and epiphyton

298   (Rodrigues et al., 2014) reinforcing the importance of epiphyton for lake production (Liboriussen & Jeppesen, 2003;

299   Vadeboncoeur et al., 2008). Indeed, macrophytes as non-inert substrates can be a significant C source for epiphyton,

300   furnishing to the biofilm metabolites such as calcium carbonate (Burkholder & Wetzel, 1989). Besides that, living

301   substrates could favor epiphyton colonization (Pip & Robinson, 1984) and also great contributing to carbon

302   production (e.g. 1770 g m^{-2} year, Villar et al., 1996). Moreover high TP concentration in southern part of the lake is

303 clear water, and production was superior that found for eutrophic lakes, which usually presents turbid waters (e.g.

304 1279 mg C m^{-2}, Liboriussen & Jeppensen, 2003).

305   Autochthonous process and light regulated primary production whereas maximum production value was

306 coincident with heterogeneous community. Peak of phytoflagellates, as we registered on day 6, is also known to

307 contribute to production (Ilmavirta, 1988; Stoecker et al., 2000; Mariazziet al.,1991). High production was also

308 noted due abundance of green algae and desmids under high PAR (1806 μmol m^{-2} s^{-1}). Studies showed that green

309 algae and diatoms are favored in high light regimes (Wall & Briand, 1979) and some diatoms present chromatic

310 adaptation responding to light spectral distributions favoring algal growth (Wallen & Geen, 1971; Seiji &

311 Gianesella-Galvão, 1991). In our controlled condition summer radiation was high during all study (1326±438 μmol

312 m^{-2} s^{-1}). Liboriussen & Jeppesen (2003) showed that photosynthesis saturation happened between 100–400 μmol m^{-2}

313 s^{-1}; radiation can negatively affect phytoplankton Chl a (PAR 600–1000 μmol m^{-2} s^{-1}), increasing at PAR values

314 below it (Collos et al., 1992). However, in Mangueira Lake, shading from macrophytes (Liboriussen & Jeppesen,

315 2003) could attenuate light levels, favoring epiphyton production *in situ* and yielding increasing results from those

316 of the present study.

317   Small-sized forms of microzooplankton as ciliate and small rotifers were dominant during all succession.

318 As observed by Agasild et al. (2007) those groups could promote strong grazing impact on the small algae (5-15

319 μm) also acting as important food resource for copepods (Bundy et al., 2005). Adnate/prostrate algae increased with

320 grazing and this could be explained because predators prefer loosely attached diatoms due the facility of gather

321 (Peterson, 1987). In Mangueira Lake, the significant correlations between epiphyton and zooplankton communities

322 could indicate not only top-down regulations of epiphyton by zooplankton, but also bottom-up regulation of

323 zooplankton by epiphyton (Chen et al., 1997). Top-down theories which phytoplankton are controlled by

324 zooplankton is largely studied (Sommer et al., 2003; Sommer & Sommer, 2006), however epiphyton and

325 zooplankton relations still a lack. Fragoso Jr. et al. (2011) revealed that phytoplankton on summer are limited by low

326 N supplies and the zooplankton grazing are limited by this light -and temperature-driven phytoplankton demand, so

327 epiphyton could act as carbon resource for them. Kluijver et al. (2015) showed that macrophytes and associated

328 community great subsides carbon for zooplankton improving cascading effects of planktonic food-webs. Biofilm

329 removal by zooplankton feed preferences could favor community due light entrance, nutrients recycling or favoring

330 the settlement of other species in the epiphyton increasing richness and diversity.

331   Our data reinforce the importance of epiphytic community in subtropical shallow lakes food-webs which

332 could supply substantial amounts of carbon during summer and act as a quality food resource for zooplankton.

333 Moreover, recent study on relation between phytoplankton and zooplankton (Rosa, 2015) in Mangueira Lake as well

334 as the phytoplankton composition and biomass (Crossetti et al., 2014) showed that diatoms were not dominant in the

335 plankton making zooplankton look for another sources of food as bacterioplankton or epiphyton. Because that,

336 Copepods and Cladocerans (macrozooplankton) increased in water when diatoms biomass increased in the end of

337 succession.

338 **Acknowledgments**

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Figure captions

Fig.1 Ordination analysis of environmental data on the littoral zone during study time in summer 2012. For the legend, see Table 1.

Fig. 2 Variation of chlorophyll a (Chla), pheopigments (Pheo), PP :Chl a, solar radiation (PAR) and biomass of epiphytic algae succession during study time in summer 2012.

Fig. 3 Epiphyton and zooplankton data during study time in summer 2012. Biomass, total density (TD), diversity (H') and Richness as taxa number (R). Legend: BAC (Bacillariophyceae), CYA (Cyanobacteria), ZYG (Zygnemaphyceae), CHL (Chlorophyceae), PROTI (Protist), ROTI (Rotifera), CLADO (Cladoceran), COPE (Copepod).

Fig. 4 CCA of biotic data using algal life-forms biomass and zooplankton groups biomass, related with environmental variables. Legend for water (w) variables, see Table 1; for algae and zooplankton, see Table 3.
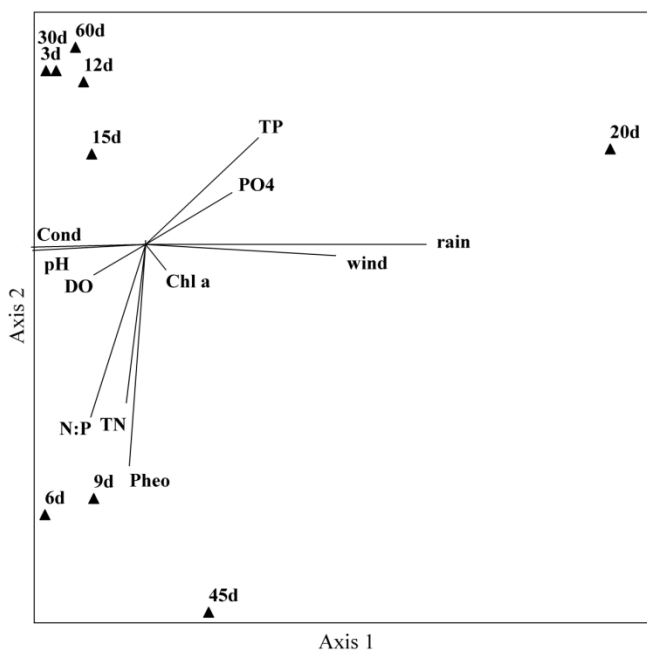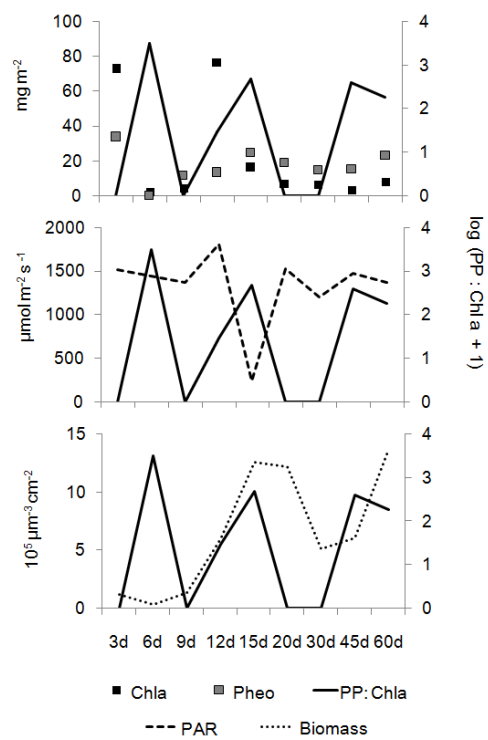

Fig.1

Fig. 2
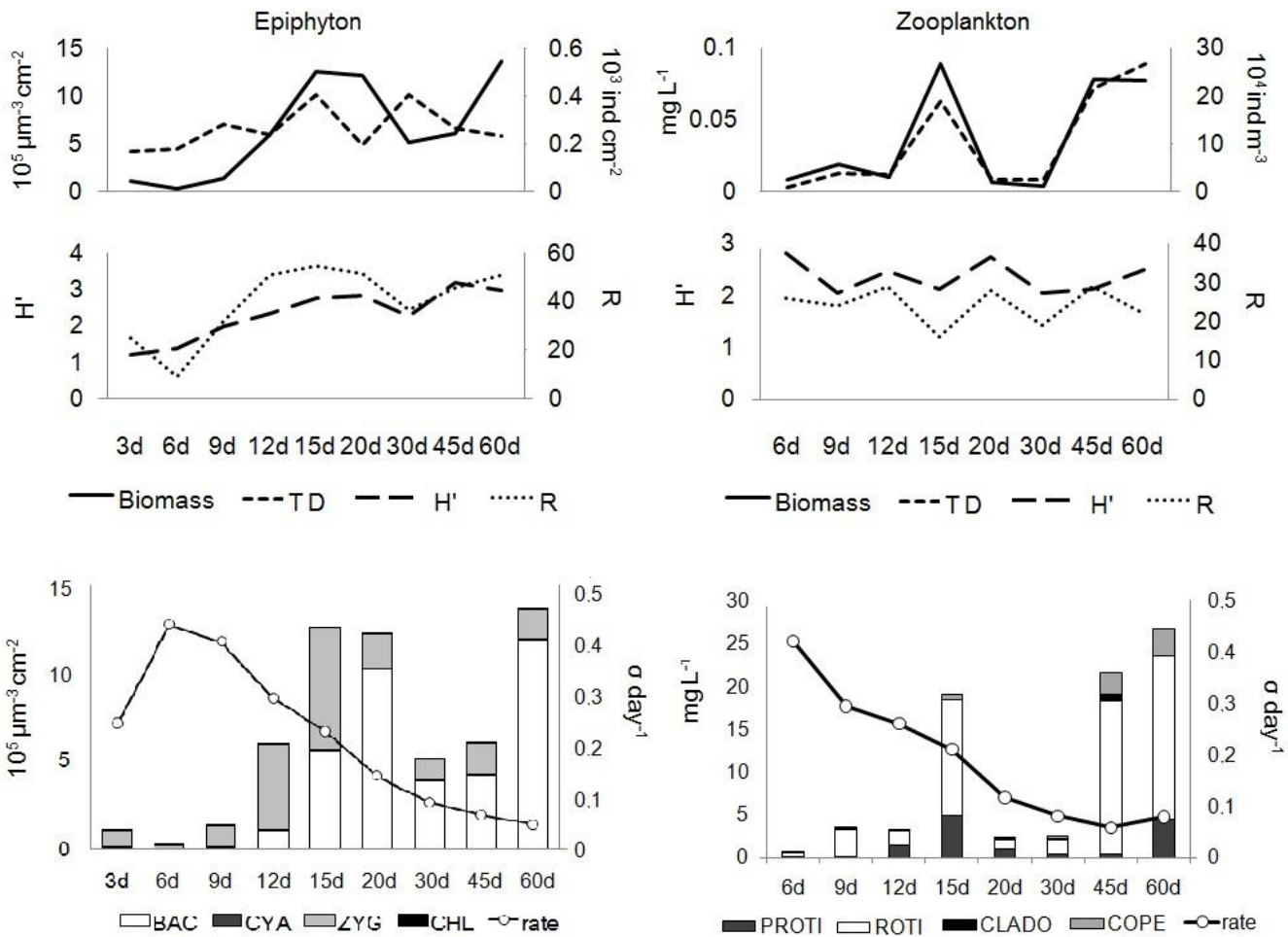
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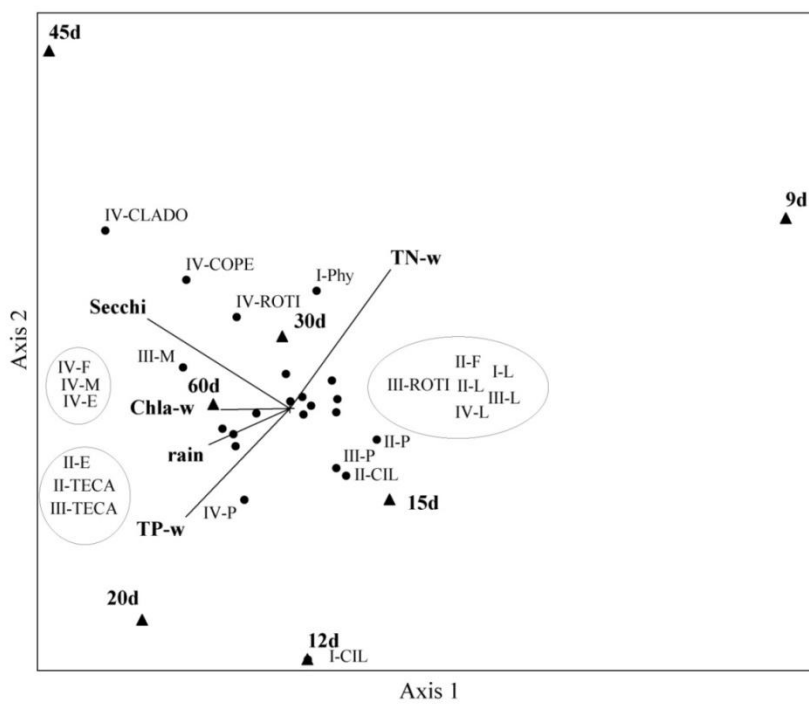
Fig. 4

Table 1 – Environmental data (SD - standard deviation and CV - coefficient of variation) on the littoral zone during study time in summer 2012.

Variables	Code	Mean ($\pm$SD); CV%
Chlorophyll a (mg L^{-1})	Chla	3.53$\pm$1.32; 37%
Pheophytin (mg L^{-1})	Pheo	0.6$\pm$0.7; 111%
Nitrate (mg L^{-1})	NO3^{-}	0.05$\pm$ 0.002; 6%
Ammonia (mg L^{-1})	NH3	0.04$\pm$0.01; 20%
Total nitrogen (mg L^{-1})	TN	0.38$\pm$0.08; 20%
Orthophosphate (mgL^{-1})	PO4	0.004$\pm$0.009; 19%
Total phosphorus (mg L^{-1})	TP	0.29$\pm$0.07; 23%
N:P molar ratio	N:P	7$\pm$3; 42%
Secchi depth (cm)	Secchi	76.33$\pm$10.33; 14%
Water temperature (^{o}C)	Temp	23.91$\pm$1.78; 7%
Conductivity (mScm^{-1})	Cond	0.41$\pm$0.08; 18%
Dissolved oxygen (mg L^{-1})	DO	8.10$\pm$0.40; 5%
pH	pH	8.62$\pm$0.10; 1%
Precipitation (mm)	mm	2.94$\pm$7.89; 268%
Wind velocity (m s^{-1})	wind	15.06$\pm$5.83; 39%

Table 2- Nutrient content, Chlorophyll a and primary production of epiphyton during succession (n=9) and biomass, richness and diversity (SD - standard deviation) of principal algae groups in epiphyton and zooplankton community during study time in summer 2012.

Biofilm content	Mean± SD
TN (mg m^{-2})	2.5±0.4
TP (mg m^{-2})	4.0±2.0
N : P molar ratio	4±1
Carbon uptake (mg C m^{-2} h^{-1})	2348.3±3294.7
Chla (mg m^{-2})	22.1±30.2
Pheo (mg m^{-2})	17.3±9.5
Epiphyton	**Mean± SD**
Bacillariophyceae (10^5 μm^{-3} cm^{-2})	4.69±4.50
Cyanobacteria (10^5 μm^{-3} cm^{-2})	0.01±0.02
Zygnemaphyceae (10^5 μm^{-3} cm^{-2})	2.45±2.22
Chlorophyceae (10^5 μm^{-3} cm^{-2})	0.01±0.01
Phytoflagellate (10^5 μm^{-3} cm^{-2})	0.01±0.02
Total biomass (10^5 μm^{-3} cm^{-2})	6.50±5.20
Richness	40±15
Diversity (H')	2.3±0.7
Zooplankton	**Mean± SD**
Protist (10^3 mg L^{-1})	1.00±1.18
Rotifera (10^3 mg L^{-1})	28.60±30.51
Cladoceran (10^3 mg L^{-1})	0.50±0.92
Copepod (10^3 mg L^{-1})	6.52±9.73
Total biomass (10^3 mg L^{-1})	36.66±38.11
Richness	24±5
Diversity (H')	2.4±0.3

Table 3–Algal life-forms and zooplankton groups related to the largest linear dimension axis (GALD).

Algal life-forms	Taxa	GALD	Code
Erect or with mucilage pads or tubes	*Achnanthidium minutissimum, Rhoicosphaenia* sp.	II	II-E
Erect or with mucilage pads or tubes	*Fragilaria* spp., *Gomphonema* spp., *Ctenhophora pulchella*, *Cymbella* spp, *Synedra* spp., *Ulnaria* spp.	IV	IV-E
Adnate and/or prostrate	*Amphora* spp.	II	II-P
Adnate and/or prostrate	*Cocconeis* sp, *Epithemia sorex*, *Amphora* spp.	III	III-P
Adnate and/or prostrate	*C. placentula*, *E. turgida*	IV	IV-P
Motile diatoms	*Nitzschia* spp.	III	III-M
Motile diatoms	*Nitzschia* spp.	IV	IV-M
Filamentous	*Pseudanabaena mucicola*, Nostocales	II	II-F
Filamentous	*P. galeata*, *Mougeotia* sp.	IV	IV-F
Loosely attached	*Scenedesmus ecorni, Synechococcus nidulans*	I	I-L
Loosely attached	*Aphanothece stagnina, Crucigenia tetrapedia, Scenedesmus* spp.,*Tetraedrum* spp.	II	II-L
Loosely attached	*Aphanocapsa* spp., *A. smithii, Merismopedia tenuissima, Cosmarium subtumidum, Monoraphidium* spp.	III	III-L
Loosely attached	*Pediastrum tetras, A. delicatissima, Cosmarium* cf *subspeciosum*	IV	IV-L
Phytoflagellate	Unindentified phytoflagellate	I	I-Phy

Zooplankton groups	Taxa	GALD	Code
Protist-Ciliate	Unindentified, *Vorticella* sp., and Ciliate	I	I-CIL
Protist-Ciliate	*Codonella* spp., *Vorticella* spp.	II	II-CIL
Protist-Tecamoeba	*Arcella* spp., *Centropyxis* spp., cf. *Corythion* sp., cf *Curcubitella* sp., *Difflugia* spp., cf *Nebela* spp., cf *Pontigulosia compressa*	II	II-TECA
Protist-Tecamoeba	*A. polypora, Difflugia* sp.	III	III-TECA
Microzooplankton-Rotifera	*Anuraeopsis* sp., *Collotheca* spp., *Keratella* spp., *Lecane* spp., *Lepadella* sp., *Paranuraeopsis* sp., *Polyartha* sp., *Pompholyx* sp., *Trichocerca* spp.	III	III-ROTI
Microzooplankton-Rotifera	*Collotheca* sp., *Filinia longiseta, Hexartha* sp., *Ploessoma* sp., *Ptygura* sp., *Synchaeta* sp., *Trichocerca* spp.	IV	IV-ROTI
Macrozooplankton-Cladoceran	*Bosmina longirostris, Bosminiopsis deitersii*	IV	IV-CLADO
Macrozooplankton-Copepod	Copepodits, Nauplii	IV	IV-COPE

Capítulo III

Wind-driving dynamics of epiphyton during winter in a large shallow lake

1   **Wind-driving dynamics of epiphyton during winter in a large shallow lake**

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7   Abstract: Shallow littoral zones are exposed to wind and hydrodynamics affects the development of attached

8   community. Mangueira Lake is a shallow lake under continuous wind influence ranging from oligo- to mesotrophic

9   conditions, and in this study we tested the response of the epiphyton to the wind dynamics (velocity and direction)

10   during cold-fronts (2013 Winter) in three different situations: Natural community, short-term succession in a

11   macrophyte bank and in an enclosure (protected from the wind). Natural community was dominated by an

12   assemblage formed by *Epithemia* spp and green filaments. Open experiment showed a rapidly colonization due

13   diatoms cells settlement; fluctuations on densities and richness were observed, however community became similar

14   to the natural community within 12 days of succession. Enclosure acted buffering wind forces delaying succession

15   derived by settlement of metaphytic cells and the succession only started after a huge disturbance (wind 10 m s^{-1})

16   which leveled the enclosure water and the lake water. Dominance of diatoms was registered in all experiments. The

17   communities' diversities responded to wind dynamics, whereas all experiments showed lower diversities when wind

18   velocity exceeded the system's means (5 m s^{-1}). Epiphyton revealed to be resilient rapidly recovering after

19   disturbance and wind favored colonization.

20   Keywords: disturbance, natural substrata, periphyton, succession

21   **Introduction**

22   Algal successional process is characterized by species growing and replacement along community

23   development (McCormick & Stevenson, 1991) following a sequence defined on time and space reaching a mature

24   state (Biggs, 1996; Stevenson, 1996). The successional sequence is driven by a complex interaction of factors as

25   light, grazing, temperature and water chemistry (Patrick & Reimer, 1966; Stevenson, 1996), propagules and

26 substrate availability (Hutchinson et al., 1975) and efficiency in resources competition (Ferragut & Bicudo, 2010)

27 responding to local conditions (Hoagland et al., 1982; McCormick & Stevenson, 1991). Different growth strategies

28 of species are evident during succession, whereas early successional species have fast reproductive rates and late

29 successional species are low immigration rates (McCormick & Stevenson, 1991). Recent studies showed that during

30 successional process growth forms change and are related to compete for the same resources (Passy, 2007; Kelly et

31 al., 2009). Attachment strategies can furnish reliable information about biofilm structure (Rimet & Bouchez, 2011)

32 and resistance and resilience of physical disturbances (Schneck & Melo, 2012).

33   Littoral zone of shallow lakes provides a great variability of substrata for algae development (Wetzel, 1990;

34 Lowe, 1996; Liboriussen & Jeppensen, 2006). At shallow depths, attached algae are exposed to wind action and

35 consequent wave action, water-level and high radiation (Cantonati & Lowe, 2014). Moreover, community also

36 suffers hardly changes responding to rains, watershed and river flows (Rimet et al., 2015). Shallow littoral zones

37 undergo waves generated by wind forces acting as a disturbance and driving algae communities (Cantonati & Lowe,

38 2014). Disturbance events are determinant of algal community structure (Peterson & Stevenson, 1992). Periphyton

39 in mature stages seems to be more resistant to disturbance (Zanon et al., 2013) however frequency and intensity of

40 disturbances can act like regulatory factors that can redirect the successional trajectory (Sommer et al., 1993).

41 Disturbance could affect attached community diversity (Ács & Kiss, 1993) and ability to recover after them will

42 depend of disturbance origin and intensity, as well as the propagules and refuges availability (Lake, 2000). For

43 streams, availability of refugia favoring recolonization could be used as a critical measure of resistance and

44 resilience (Lake, 2000).

45   Wind dynamics drives the changes in phytoplankton and zooplankton community in subtropical shallow

46 lake (Cardoso & Motta Marques, 2004; 2009). Continuous wind influence in Mangueira Lake results an intense

47 water circulation which communities' distribution are driven by hydrodynamics (Cardoso et al., 2012) which

48 directly influences their physical and chemical properties (Scheffer, 1998). Central area of the lake acts as a

49 transitional point, whereas attached diatoms community assumes characteristics of the both extremes of the lake

50 (North and South) due wind dynamics (Faria et al., 2015). Wind action in littoral zone also showed to model

51 attached algae community selecting them by their adaptations (Faria et al., 2015; Rimet et al., 2015) and even with

52   the stabilization of the water due macrophyte bank (Jeppesen et al., 1998) the effect of disturbances still remains

53   poorly understood, particularly in terms of establishment of equilibrium states and non-equilibrium theories

54   (Lengyel et al. 2014).

55   Previous study in southern area of Mangueira Lake showed that disturbance drives epiphyton successional

56   process during summer, whereas high wind velocity (15 m s^{-1}) and high precipitation (29 mm) favored tightly

57   attached diatoms (Faria et al., in prep). In this study our goal was to characterize the natural community in the center

58   area of Mangueira Lake and investigate how wind forces affect natural epiphytic community and epiphyton short-

59   term succession during winter 2013, in a period of cold-front, when wind changes from NE dominant to SWS

60   direction. We also hypothesized that wind models community structure and algae growth forms, and if intensity of

61   that disturbance affects diversity, resistance and resilience of community. We also aimed to test the effect of absence

62   (or strongly reduction) of wind disturbance in algae successional trajectory, by comparing succession in an

63   enclosure built for isolation of disturbance with a succession in natural environment, testing if the course of them

64   differs between experiments.

65   **Material and Methods**

66   Study area

67   Mangueira Lake is a shallow coastal lake located in southern Brazil on a narrow strip of land between the

68   Atlantic Ocean and Mirim Lake (Crossetti et al., 2013). The lake covers a large area (approximately 820 km^2), 90

69   km long and 3–10 km wide, and the average depth is 3 m (Zmax = 6 m). The lake ranges from oligo to -mesotrophic

70   conditions and is under continuous wind influence, causing intense water mixture (Fragoso Jr et al., 2008), with

71   predominantly NE direction and SWS direction during cold-fronts (Cardoso et al., 2012).

72   Field and laboratory procedures

73   Wind, precipitation and air temperature data were obtained from Santa Vitoria do Palmar-RS

74   Meteorological Station (maintained by INMET, Meteorological National Institute) from July 12 (10 days before

75   sampling) to August 20 of 2013 three times per day (0 am, 12 pm and 6 pm) to describe the winter wind and

76   precipitation patterns. We also used the wind data which was monitored by a RM Young Ultrasonic Wind Sensor

77   located on a structure maintained on the pelagic zone, in center area of the lake to evaluate the wind disturbance *in*

78   *loco*. This structure also holds an YSI 6600 probe by which were measured dissolved oxygen, pH and conductivity.

79   Water was sampled with plastic bottles (n=3), in littoral zone of center area of the lake (33°13′34.41″S;

80   52°52′8.51″W), that were stored frozen for nutrient (nitrogen and phosphorus series) and carbon analysis (day 24,

81   missing data). Carbon (dissolved inorganic carbon, DIC; dissolved organic carbon, DOC; total organic carbon,

82   TOC) and total nitrogen (TN) were analyzed using a total organic carbon analyzer (Shimadzu VCPH) and filters

83   GF-3 (MN), pore size 0.2 μm. Ammonia (NH_3) and total phosphorus (TP), followed Mackereth et al. (1989) and

84   orthophosphate (PO_4) were provided by chromatography (Metrohm 881). In addition to measurements, TN and TP

85   molar ratios were calculated. Water and epiphyton chlorophyll (Chl a) and pheophytin (Pheo) were extracted from

86   GF/F filters in 90% ethanol (Jespersen and Christoffersen, 1987) and measured by spectrophotometry (APHA,

87   2005).

88   We conducted the study *in situ* in the littoral zone (West edge) in central part of the lake over 30 days in

89   winter 2013 (from July 22 to August 20) comparing three different conditions: two epiphyton short-term succession

90   process under different wind influence and a natural community. For that, we chose a large bank of *Schenoplectus*

91   *californicus* L. in the littoral zone. For successional experiments, we randomly choose 200 leaves of macrophytes

92   (100 leaves for each successional experiment, sub-divide in three replicates distant 2–5 m) and carefully cleaned

93   them with a soft sponge to remove the preexistent biofilm. We marked the top of the leaves with adhesive tape for

94   identification. The experiment named as "Enclosure" occurred on an aquatic mesocosm (polyethylene enclosure, ±7

95   length and ±2 m width) developed for isolation of winds and waves disturbance. The other experiment was named as

96   "Open" whereas the successional process occurred on natural environment, near to the "Natural" experiment, which

97   was the experiment that we sampled the preexistent community growing on littoral zone, without clean the biofilm.

98   We also sampled epiphyton in the same day of the successional experiment's implementation (from Natural

99   experiment), and call them as "day one", thus we could monitory the influence of disturbances in natural epiphyton

100   community.

101   Sampling (n=3 for each experiment) was performed at each 3 days of interval during 30 days. Except by a

102   strong precipitation occurred on day 12, and water invaded the enclosure, so we also sampled all experiments on day

103   13 aiming to verify the influence of that precipitation on the experiments. For samples conservation, the biofilms

104   were removed from the substrate with toothbrushes, fixed in Lugol 5% for quantitative analysis and stored frozen

105   for pigments and ash free dry mass (AFDM) analysis (APHA, 2005). Samples from day 3, 9 and 15 of Natural and

106   day 3 of Open experiment are missing data.

107   Algae were identified and counted according to Utermöhl's (1958) method which yields 90% counting

108   efficiency (Pappas & Stoermer, 1996). Species diversity (H') was calculated as the Shannon-Wiener index. We also

109   classified taxa (total density > 1%, according to Lavoie et al., 2009) into five categories of life-forms (modified from

110   Berthon et al., 2011; Schneck & Melo, 2012; Rimet & Bouchez, 2012; Rimet et al., 2015) being "erect/mucilage

111   stalks" that were diatoms attached by mucilage pads or stalks growing perpendicular to the substrata

112   (*Achnanthidium*, *Ctenophora*, *Fragilaria*, *Gomphonema*, *Rhoicosphaenia*, *Ulnaria*), "adnate/prostrate" were

113   diatoms attached by pads and growing parallel to substrata (*Cocconeis*, *Epithemia*, *Rhopalodia*), "Motile diatoms"

114   (*Navicula*, *Nitzschia*), "Filamentous" were the filamentous Chlorophyta, Cyanobacteria and diatoms forming chains

115   (*Achnanthidium catenatum*, *Staurosirella, Melosira, Heteroleibleinia, Mougeotia, Spirogyra, Oedogonium*) and

116   "Metaphyton" (*Aphanocapsa*, *Pseudanabaena*, *Synechococcus*, *Chlorella*, *Monoraphidium*, *Cosmarium*,

117   *Chlamydomonas*, unidentified Chrysophyceae and unidentified Chroococcales). In the case of *Epithemia* and

118   *Rhopalodia* which are commonly known as epiphytic both in macrophytes and filamentous algae but are also motile,

119   we choose to classify them as prostrate (attached by mucilage pads and parallel to substrate) (Schneck & Mello,

120   2012).

121   Data analyses

122   The succession rate of the community composition (σ) was calculated according to the method of the sum

123   of differences (Lewis, 1978). T-tests of dependent samples were applied among days (on successional sequence) to

124   investigate the responses of community structure, life-forms and diversity to disturbances. Analysis of variance

125   (ANOVA) were performed using community attributes using the software Statistica 7.1 (StatSoft Inc. 2005),

126   followed by Tuckey HDS *post-hoc* tests for pairwise comparisons. We also performed correlation analyses (*r-*

127   Pearson p<0.05) between the epiphyton community and environmental data (meteorological data and water data) to

128   identify relationships among them and explanatory variables to include in the subsequent multivariate analyses.

129   Ordination analyses were performed using the software PC-ORD version 6.08 for Windows (McCune and Mefford,

130   2011). PCA of water attributes was performed to reveal environmental changes over the course of the experiment.

131   PCA with biotic data was also performed aiming to select species based on the length of the eigenvector ($r > 0.60$

132   for the first two axis), to perform a RDA. The data were log x+1 transformed prior to ANOVA and multivariate

133   analysis.

134   **Results**

135   Environmental data

136   Winds from SWS–S predominated during 10 days before the beginning of experiment until day 14, with

137   some daily changes on days 7–10 (ENE-ESE). Southern winds also occurred on days, 19–20, 23–24 and 27 (Fig.1).

138   High daily changes on wind direction were noted, mainly with the output of cold front (13–14 day) whereas wind

139   ranged from WNW to E. During experiment, wind velocity was constant (4.9 ± 1.9 m s^{-1}) peaking on day 23 (10 m

140   s^{-1}) being also high on days 12, 19 and 24 (8 m s^{-1}) (Fig.1). High precipitation was registered on days 12 (23.2 mm),

141   13 (40.6 mm) and 18 (23.8 mm) (Fig.1). Temperatures ranged about 10.4$\pm$2.5 ºC, pH was alkaline (8.4$\pm$0.10) and

142   water was oligohaline (0.31$\pm$0.05 mS cm^{-1}) with great availability of dissolved oxygen (10.3 mg L $^{-1}$). Water was

143   oligo to -mesotrophic (TP, 0.04$\pm$0.02 mg L^{-1}), showing low TN:TP ratios from days 6–18 (TN:TP < 10) and high

144   rations from days 21– 30 (TN:TP >37).

145   Ordination analysis (PCA) was significant for the first two axis (58.83%; first axis 37.95%, p = 0.004)

146   grouping on positive side the days that were marked by low wind and no precipitation, being correlated with PO4 (r

147    $= 0.60$) and DIC ($r = 0.73$) availability on water (Fig.2). Negative side of first axis revealed that high precipitation

148   registered on days 12–13 increased nutrients and carbon availability in water (prec, r =-0.62; Si, r =-0.62; DOC, r =-

149   0.77; TOC, $r = -0.80$; TP, r =-0.82; TN, $r = -0.91$). Days 18 and 30 were marked by increase of temperature ($r = -

150   0.47$). Days with high wind velocity increased TSS ($r = 0.52$), NH4 ($r = 0.74$) and POC ($r = 0.78$) in water (second

151   axis).

152   Biotic data

153   Natural community revealed that epiphyton was dominated by diatoms (>80% of total density). Control

154   sample (day 1) presented dominance of *Epithemia sorex* and *E. turgida*, green filaments (*Mougeotia* and

155   *Oedogonium*) and great densities of *Melosira varians* (Fig. 3); this assemblage characterized Center area in

156   Mangueira Lake, in a case of co-existence ($r = 0.92$, $p < 0.001$) once diatoms can colonize those filaments, and both

157   contributed to ash free dry mass (AFDM) in epiphyton ($r = 0.56$, $p = 0.002$; $r = 0.40$, $p = 0.0034$; respectively) and

158   Chl a ($r = 0.67$, $p < 0.001$; $r = 0.57$, $p = 0.001$). High wind velocity was registered after we sampled control

159   community (11 m s^{-1} on day 1, and 10 m s^{-1} day after), and total density (TD) strongly decreased on day 3 removing

160   filamentous algae. Community was composed by adnate/prostrate and erect/mucilage stalks diatoms showing low

161   TD until day 12. High rate of change revealed that high precipitation (23.2 mm) favored community also in density

162   and biomass (AFDM and Chl a) (Fig. 3). Richness on natural community showed ±54 taxa during 30 days, and

163   peaks occurred on days 13 (83 species) and 21 (78 species), days with low winds (±3.8 m.s^{-1}). T-test for dependent

164   samples revealed that community changed between days 13–15 ($T= -2.48$, $p = 0.01$) and 15–18 ($T = 2.71$, $p = 0.008$)

165   and it was related to the abruptly changes in wind velocity with the output of cold front and also in wind direction,

166   coming from the Northern-East quadrant (Fig. 1) favoring erect/mucilage stalks (*Gomphonema* spp, *Fragilaria* spp.,

167   *Ulnaria* spp, *Ctenophora pulchella*) and motile (*Navicula* spp., *Nitzschia* spp) diatoms and reduction on green

168   filaments and *Epithemia* spp which were recovered on day 27. Pheophytin peaked on day 21, with low wind (3.2

169   m.s^{-1}) and no precipitation. Subsequent days were marked by increases in Chl a due diatoms and richness mean was

170   maintained (54 taxa).

171   Enclosure experiment showed very low densities during beginning of succession (Fig. 3). First day was

172   dominated by flagellate algae (Chlamydophyceae and Crysophyceae) and metaphytic taxa as *Monoraphidium* spp,

173   *Pseudanabaena galeata* and *Synechococcus nidulans* (Fig. 3). After precipitation on day 12, water level increased

174   (±0.4 m) and water invaded the enclosure. As a result, community showed a high rate of change (Fig. 3), increasing

175   richness (57 taxa). As natural community, enclosure also showed community changes in species between days

176   13–15 ($T= -2.23$, $p = 0.30$) and 15–18 ($T = -2.54$, $p = 0.01$) due wind action (direction and velocity). Peak on

177   richness occurred on day 21 (60 taxa) decreasing thereafter between days 21–24 (N = 36, $T = -2.46$, $p =0.01$) also

178 related to wind changes. Biomass (AFDM and Chl a) was low during all experiment and diatoms dominate the end

179 of succession also decreasing richness (19 taxa).

180   Open experiment showed more variability during succession process (Fig. 3). Community on day 3 was

181 very heterogeneous, with high abundance of *Monoraphidium* spp, Crysophyceae, *Pseudanabaena galeata* and

182 *Synechococcus nidulans* but also showing settlement of diatoms (*Gomphonema* spp, *Fragilaria* spp., *Ulnaria* spp,

183 *Staurosirella* spp, *Navicula* spp., *Nitzschia* spp and *Ctenophora pulchella*). Peak of richness occurred on day 6 (66

184 taxa). Species substitution were registered earlier than in the enclosure experiment, between days 6–9 (T= 2.06, p =

185 0.04) when *Epithemia* spp started to grow. T-test for dependent samples showed that changes was also recorded

186 between days 9–12 (T = -2.06, p = 0.04) and 13–15 (T =-2.22, p = 0.03). Rate of change peaked on day 13 due

187 disturbance (prec 40.3 mm). Low total density and biomass were registered until day 18 which was marked by

188 increases in wind velocity (5.6 m.s^{-1}) and precipitation (23.8 mm) with increases in temperature (12.6 ⁰C), and

189 community was dominated by Cyanobacteria, decreasing diversity (r = -0.62, p< 0.001); we also noted that small

190 snails appeared on the macrophytes. On day 24 another peak on wind velocity (8 m s^{-1}) occurred and a dominance of

191 Chroococcales was registered improving total density (r = 0.63, p< 0.001) and biomass (AFDM r = 0.84, p<0.01;

192 Chl a r = 0.70, p< 0.001, Table 2). After that, community showed low richness (29 taxa) and was dominated by

193 diatoms and green filaments.

194   Disturbance caused by wind drove community changes (Fig. 4) and diversity was negatively correlated

195 with wind velocity (r = -0.45, p = 0.017). Diversity increased with wind velocity ≤ 5 m s^{-1}; velocity higher than

196 system's means decreased the diversity. Wind dynamic drove communities changes whereas in the Enclosure

197 experiment, T-test between diversity revealed different composition between days 12–13 (T = -11.88, p < 0.001),

198 when the water level increased and covered the enclosure, 13–15 (T = -19.04, p < 0.001) and 15–18 (T = -8.03, p <

199 0.001). In the Open experiment, those influences were noted only in days 13–15 (T = -3.55, p < 0.001). Life-forms

200 revealed that adnate/ prostrate, motile diatoms and filamentous life-forms were higher on Natural and Open

201 experiments than Enclosure. T-test for dependent samples was also applied to them and only metaphyton life-form

202 proved to increase with disturbance (T = 5.23, p = 0.03). ANOVA was run between wind velocity higher and above

203 the mean (5 m s^{-1}) and only to metaphyton was significant (F = 4.46, p = 0.042).

204   Sixteen species and the five life-forms were used to perform the Redundancy Analysis (RDA) with the

205   three experiments and the Day 1 community (Fig.5). RDA (36.7% of the variance explained for the first two axis)

206   grouped on positive side of first axis those samples related to the initial phase of succession (Enclosure, 3–15d and

207   Open, 3–9d) as well as samples from Natural community (6d –9d), all opposite to the nutrient negative quadrant.

208   Negative side of first axis showed that Day 1, or the control sample for the natural community, was characterized by

209   filamentous (r = -0.94) and adnate/prostrate diatoms (r = -0.91), and community was dominated by *Mougeotia* (r = -

210   0.78), *Melosira varians* (r = -0.88), *Epithemia sorex* (r = -0.88), *E.turgida* (r =-0.90) but also an erect diatom

211   *Ulnaria ulna* (r = -0.86). Open experiment presented this assemblage on the advanced phase of succession (days

212   27–30). Wind velocity (r = -0.23) and temperature (vector suppressed, r = -0.32, third axis) were related with day18

213   (r = -0.23) and to metaphyton increases (r = -0.70) which was also higher on initial phase of succession. After

214   disturbance on day 13 by the precipitation (40.6 mm), chlorophyll a (r = -0.50) and carbon (DOC, r = -0.52; TOC, =

215   -0.59) increased in water as well nitrogen (TN, r = -0.43; NH4,r = -0.45) and TSS (vector suppressed, r = -0.12).

216   Low wind velocity was registered on day 21 (r = -0.33, second axis), and related to dominance of erect/mucilage

217   stalks (*Gomphonema* spp [r = -0.89], [r = -0.63], [r = -0.55] and *Ctenophora pulchella* [r = -0.90]) and motile

218   diatoms (r = -0.85).

219   **Discussion**

220   Natural community was dominated by diatoms, mainly *Epithemia sorex* and *E. turgida*, that were enlaced

221   in large amounts of green filaments (mainly *Mougeotia* and *Oedogonium*) which was not dominant in microscopic

222   count due cell size and/or cell distribution in Utermöhl camera, but forming gross masses *in situ*. *E.sorex* and *E.*

223   *turgida* often occurred together although Europe and knowing to be N-fixing diatom presenting nitrogen

224   endosymbionts (Deyoe et al., 1992). This genera was characteristically dominant in central area of Mangueira Lake,

225   as showed in our previous study but curiously occurred in high TN:TP ratios > 12 (Faria et al., 2015). Nutrients

226   concentration was low during winters due low watershed nutrient load (Fragoso Jr. et al., 2011), however

227   precipitation causes nutrient inputs and attached community in lakes can display substantially biomass changes with

228   nutrient levels changes (Vadeboncoeur et al,. 2001). Succession experiment in a Mediterranean river revealed

229   Rhopalodiaceae dominates under low N (7µg L⁻) and changes in N availability favored non N-fixing taxa in

230 epiphyton and their host development (Marks & Power, 2001; Power et al., 2009). In our study, we verified three

231 distinct periods with a nutrient gradient: (1) dominance of *Epithemia* spp under low N, (2) algal increases with

232 dominance of N-non fixing diatoms (erect and motile diatoms) under TN:TP> 37, and (3) a recover of *Epithemia*

233 densities when green filaments became to grow. TN led to faster algal growth (Murdock et al., 2011). An

234 explanation for *Epithemia* success Center are is (1) shading by the large amounts of green filaments once they are

235 adapted to extreme low light intensity (Mueller, 1999) and (2) following Burkholder et al. (1990), in mature biofilms

236 in P-poor environments, adnate algae are isolate from water nutrient source, and host plants and small animals

237 excretion can supply phosphate availability to epiphytes, decreasing biofilm TN:TP. This could guarantee the

238 success of *Epithemia* during high TN:TP periods.

239   Green filaments were abundant in all littoral zone during winter, and also colonized the Enclosure nets and

240 it has also been reported to clogging fishermen nets in Mangueira Lake. Green filaments as *Mougeotia*,

241 *Oedogonium*, *Spirogyra* were registered in high abundance on natural substrata in Everglades at low TP

242 concentrations (Vymazal et al). Tapolczai et al. (2014) reported *Mougeotia* blooms on phytoplankton community in

243 large and deep lakes occurring in meso-oligotrophic conditions (phosphorus < 20 μg L^{-1}) and especially in Lake

244 Geneva, wind forces could cause nutrient replenishment favoring the bloom. Smith (1983) concluded for temperate

245 lakes that TN:TP < 29:1 favored Cyanobacteria dominance and can proliferate in non-eutrophic rivers in winter

246 floods that reduce grazers, providing a window time before grazing populations recover (Power et al, 2008). In

247 Mangueira Lake the low TP could favored *Mougeotia* development once those filamentous algae is a great

248 competitor in low phosphorus conditions (Sommer, 1983).

249   Green filaments were not resistant to disturbance. Wind velocity and direction from NE-E, removed them

250 carrying biomasses to the lake margin causing filaments accumulation. Senescent cells could be dislodged by

251 mechanical forces (as wind) carrying with them other organisms as loosely attached ones. Disturbance was

252 responsible to increase metaphytic life-form in Open succession. This group is low resistant and resilient, and is

253 benefited by presence of refuges (Schnek & Mello, 2011; 2012). Metaphytic life-form was dominate by loosely

254 attached Cyanobacteria related to (1) increases in temperature, once planktonic Cyanobacteria showed to be

255 sensitive and favored during winter warming (He et al., 2015) and (2) changes in wind direction, because this group

256　growed in epiphyton when wind came from NE-E direction, maybe dislocating pelagic community to littoral zone.

257　Moreover, Ferragut & Bicudo (2012) revealed that Cyanobacteria (*S. nidulans* and *P. galeata* as we found) are

258　favored by N addictions. We do not monitored grazers, however based in our observations on the field, snails

259　populations appeared after day 18. Attached community biomass is direct and indirect controlled by snails having a

260　negative effect on Chl a (Mahdy et al., 2015) as we observed on day 18. Filamentous algae have inferior food

261　quality being mechanically resistant to grazing (Roll et al., 2005). Thus an explanatory hypothesis is that grazers

262　could prefer the community with low densities of filaments, as in Open experiment. So, the epiphyton removal by

263　grazing could open space for settlement of cells, once biofilm need to be at a certain level of development for

264　planktonic algae be able to settle (Ács at al., 2007) and we do not registered the same response on Natural

265　community.

266　　　　Life-forms as adnate/prostrate and erect/mucilage stalks are primarily formed by diatoms tightly adhering

267　to the substrate (Peterson & Stevenson, 1992), and as for lotic environments (Schneck & Melo, 2012) were resistant

268　life-forms, persisting after disturbance (Stevenson, 1996). We do not observed statistical differences among tightly

269　attached life-forms before and after disturbance. As observed for riverine periphyton under constant disturbance,

270　algae showed to be supple to some disturbance levels (Ács & Kiss, 1993), in this case, wind velocity. Diversity also

271　responded to wind dynamics: higher diversity was registered under mean wind velocity (5 m s^{-1}), tending to follow

272　intermediate disturbance hypothesis (Connell 1978), and reduced with higher wind velocity. However our data do

273　not agreed completely with the theory once low diversities were also registered during lower winds.

274　　　　Enclosure buffered wind action acting as a barrier for substrata colonization, once early successional phase

275　was longer in the mesocosm. The early phase that was characterized by settlement and reproduction of ruderal

276　species (McCormink & Stevenson, 1991) predominate until day 18 of succession which are commonly reported in

277　tropical reservoirs during early colonization (Ferragut & Bicudo, 2012; Rodrigues dos Santos & Ferragut, 2013). We

278　believe that this early phase may last more if lake water hadn't invaded the enclosure. The number of algae settling

279　on the substratum is increased by immigration and reproduction, and decreased by emigration, mortality and grazing

280　(Ács et al., 2007) and in our study, also by wind. Ács et al. (2007) in mesocosm experiment revealed that the

281　settlement of cells and the "undulation" between planktonic and benthic algae during succession initial phase varied

282　depending on physic-chemical conditions of biofilm and alga life-forms strategies from adherence. The time of the

283 phases depended of the disturbance experienced (Szlauer-Łukaszewska, 2007) and here, waves in macrophyte banks

284 improved succession by settlement of cells, and absence of them delayed the process.

285   For Natural community and Open experiment macrophyte banks acts as a refuge for epiphyton protecting

286 them from recurrent wind action and providing habitat heterogeneity (Jeppesen et al., 1998). Maybe this continuous

287 perturbation can indeed be understood as a steady condition that resulted to steady-state community (Chorus &

288 Schlag, 1993). Nevertheless, community suffered with strong winds and with turbulence during changes in wind

289 direction both affecting community structure favoring different assemblages of tightly attached diatoms. Moreover,

290 water circulation promoted by intermediate wind provided propagules for recolonization after huge losses due high

291 wind velocity. On Enclosure, we observed a case of recruitment incited by disturbance (Fraterrigo et al., 2008).

292 Disturbances caused community heterogeneity once species diversity could be conserved by local immigration

293 (Naselli-Flores et al., 2003). Epiphyton in Mangueira Lake showed high capacity to recover increasing community

294 resilience (Lake, 2000) and species tended to return to pre-disturbance patterns of heterogeneity (Fraterrigo et al.,

295 2008).

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446   **Figure captions**

447   **Fig.1** Wind velocity (wind) and precipitation (prec) from ten days before the beginning of samplings (10d bs) and

448   during 30 days (d) of winter 2013 experiment. South winds are highlighted by the black lines with dominance of

449   WSW–S wind direction.

450   **Fig. 2** Ordination analysis of environmental data on the littoral zone during 30 days (d) of winter 2013 experiment.

451   For the legend, see Table 1.

452   **Fig. 3** Densities of principal algae groups in natural community (N), in the enclosure (E) and open (O) experiments

453   *versus* their community rate of change (rate) during days (d) of experiment, and ash free dry mass (AFDM),

454   Chlorophyll a (Chl a) and pheopigments (Pheo) (log x +1).

455   **Fig. 4** Wind velocity relations with diversities among the natural community (N), enclosure (E) and open (O)

456   experiments (d, days). The double black line represents the wind mean for the period (5 m s^{-1}).

457   **Fig. 5** Redundancy Analysis showing epiphyton succession during 30 days (d) in littoral zone of Mangueira Lake.

458   Principal species and life-forms are showed on natural, enclosure and open experiments answering to environmental

459   data. For the water variables legend, see Table 1. For species: *Acat* (*Achnanthidium catenata*), *Cocc* (*Cocconeis*

460   *placentula*), *Cpul* (*Ctenophora pulchella*), *Esox* (*Epithemia sorex*), *Etur* (*E. turgida*), *Gom1*(*Gomphonema*

461   *capitatum*), *Gom5* (*G. parvulum*), *Gom6* (*Gomphonema* sp), *Nit1* (*Nitzschia palea*), *Nav3* (*Navicula* complex), *Sta2*

462 (*Staurosirella* complex), *Syni* (*Synechococcus nidulans*), *Mvar* (*Melosira varians*), *Moug* (*Mougeotia*), *Rhop*
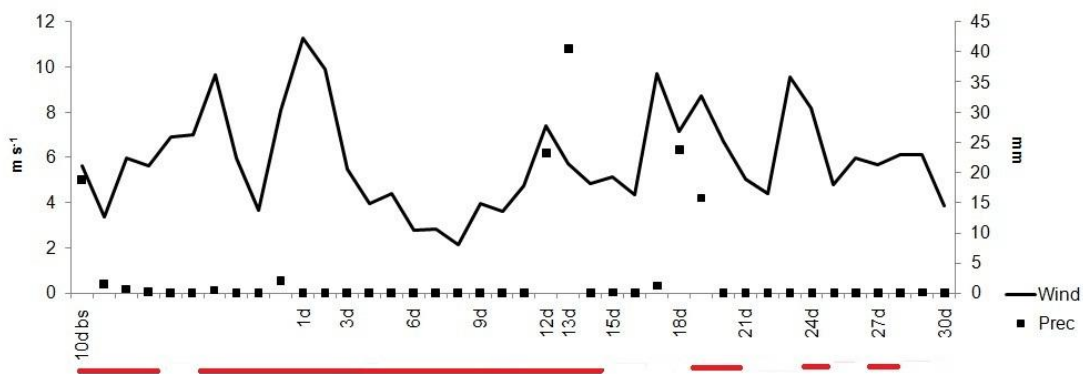
463 (*Rhopalodia gibba*), *Ulna* (*Ulnaria* complex).
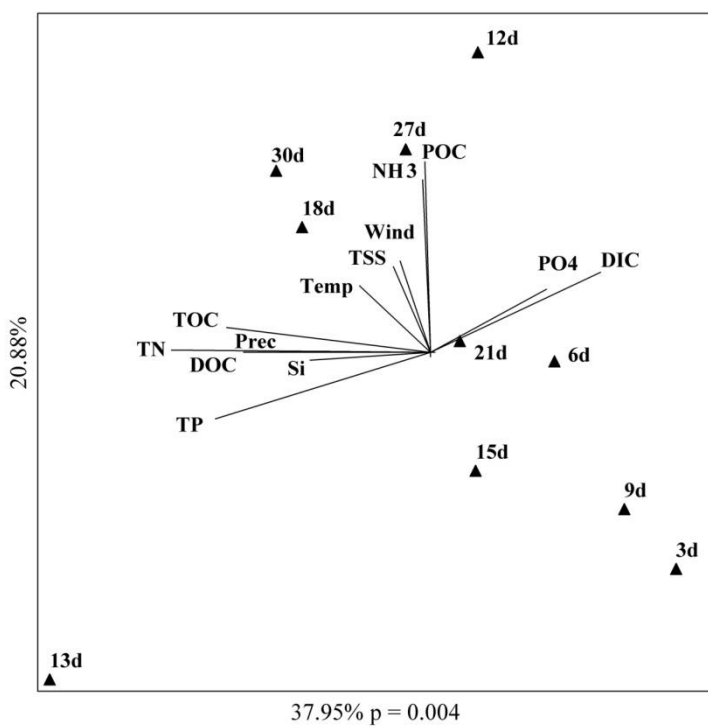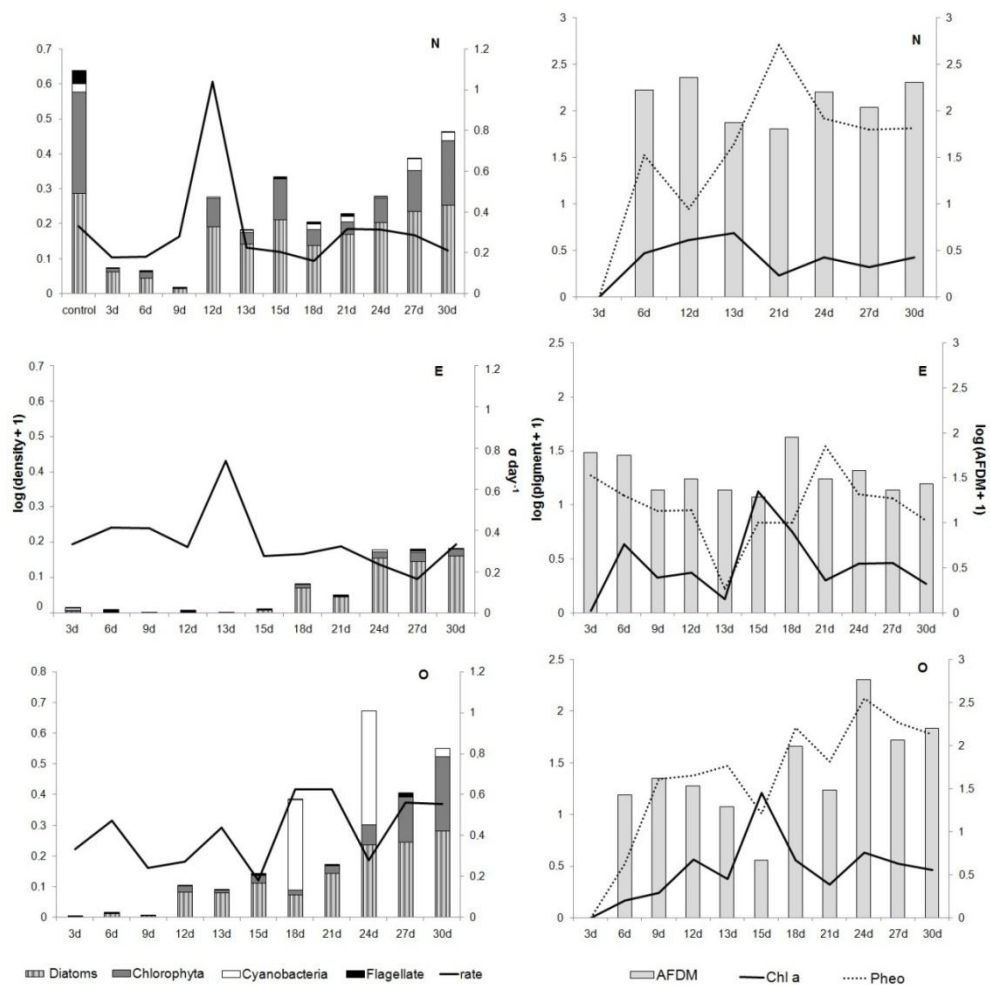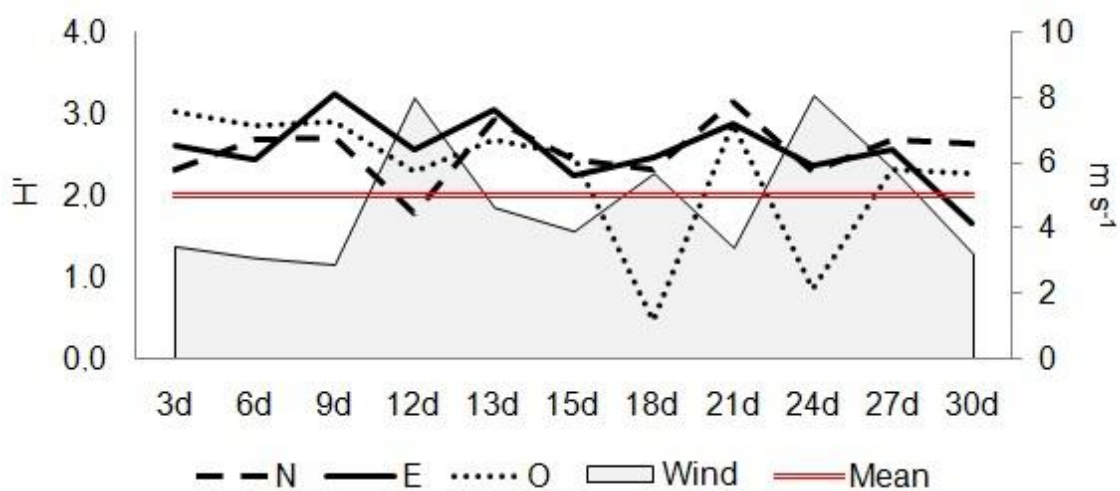
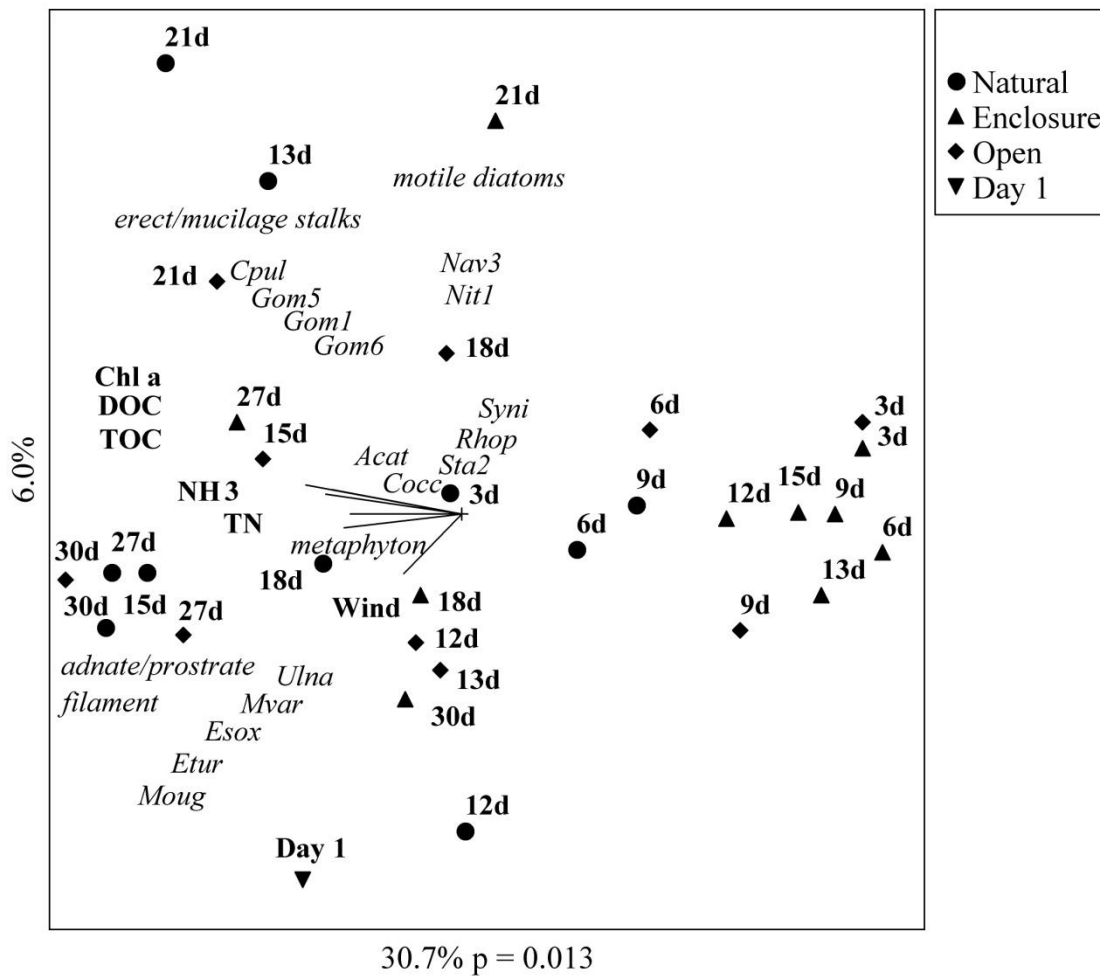Fig. 1

Fig.2

Fig. 3

Fig. 4

Fig.5

Table 1 – Environmental data (SD - standard deviation and CV - coefficient of variation) on the littoral zone during winter 2013 experiment (*data from Meteorological Station *[a] – amplitude of the data).

Variables	Code	Mean (±SD); CV%
Chlorophyll a (μg L^{-1})	Chla	5.2±2.6; 50%
Pheophytin (mg L^{-1})	Pheo	8.0±4.9; 62%
Ammonia (mg L^{-1})	NH3	0.09±0.07; 77%
Total nitrogen (mg L^{-1})	TN	0.51±0.15; 28%
Orthophosphate (mgL^{-1})	PO4	0.004±0.002; 49%
Total phosphorus (mg L^{-1})	TP	0.04±0.02; 48%
Silica (mg L^{-1})	Si	0.04±0.02; 52%
Total organic carbon (mg L^{-1})	TOC	8.45±1.89; 22%
Dissolved organic carbon (mg L^{-1})	DOC	6.91±1.81; 26%
Dissolved inorganic carbon (mg L^{-1})	DIC	12.59±4.73; 37%
Particulate organic carbon (mg L^{-1})	POC	1.54±0.68; 44%
Total suspended solids (mg L^{-1})	TSS	53.3±30.7; 57%
Temperature (^{o}C)	Temp	10.4±2.5; 24%
Conductivity (mS cm^{-1})	Cond	0.31±0.05; 1.8%
Dissolved oxygen (mg L^{-1})	DO	10.3±0.00; 0.2%
pH	pH	8.4±0.10; 1%
Wind (m s^{-1})*	Wind	4.9±1.9
Wind direction (º)*[a]	WindDir	146–258 (mainly SWS)
		78.5–281 (mainly NE-E)
Precipitation (mm)*	Prec	8.8±14.8

Table 2 – Means ± standard deviation (sd) of epiphyton attributes, principal algae classes and life forms and analysis of variance (followed by Tuckey HDS post-hoc) among the three experiments (AFDM – ash free dry mass, Chla – Chlorophyll a, TD – total density, H'- Shannon-Wienner diversity index, NS – No Significant).

Variable	Mean±sd			MS (df=2)	F	p	Pairwise comparison
	Natural (N)	Enclosure (E)	Open (O)				
AFDM (mg cm^{-2})	143.39±63.82	37.37±21.81	110.74±173.94	0.074	4.98	**0.015**	**E = N < O**
Chl a (mg cm^{-2})	1.99±1.11	2.60±3.46	3.16±4.31	0.012	0.17	0.842	NS
Richness	58±17	39±14	51±14	0.064	3.29	0.050	NS
H'	2.59±0.44	2.55±0.42	2.21±0.86	0.009	1.04	0.364	NS
TD (10^5 ind cm^2)	6.21±9.29	0.62±0.82	5.38±8.08	2.72	4.35	**0.021**	**N = O > E**
Diatoms (ind cm^{-2})	2.69±1.66	0.55±0.75	2.07±2.48	0.027	3.82	**0.033**	**N = O > E**
Chlorophyta (ind cm^{-2})	0.18±0.16	0.01±0.01	0.15±0.24	0.016	3.80	**0.033**	**N = O > E**
Cyanobacteria (ind cm^{-2})	0.07±0.08	0.01±0.01	3.03±7.02	0.012	2.06	0.144	NS NS
Flagellate algae (ind cm^{-2})	0.01±0.02	0.01±0.01	0.01±0.02	0.000	1.44	0.25	NS
Life forms				MS (df=2)	F	p	Pairwise comparison
Erect/mucilage stalks	5.88±5.66	2.49±3.25	4.30±4.53	1.836	2.86	0.072	NS
Adnate/prostrate	15.03±16.51	3.27±5.33	11.07±12.81	4.605	6.44	**0.004**	**N= O > E**
Motile diatoms	1.53±1.64	0.26±0.48	1.40±1.81	4.157	5.07	**0.012**	**N = O > E**
Filamentous	5.92±6.32	1.66±2.31	8.37±12.80	2.962	3.88	**0.031**	**N = O > E**
Metaphyton	1.15±1.16	0.30±0.32	25.46±64.45	1.44	2.226	0.125	NS

Considerações finais

Considero que as metas estabelecidas e que nortearam as hipóteses testadas nesta tese foram alcançadas, pois explicitaram a importância de conhecer a composição e a estrutura da comunidade de algas epifíticas na Lagoa Mangueira. Nesta pesquisa pioneira em lagoa costeira, os estudos apresentados evidenciaram que o epifíton é regido pela hidrodinâmica corroborando com os estudos realizados para as demais comunidades bióticas do sistema. Os distúrbios causados pelo vento atuaram diretamente na estruturação da comunidade, uma vez que as algas responderam à frequência e intensidade do distúrbio vastamente discutida na literatura, mas até então não aplicada para o sistema. O uso do mesocosmo mostrou através da ausência de distúrbio que o vento é o norteador para o desenvolvimento e estruturação das comunidades aderidas. O uso das formas de vida e também das guildas para as diatomáceas já nos sugeria esta hipótese, que conseguimos comprovar.

O epifíton também comprovou ser principal fornecedor de carbono para o sistema, regulando o controle *bottom-up* do zooplâncton. Este estudo confirma dados encontrados em estudo anterior realizado por pesquisadores do grupo, que mostraram através de isótopos estáveis a relação desta comunidade com a predação, uma vez que é uma comunidade rica nutricionalmente quando comparada, por exemplo, ao fitoplâncton da Lagoa Mangueira que é dominado por Cianobactérias.

Por fim, este estudo ainda abre portas para novas investigações, pois alguns dos resultados encontrados podem embasar e incentivar novas pesquisas quanto à autoecologia das espécies, teorias ecológicas de estados de equilíbrio, regulação *bottom-up* das algas e relações com a produtividade das macrófitas.