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The structuring role of submerged macrophytes in a large subtropical shallow lake: Clear effects on water chemistry and phytoplankton structure community along a vegetated-pelagic gradient

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A B S T R A C T

It is well known that submerged macrophytes exert positive feedback effects that enhance the water transparency, stabilizing the clear-water state in shallow temperate lakes. However, the structuring effect of macrophytes on the food web of subtropical and tropical ecosystems is still poorly understood. In this study we investigated the influence of dense submerged vegetation beds on the water chemistry and phytoplankton structure along a littoral-pelagic gradient of large subtropical shallow lake in southern Brazil. Seasonal monitoring was carried throughout one year following along a submerged vegetated-pelagic transect in order to analyze the effects of macrophyte's coverage (percentage of volume infested- PVI) on the water chemistry and phytoplankton community structure. Clear variations on nutrient concentration and phytoplankton biomass/composition could be observed permanently along the transect. Nutrients as orto-phosphate (PO_4^-) and bicarbonate increased linearly towards the pelagic zone, whereas dissolved organic carbon and humic substances decreased linearly as PVI decreased. Concomitantly, a significant increase in the phytoplankton biomass was observed outwards from the submerged vegetation bed. In the vegetated area, small species (C-R strategists), unicellular flagellates were selected; whereas in the pelagic zone, larger (K-selected) species of cyanobacteria occurred, especially representatives of the functional groups **M**, $\mathbf{L_O}$, **SN**, **S1** and **K**. Such results indicate that the macrophytes and inherent metabolism, such as potential excretion of dissolved organic compounds with allelochemicals and nutrient uptake from water column influence the structure of the phytoplankton community reducing also significantly the biomass of cyanobacteria within the dense submerged vegetated zone. Because of the continuous growth of macrophytes over the year in low latitude systems, their feed-back effect pattern tends to also dictate a different role in ecosystem dynamics and structure of the food web. These findings contribute to the management and conservation of subtropical and tropical lakes.

1. Introduction

Submerged macrophyte communities promote physical and chemical changes in shallow freshwater ecosystems (Wetzel, 1992). The formation of densely-packed submerged stands depends on the underwater light regime (Moss, 1990; Scheffer et al., 1993) and hydrodynamics (Barko and James, 1998). By their structuring effect, the macrophytes create an environment that is different from that of the open water and that potentially may have different impact on water quality and interactions between different trophic levels, especially on phytoplankton (Søndergaard and Moss, 1998).

Once a submerged vegetation stand is established, water transparency is enhanced through several positive feed-back mechanisms which, in turn, stimulate plant's growth (Van Nes et al., 2003). In temperate freshwaters, the mechanisms of macrophytes proposed to stabilize the clear state are: protection for the grazers on the algae as larged-bodied zooplankton (Jeppesen et al., 1997), attenuation of water currents and stabilization of sediments (James and Barko, 1990), support of epiphyton that sequesters nutrients (Burkholder and Wetzel, 1990), reduction of inorganic macronutrients by uptake from the water

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column, and through production of allelopathic compounds (Gross et al., 1996). Although, the confirmation of allelopathy is still speculative at the ecosystem level (Hilt et al., 2006; Lurling et al., 2006), submerged plants are known to prevent excessive phytoplankton growth (Blindow et al., 1993; Van den Berg et al., 1998) causing the clear state to be self-stabilizing (Moss, 1990; Sheffer et al., 2001; Van Nes et al., 2003). Although many of these processes have been well investigated in temperate ecosystems, the dynamics of macrophytes in subtropical and tropical lakes is still poorly known.

Despite the little knowledge we have on subtropical systems, marked differences were already found about interactions and natural regulating mechanisms which structure the higher complexity of tropical and subtropical ecosystems (Jeppesen et al., 2005). A major contrast is that macrophytes grow continuously throughout the year, differently from the seasonal die-off process observed in temperate ecosystems (Finkler Ferreira et al., 2008). Therefore, their effects on the environment are permanent and consequently this may enhance the resistance of the clear water state against the phytoplankton domination (Finkler Ferreira et al., 2008). Moreover, because of the higher diversity of plant and animal species and dominance of fish omnivory, the trophic interactions that structure the phytoplankton community proceed in different ways (Meerhoff et al., 2006) that still need to be elucidated both *in situ* and experimentally.

In complex systems comprised of shallow lakes, adjacent wetlands are known to influence function and nutrient economy of littoral and pelagic waters (James and Barko, 1991). The high productivity of emergent macrophytes, at the interface, contributes with large amounts of soluble organic matter that can be transported to open areas and affect major changes into the pelagic metabolism (Jones, 1990; Wetzel, 1992). The decomposition and metabolism of both emergent and submerged macrophytes, within littoral zones, generate recalcitrant organic compounds that complex chemically with many enzymes produced by phytoplankton and bacteria (Stewart and Wetzel, 1982b). Therefore, it is expected that lake-wetland systems with dense macrophyte coverage would have stronger effect on the dynamics and structure of phytoplankton community along the gradient of macrophyte domination (Søndergaard and Moss, 1998). These interactions become more intrinsic in shallow systems influenced by intense wind driven hydrodynamic regimes, which end up dictating spatial heterogenity of biotic components (Cardoso and Motta Marques, 2009; Fragoso et al., 2008).

Few studies have focused on phytoplankton in relation to the presence of submerged macrophytes along a littoral-pelagic gradient. Moreover, the influence of humic compounds produced in adjacent wetlands on phytoplankton production is poorly documented (Wetzel, 1992). Considering these gaps, the aiming of this work was to evaluate the effects of a densely submerged macrophyte bed on the water quality and phytoplankton community structure along a littoral macrophyte dominated-pelagic gradient in a large shallow lake-wetland ecosystem, in southern Brazil. In this work, we show the role of subtropical submerged macrophytes over the nutrient pool and structuring effects on phytoplankton, indicating traces of the antagonistic relationship with cyanobacteria.

2. Material and methods

2.1. Study site

The study was carried out in the large shallow lake Mangueira (max. depth 6m). It is situated along the Atlantic Ocean, southern Brazil (33°31′22″S 53°07′48″W) (Fig. 1), with 90 km in length and 3–10 km in width. This ecosystem originates from the last glaciation event on the southeast coast of South America (during the Pleistocene ~5000 years ago). Due to the last ocean regression, large amounts of bicarbonate were burried by the sand, but remain in the system. Turbulence from constant winds ensures a high concentration of dissolved oxygen in the water column. These factors lead to high redox conditions in the water and a neutral pH. Despite its proximity to the Atlantic Ocean (≅3 km), salt sprays do not enhance the low salinity of the lake.

Along the lake's shoreline, there is a continuous formation of several sand benches due to intense hydrodynamics. Such areas are colonized by dense belts of emergent macrophytes, as *Zizaniopsis banariensis,* the dominant species (Finkler Ferreira, 2009), that reduce water currents, allowing the establishment of submerged macrophyte communities. Generally, the emergent belts create shallow ponds (5–300 ha) that are connected to the lake through narrow canals. Within the belts, the ponds are colonized by several submerged plants up to 2 m depth. Together, they form densely packed submerged communities with high biomass in areas with lower water velocity ($< 1\ m\,s^{-1}$).

At its northeast and southwest edges, the lake is hydrologically linked to two large wetlands. Together, they constitute a synergetic system driven by intense winds (SW-NE) that carry large amounts of organic matter, generated by the decomposition of macrophytes, from the wetlands into the lake. The inflow of humic substances turns the water darker in the areas near the wetlands.

The region climate is classified as subtropical humid, without wet or dry season; the rainfall is well distributed along the year.

2.2. Sampling along the macrophyte-pelagic gradient

In order to asses the effect of the submerged macrophytes on the water quality and phytoplankton community structure, sampling was undertaken along a transect, near the surface of water column (~15 cm), ranging from a submerged, densely vegetated littoral to an unvegetated pelagic zone, in the southern part of the lake Mangueira. At the vegetated area, the margin was covered by emergent macrophytes being surrounded by a large belt of wetland. The transect had approximately 3220 m, comprising eight sampling points (Fig. 2). The distribution of the points was not regular, but arbitrarily chosen to cover the heterogeneity of the habitats along the macrophyte-pelagic gradient.

Samplings were carried out seasonally. In total, five campaigns were conducted from May 2007 until March 2008. Water samples were collected near the surface of water column (~15 cm) for nutrients, phytoplankton and zooplankton evaluation in laboratory. All water samples were storage in a box with ice to preserve the natural features and after the sampling, in a period less than 24 h, all of them were transported to laboratory to perform analysis. Concomitantly the samplings, analysis of the submerged macrophytes community and immediate measures of limnological variables were taken in field.

2.3. Submerged macrophyte sampling

The abundance of submerged macrophytes was estimated as the percentage of volume infested (PVI) under water (Canfield et al., 1984). PVI was calculated by the following equation 1:

$$PVI\ (\%) = \frac{MacC\ \times MacL}{D} \tag{1}$$

Where, *MacC* is the macrophyte coverage (%) of each species, *MacL* is the macrophyte length (m) and *D* is the depth (m). The coverage of each species was estimated visually as the percentage covered by each species within plots of $9\ m^2$.

2.4. Limnological variables

In the field, dissolved oxygen concentration/saturation, pH, temperature, Oxi-Redox potential and salinity were taken with a multiprobe (YSI-6600, Yellow Springs, Ltd.). Yellow substances were estimated using a submergible espectrofluometer (BBE-Moldaenke). The vertical downward attenuation coefficient of light (K_d) was measured using a photosynthesis active radiation sensor (LICOR). The