

Hydrology-Driven Regime Shifts in a Shallow Tropical Lake

Simoni Maria Loverde-Oliveira,^{1*} Vera Lúcia Moraes Huszar,² Nestor Mazzeo,³ and Marten Scheffer⁴

¹Depto. Ciências Biológicas, Universidade Federal do Mato Grosso, Rondonópolis, MT 78000-000, Brazil; ²Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ 20940-040, Brazil; ³Depto. de Ecología, Laboratorio de Ecología y Rehabilitación de Ecosistemas Acuáticos, Universidad de la República, Montevideo, Uruguay; ⁴Department of Aquatic Ecology and Water Quality Management, Agricultural University, Wageningen, The Netherlands

ABSTRACT

Shifts between alternative stable states have become a focus of research in temperate shallow lakes. Here we show that sharp transitions between a clear, macrophyte-dominated state and a turbid state without submerged plants can also occur in tropical floodplain lakes, albeit driven by a largely different set of mechanisms. We show how a shallow lake in the Pantanal becomes covered by an exploding population of the submerged macrophyte *Egeria najas* Planchon as the water level rises during the annual high-water period. Water clarity increases spectacularly in this period due to flushing with river water that has lost most of its suspended matter during its slow flow over the flooded vegetated plains. A few months later when the water level drops again, the submerged plant beds die and decompose rapidly, triggering a phase of increasing turbidity. During this period an increase in dissolved organic matter, suspended

matter, and phytoplankton biomass results in a sharp deterioration in water clarity. The concomitant water level decrease largely counteracts the effects on the underwater light climate, so that the amount of light at the bottom may not differ in comparison with the high-water period. Therefore, changes in light climate seem unlikely to be the sole driver of the vegetation shifts, and other mechanisms may prevent recovery of the submerged vegetation until the next high-water episode. Also, contrary to what is found in temperate lakes, there is no evidence for top-down control of phytoplankton biomass associated with the macrophyte-dominated state in our tropical lake.

Key words: alternative states; shallow lake; *Egeria najas*; phytoplankton; macrophytes; pantanal; freshwater wetlands.

INTRODUCTION

Temperate shallow lakes are among the best-understood examples of ecosystems with alterna-

tive states (Scheffer and Carpenter 2003). At intermediate nutrient loadings, such systems may be dominated either by phytoplankton or by submerged macrophytes. Much work has focused on the mechanisms that explain the stability of both states (Scheffer and van Nes 2007). More recently, there has been an increase in studies focusing on mechanisms that may tip lakes from one state to the other (Scheffer and Jeppesen 2007). A shift from the clear, macrophyte-dominated state, to the turbid state dominated by phytoplankton in such

Received 5 November 2008; accepted 30 April 2009;
published online 26 June 2009

Author Contributions: Simoni Maria Loverde-Oliveira, Vera Lúcia Moraes Huszar—conceived the study, Simoni Maria Loverde-Oliveira—performed research and analyzed data, Simoni Maria Loverde-Oliveira, Vera Lúcia Moraes Huszar, Nestor Mazzeo, Marten Scheffer—wrote the paper.

*Corresponding author; e-mail: loverde@terra.com.br

lakes is often related to an increase in nutrient load (Moss and others 1996; Scheffer 1998). However, lakes have also been shown to shift from clear to turbid as a result of heavy storms uprooting plants (McKinnon and Mitchell 1994; Schelske and others 1995), increasing salinity releasing phytoplankton from top-down control by cladocerans (Jeppesen and others 2007b), water level fluctuations (Wallsten and Forsgren 1989; Blindow and others 1993; Beklioglu and others 2007), natural or human-induced fish kills (Scheffer 1998), or a combination of several factors (Hargeby and others 2004). Finally, some lakes show recurrent shifts between a clear and a turbid state in an almost periodic multi-year pattern that appears to be driven by a combination of internal processes and forcing by weather-related cycles in nutrient load (Perrow and others 1994; Hargeby and others 2004; Rip and others 2005).

It has become clear over the past years that some of the key mechanisms that regulate the stability of temperate lakes do not operate the same way in the tropics. For instance, in contrast to what is observed in vegetated temperate lakes, top-down control of phytoplankton appears to be unimportant in tropical and subtropical lakes (Jeppesen and others 2007a; Meerhoff and others 2007; Teixeira-de-Mello and others 2009). Nonetheless, it has been observed that, just as their temperate counterparts, tropical and subtropical lakes or reservoirs may shift between a submerged macrophyte-dominated state and a contrasting turbid state without macrophytes (Adler 2002; Bini and Thomaz 2005).

An annual flood pulse has a major impact on tropical and subtropical (Junk and others 1989; Neiff 1990; Carignan and Neiff 1992; Junk 2005; Wantzen and others 2008), as well as, temperate floodplain lakes (Van Geest and others 2005; Van Geest and others 2007; Roozen and others 2008; Wantzen and others 2008). The impact of the flood pulse in the Pantanal depends on the distance and degree of connectivity to the main river (Fantin-Cruz and others 2008). This results in at least three different types of lakes (Loverde-Oliveira 1999, 2005): (i) lakes permanently connected and located close to the main river, which never reach a clear state, independently of the hydrological phase; (ii) lakes fed by tributaries of different water quality resulting in a spatial pattern of clear and turbid states in the same system; and (iii) lakes that are located far away from the main river and are isolated much of the year. Anecdotal evidence suggests that the last group can alternate between clear to turbid states.

Here we report on a detailed study of the dynamics of an example of such a switching lake in the Pantanal floodplain. In contrast to what is observed in many temperate lakes, this lake shifts to a clear, vegetated state, during periods of high-water levels. We attempt to infer the driving mechanisms from our time series, and discuss how this type of lake appears to differ from the well-studied lakes at higher latitudes.

METHODS

The Ecosystem

The Pantanal in the state of Mato Grosso in central Brazil is an extensive flooded area of about 140,000 km², where the hydraulic gradient varies from 0.7 to 6.5 cm km⁻¹ (Ponce 1995). In 2000, the Pantanal was recognized by UNESCO as a World Biosphere Reserve (www.mma.gov.br). The area contains large numbers of shallow lakes with a seasonal (recurring) water-level fluctuation. The complex hydrography of the region, together with the geomorphologic and edaphic heterogeneity, shapes a patchwork of landscapes with different hydrologic conditions. The annual flood pulse results in an extensive area covered by 0.4–1.0 m of water, depending on the proximity to the main river or associated stream. The regional climate is warm and humid (Köppen AW), with a total annual precipitation ranging from 800 to 1,600 mm and a mean annual temperature of 27°C (PCBAP 1997). A summary of ecological characterization of the Pantanal wetland is found in Junk and others (2006).

The shallow lake considered, Coqueiro Lake, is located in Pantanal de Poconé (16°15'12"S; 56°22'12"W, Figure 1) in a little-populated area with extensive cattle ranching. During the high-water period, the lake is connected to the main river of the drainage basin (Cuiabá River) through natural connection channels, known locally as *corixos*, bordered by riparian vegetation. Coqueiro Lake is an elongated (total area: 2.2 km²) and shallow (maximum depth: 2.3 m) ecosystem (Loverde-Oliveira and others 2007). It is continuously warm polymictic, as well as eutrophic if the annual mean concentrations of chlorophyll-*a* (22 µg l⁻¹) and total phosphorus (230 µg l⁻¹) are considered, but mesotrophic as regards the annual means of total nitrogen (481 µg l⁻¹) (Loverde-Oliveira 2005), taking into account the classifications for temperate (Vollenweider and Kerekes 1980; Nürnberg 1996) and tropical (Salas and Martino 1991) regions.

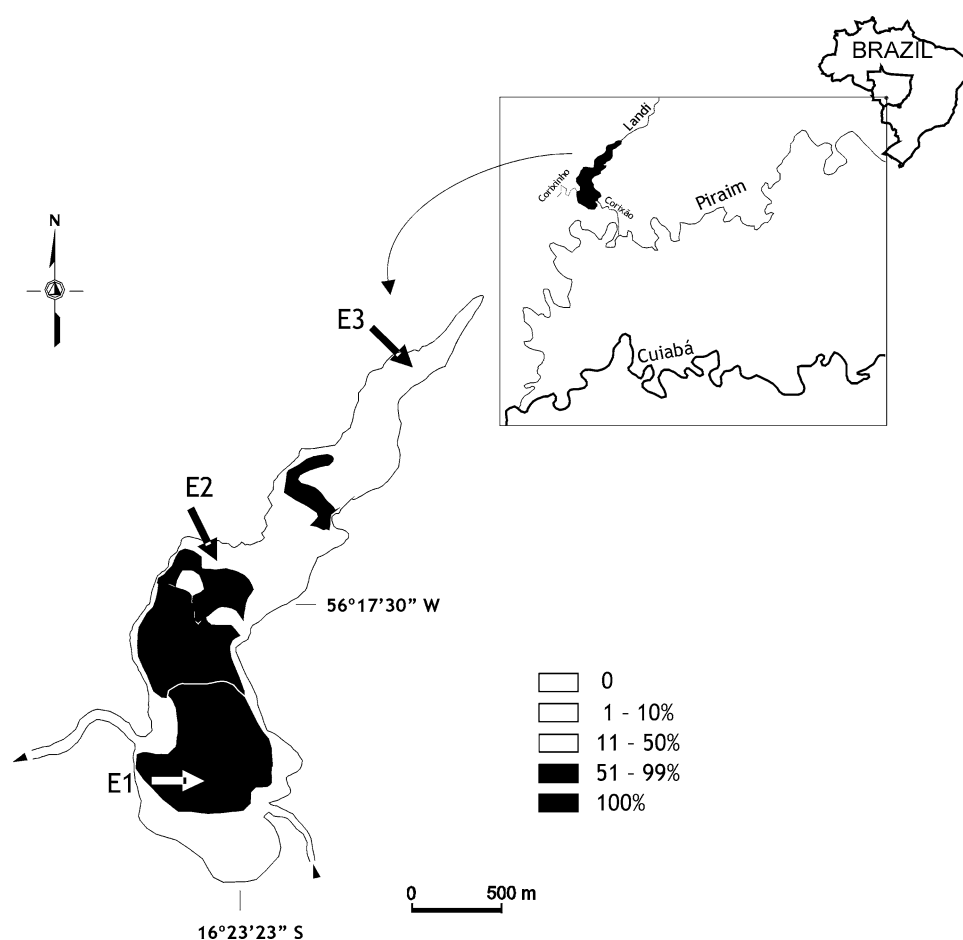


Figure 1. Map and location of Coqueiro Lake and sampling stations E1, E2, and E3. Schematic representation of the spatial distribution of *Egeria najas* (PVI percentage of volume infested) in the period of high abundance during high-water level (30 April 2003).

During the period of high water, the populations of floating (*Salvinia*, *Pistia*, *Nymphaea*) and emergent aquatic plants (*Sagittaria*, *Echinodorus*, among others) increase. In the littoral areas, *Eichhornia azurea* Kunth and *E. crassipes* (Martius) Solms predominate. Sometimes, the last species, together with other macrophytes, become detached from the littoral region and generate floating islands, locally known as *camalotes*. In an earlier study the cover of *E. azurea* in Coqueiro Lake has been observed to expand in the period of rising water level, and retract during the falling period (Silva 2002). Also, interviews with residents suggest that dominance by submerged macrophytes is a recurrent feature of the lake in the annual period when the water level rises (Loverde-Oliveira 2005).

The high diversity of fish in the near-shore environments of Coqueiro Lake is comparable to other systems in the region subject to flooding (Melo, unpublished data). The fish of the Pantanal show a wide range of food preferences, and range from being strict predators (*Roeboides prognathus*

Boulenger) to generalist herbivores (*Metynnus mola* Eigenmann et Kennedy) (Machado 2003).

Sampling

The study was carried out monthly from April 2002 to May 2003, at three collection sites (Figure 1). For the physical and chemical water analysis and phytoplankton structure, samples were collected at the subsurface (using flasks) and near the bottom of the lake (using a Van Dorn bottle). To analyze the zooplankton structure, 100 l of water were collected at the subsurface and 100 l at the bottom of the water column, using a manual suction pump. The water was filtered through a 68- μ m net, and the zooplankton were preserved in 4% formaldehyde.

The percentage of volume infested (PVI) with the submerged macrophytes in the lake was estimated monthly, on average, at 110 points, along 14 transverse transects arranged in a zigzag manner along the longitudinal axis of the lake, as the product of the percentage of cover (estimated

visually) and the height of the plants divided by the depth of the water column (Canfield and others 1984).

Sample Analysis

The profiles of water temperature (T), electrical conductivity ($\mu\text{S cm}^{-1}$), pH, and dissolved oxygen (DO) were determined using a Mettler Toledo meter. Alkalinity was determined according to Golterman and others (1978) and Mackereth and others (1978), and CO_2 based on Carmouze (1994). Turbidity was measured using a Hach 2100P portable turbidimeter, color through direct reading (Nessler Quanti 200), and total suspended solids (TSS) according to Teixeira and others (1965). The water transparency was measured as the depth of extinction of the Secchi disk (SD). Total nitrogen (TN) and total phosphorus (TP), ammonium (N-NH_4^+), nitrate (N-NO_3^-), soluble reactive phosphorus (SRP), and soluble reactive silica (SRSi) were analyzed based on Golterman and others (1978). Chlorophyll- a (Chl) was estimated using the Nusch and Palme (1975) method (extraction in warm ethanol).

The phytoplankton populations were enumerated in random fields (Uhelinger 1964), by the sedimentation method (Utermöhl 1958). The units (cells, colonies, and filaments) were enumerated, at least to 100 specimens of the most frequent species ($P < 0.05$, Lund and others 1958). Specific biovolume ($\text{mm}^3 \text{l}^{-1}$) was estimated from the product of the population and mean unit volume of each species (Edler 1979). In general, mean cell size was based on measurements of at least 30 cells. The quantification of the zooplankton (ind l^{-1}) at a major-group level was carried out in a Sedgwick-Rafter chamber.

Data Analysis

Small filter-feeders (rotifers and copepod nauplii), medium-sized filter-feeders (calanoid copepods and cladocerans), and omnivorous–carnivorous (cyclopoid copepods) were lumped as functional groups of the zooplankton.

Two approaches were used to estimate the contribution of the phytoplankton and the non-phytoplankton material to the coefficient of the total extinction of light. The first approach took into consideration the coefficients of extinction for the phytoplankton and the inorganic turbidity of the water and color, calculated from the SD as $K_{\text{total}} = -1 \times \ln(\text{SD}_{\text{light}})$, with SD_{light} being the fraction of the penetration of the light from the

surface at the SD depth, generally reported as 0.1 (10%, Wetzel and Likens 1991). The total extinction of light (K_{total}) is the sum of the extinction of light by the phytoplankton (K_{phyt}) itself, the colored organic matter and the inorganic turbidity (K_{residual} , K_{res}). K_{phyt} was calculated as $\text{EP} \times \text{chlorophyll-}a$, where EP is the specific extinction by the biomass ($\text{m}^2 \text{mg chl}^{-1}$) of the phytoplankton, which generally ranges between 0.01 and 0.02 for different species of phytoplankton (McBride and others 1993). The value $0.016 \text{ m}^2 \text{mg chl}^{-1}$ was used in this study. The second approach estimated the contribution of the fractions of the phytoplankton (in terms of chlorophyll- a), detritus, and suspended inorganic solids to the total extinction of light, based on regression analysis according to Scheffer (1998). Ten samples of subsurface water were collected along a longitudinal transect of the lake in the turbid-water phase (absence of submerged macrophytes) (5 October 2003). The concentrations of inorganic suspended solids (ISS; mg l^{-1}) were calculated as the difference between the concentrations of total suspended solids (TSS; mg l^{-1}) and the suspended organic matter (SOM; mg l^{-1}). The concentrations of detritus were estimated as the difference between SOM and the dry weight of chlorophyll- a (mg l^{-1} ; APHA 1992). The concentrations of the algal biomass were estimated assuming the dry weight/chlorophyll- a ratio to be 70 (Scheffer 1998). The total extinction of light, estimated as the inverse of the Secchi disk ($1/\text{SD}$), is the sum of the extinction of light by chlorophyll- a (Chl), detritus (Det), and inorganic suspended solids (ISS) ($1/\text{SD} = \sigma_{\text{C}} \text{Chl} + \sigma_{\text{D}} \text{Det} + \sigma_{\text{I}} \text{ISS} + \sigma_{\text{O}}$; Scheffer 1998). Finally, the shade index was evaluated as K_{d} times mean depth (Scheffer 1998).

The temporal differences were tested using analysis of variance with repeated measures (ANOVAmr). The data considered were the means from the water column of each sampling station. To simplify the results analysis, the temporal series was organized in periods of 2 months as follows: H1, L1, L2, L3, L4, H2, and H3. H and L mean high and low-water level periods, respectively. *Egeria najas* occurred at H1, H2, and H3. To determine the role of *E. najas* coverage in the temporal changes, the water level was considered as a co-variable in the ANOVAmr test. The post hoc differences were tested by Tukey honest significant differences (HSD). Results were considered significant at $P < 0.05$. Finally, the relationships among biological, physical, and chemical attributes were analyzed by non-parametric correlations (Spearman, r_s), considering the data from each collection site or the mean per month.

RESULTS

Temporal Distribution of Plant Beds

The occurrence of *E. najas* (Figure 2A) was first recorded in the period of falling water level (April 2002), when the PVI varied between 27% and 35%. The covered area decreased until its total disappearance in June 2002, when *E. najas* began to decompose. The occurrence of young specimens of *Egeria* (2–5 cm) was recorded again from February 2003 (high-water level), and the beds were observed beginning in March (3–5%). The highest PVI (37%) occurred in April 2003. At the beginning of the second period of falling water level (May 2003), the *Egeria* beds decreased (1.4–3.5%) again (Figure 2A).

Physical and Chemical Water Features

The waters of Coqueiro Lake are, on average, slightly acidic, with a low alkaline reserve and high total phosphorus concentration (Table 1). The phase without *Egeria*, compared to the phase with *Egeria*, was characterized by shallower depths and lower water transparency (Figure 2A, B), more colored and turbid waters (Figure 2C), and higher concentrations of suspended matter (Table 1).

The shade index showed a complex temporal pattern (Figure 2B), with similar level in several months of the periods with and without *Egeria* (or high- and low-water periods), no significant differences were detected in the ANOVAmr test. Transparency (Secchi depth) was significantly correlated to turbidity, water color, and phytoplankton biomass (Table 2). The two approaches used to estimate the contribution of the different components to light extinction indicated that the most important factor was the non-phytoplankton fraction (84% in the first approach and 96% in the second). In the first approach, the estimated total coefficient of light extinction was 2.201 m^{-1} (mean value), and the coefficient of extinction attributable to phytoplankton was 0.345 m^{-1} . When the total light extinction was calculated by the inverse of the Secchi disk (second approach), the estimated chlorophyll-*a* contribution was only about 5% of the light extinction (Figure 3).

In the middle of the period without *Egeria*, the alkaline reserve was lower, but higher concentrations of TP and SRP (Table 1) were found. Also, a higher DIN/SRP ratio occurred during the months with higher *Egeria*'s PVI. In May 2002 (coinciding with the beginning of *Egeria* decomposition), a fivefold increase in total nitrogen was observed, followed by increases in nitrate and ammonium.

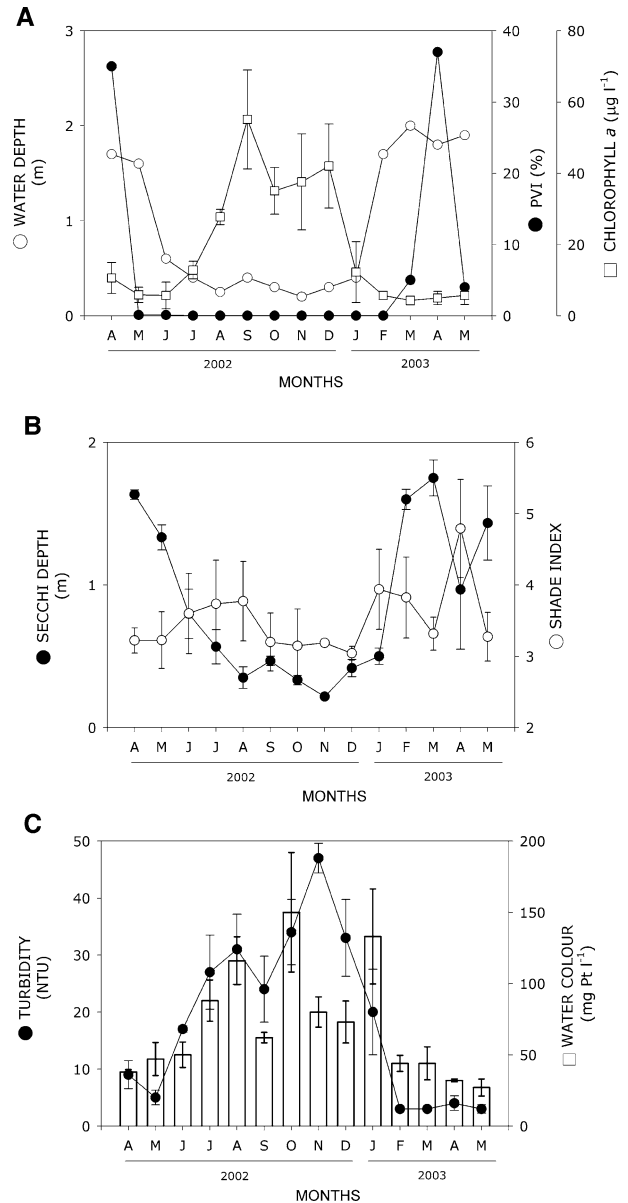


Figure 2. Temporal patterns of water depth, phytoplankton biomass (chlorophyll-*a*), and PVI (percentage of volume infested) of *Egeria najas* (A); water transparency (Secchi disk depth) and shade index (B); turbidity and water color (C). All graphs include the mean values of sampling stations and water column, and the standard errors.

Plankton Communities

The algal biomass, expressed as chlorophyll-*a*, was significantly higher in the phase without *E. najas* than in the period with plants reaching a maximum in September ($60 \mu\text{g l}^{-1}$; Figure 2A; Table 1). The phytoplankton biovolume was similar during the phases with and without *E. najas*, but composition differed somewhat. The

Table 1. Average and Standard Error of the Limnological Variables in the Periods With *Egeria najas* (April to June 2002 and March to May 2003) and Without *Egeria najas* (July 2002 to February 2003) in Coqueiro Lake

| Variables | With <i>Egeria</i> clear waters (n: 36) | Without <i>Egeria</i> turbid waters (n: 48) | Statistical differences $F_{(6,12)}$ | Post hoc comparisons | | | | | | | |
|---|---|---|--|----------------------|----|----|----|----|----|----|----|
| | | | | H1 | L1 | L2 | L3 | L4 | H2 | H3 | |
| Temperature (°C) | 26.8 ± 0.4 | 28.6 ± 0.2 | 34.4, $P < 0.001$ | C | A | C | C | C | C | C | B |
| Conductivity ($\mu\text{S cm}^{-1}$) | 29.9 ± 1.6 | 24.3 ± 0.9 | NS | | | | | | | | |
| Alkalinity ($\text{mgCaCO}_3 \text{ l}^{-1}$) | 16.7 ± 0.9 | 9.8 ± 0.4 | 3.7, $P < 0.05$ | B | B | B | A | B | B | B | B |
| pH | 5.8 ± 0.1 | 5.9 ± 0.1 | 6.2, $P < 0.01$ | AB | A | B | B | AB | A | A | A |
| Dissolved oxygen (%) | 33.0 ± 2.7 | 34.3 ± 2.2 | 57.8, $P < 0.001$ | A | A | A | B | B | B | B | B |
| Water color (mg l Pt^{-1}) | 48.1 ± 3.0 | 95.8 ± 6.4 | 4.9, $P < 0.01$ | A | A | B | B | B | A | A | A |
| Turbidity (NTU) | 13.6 ± 2.2 | 33.8 ± 3.1 | 12.7, $P < 0.001$ | A | AB | B | B | AB | A | A | A |
| Suspended matter (mg l^{-1}) | 29.0 ± 6.2 | 51.4 ± 8.6 | NS | | | | | | | | |
| Euphotic zone (m) | 1.7 ± 0.04 | 1.2 ± 0.07 | 42.0 $P < 0.001$ | C | B | AB | A | AB | C | C | C |
| TP ($\mu\text{g l}^{-1}$) | 180 ± 12.5 | 278 ± 26.8 | 3.61, $P < 0.05$ | A | AB | B | B | B | AB | AB | AB |
| SRP ($\mu\text{g l}^{-1}$) | 15 ± 2.2 | 56 ± 9.9 | 3.0, $P < 0.05$ | A | AB | AB | B | AB | A | A | A |
| TN ($\mu\text{g l}^{-1}$) | 442 ± 61.2 | 519 ± 32.0 | 54.8, $P < 0.001$ | C | B | B | C | BC | A | A | A |
| N-NO ₃ ⁻ ($\mu\text{g l}^{-1}$) | 39 ± 3.1 | 49 ± 6.2 | 3.8, $P < 0.05$ | A | B | A | A | A | A | A | A |
| N-NH ₄ ⁺ ($\mu\text{g l}^{-1}$) | 47 ± 3.9 | 92 ± 12.4 | NS | | | | | | | | |
| SRSi ($\mu\text{g l}^{-1}$) | 252 ± 30.5 | 128 ± 22.3 | 46.7, $P < 0.001$ | C | C | B | A | A | A | A | A |
| CO ₂ ($\mu\text{M l}^{-1}$) | 41 ± 4.6 | 30 ± 4.7 | 5.9, $P < 0.01$ | A | A | A | A | A | B | B | B |
| Chlorophyll- $(\mu\text{g l}^{-1})$ | 11.5 ± 2.2 | 31.5 ± 3.2 | 13.3, $P < 0.001$ | A | A | B | B | B | A | A | A |
| TN:TP (molar base) | 8.4 ± 1.8 | 5.9 ± 0.6 | 37.3, $P < 0.001$ | C | B | AB | AB | AB | A | A | A |
| DIN:SRP (molar base) | 40.8 ± 10.2 | 14.3 ± 1.9 | 6.1, $P < 0.01$ | B | A | A | A | A | B | A | A |

The variance analyses include ANOVA_{mr} considering the water level as co-variable. *Egeria najas* occurred at H1, H2, and H3. H high-water level; L low-water level; NS non-significant differences. Same capital letters indicate groups with significantly similar mean values (TP total phosphorus, SRP soluble reactive phosphorus, TN total nitrogen, DIN dissolved inorganic nitrogen).

Table 2. Spearman Non-Parametric Rank-Order Test Results (rs) and Their Significance (P)

| Variables | rs | P | n |
|--|-------|--------|----|
| Water transparency vs turbidity | -0.80 | <0.001 | 41 |
| Water transparency vs water color | -0.77 | <0.001 | 41 |
| Water transparency vs phytoplankton biomass | -0.62 | <0.001 | 41 |
| Water transparency vs water level | -0.92 | <0.001 | 14 |
| PVI of <i>Egeria najas</i> vs water level | 0.64 | <0.01 | 14 |
| Phytoplankton biomass vs water level | -0.83 | <0.001 | 14 |
| PVI of <i>Egeria najas</i> vs phytoplankton biomass | -0.57 | <0.05 | 14 |
| Phytoplankton biomass vs N-NH ₄ ⁺ | 0.69 | <0.01 | 14 |
| Phytoplankton biomass vs SRP | 0.65 | <0.01 | 14 |
| Phytoplankton biomass vs small/medium filter-feeders ratio | 0.64 | <0.01 | 14 |

PVI percentage of volume infested; SRP soluble reactive phosphorus.

main groups in both phases were small-celled colonial cyanobacteria [*Aphanocapsa holsatica* (Lemmermann) Cronberg et Komárek and *Aphanothece minutissima* (W. West.) Komárková-Legnerová et Cronberg], colonial green algae [*Botryococcus braunii* Kützing, *Coelastrum reticulatum* (Dangeard) Senn], and diatoms [*Aulacoseira granulata* (Ehrenberg) Simonsen]. Differences in composition were due to the absence of N-fixing cyanobacteria (*Anabaena circinalis* Rabenhorst ex

Bornet & Flahault) and the higher proportion of flagellates (*Synura* sp., *Cryptomonas* spp., and nanoplanktonic Chromulinales) during the phase with *Egeria* (Table 3). The algal biomass increase was especially associated with coccoid colonial cyanobacteria, diatoms in chains, and colonial chlorophytes covered by mucilage. The contribution of flagellates, which may have mixotrophic nutrition (Table 3), increased slightly during the period with *E. najas*.

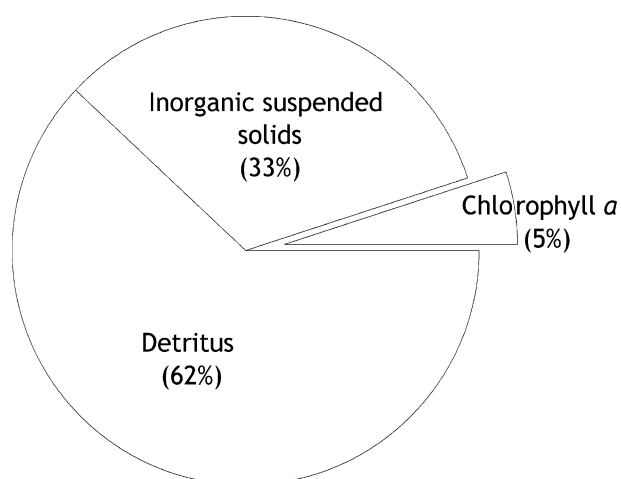


Figure 3. Average contribution of the seston fractions to the vertical extinction of light, estimated from the regression $1/SD = 2.140 + (0.166 \cdot Chlo) + (0.00641 \cdot Det) + (0.00605 \cdot ISS)$. *SD* Secchi depth; *Chlo* chlorophyll-*a*; *Det* detritus; *ISS* inorganic suspended solids.

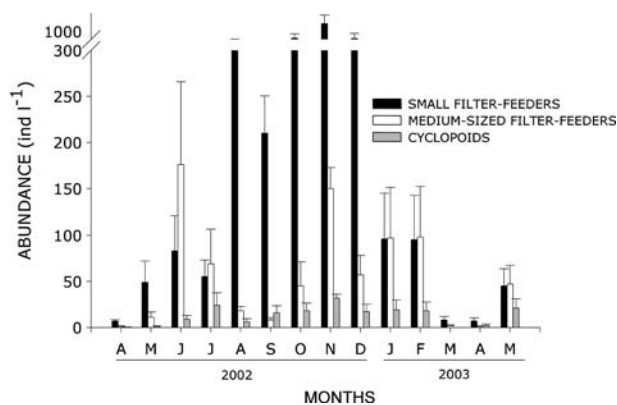


Figure 4. Temporal distribution of the main zooplankton functional groups in terms of abundance. Small filter-feeders (rotifers and nauplii). Medium-sized filter-feeders (cladocerans and calanoids). The graph includes the means and standard errors.

Table 3. Average Percentage of the Main Phytoplankton Groups (in Terms of Biomass) Among Sampling Stations, During the Phases With and Without *Egeria najas*

| | Phase without <i>Egeria</i> | Phase with <i>Egeria</i> |
|-------------------------------------|-----------------------------|--------------------------|
| Colonial small-celled cyanobacteria | 21,8 | 26,6 |
| Colonial greens | 22,1 | 12,3 |
| Diatoms | 16,5 | 8,7 |
| N-fixing cyanobacteria | 13,4 | 0,0 |
| Flagellates | 6,8 | 19,0 |
| Desmids | 4,0 | 5,5 |
| Oscillatoriales | 1,4 | 2,7 |
| Filamentous greens | 3,8 | 3,8 |

Table 4. Average and Standard Error of the Zooplankton Functional Group Abundances in the Periods With *Egeria najas* (April to June 2002 and March to May 2003) and Without *Egeria najas* (July 2002 to February 2003) in Coqueiro Lake

| Functional group (ind l ⁻¹) | With <i>Egeria</i> clear waters (n: 36) | Without <i>Egeria</i> turbid waters (n: 48) | Statistical differences F _(6,12) | Post hoc comparisons | | | | | | | |
|---|---|---|---|----------------------|----|----|----|----|----|----|--|
| | | | | H1 | L1 | L2 | L3 | L4 | H2 | H3 | |
| Zooplankton abundance | 66 ± 17.5 | 578 ± 85.1 | 6.2, P < 0.01 | A | A | AB | B | AB | A | A | |
| Small filterers | 33 ± 9.7 | 441 ± 108.2 | 14.7, P < 0.001 | A | A | AB | B | AB | A | A | |
| Medium filterers | 40 ± 20.0 | 68 ± 13.4 | 14.7, P < 0.001 | A | B | A | AB | AB | A | A | |
| Omnivores carnivores | 5 ± 2.4 | 19 ± 2.9 | 6.3, P < 0.01 | A | AB | AB | B | B | AB | AB | |

The variance analyses include ANOVAmr considering the water level as co-variable. *Egeria najas* occurred at H1, H2, and H3. H high-water level; L low-water level; NS non-significant differences. Same capital letters indicate groups with significantly similar mean values.

The total zooplankton abundance differed significantly between the phases with and without *E. najas* (Table 4). The community was dominated

by small filter-feeders, reaching a maximum in November 2002 (Figure 4), 2 months after a chlorophyll-*a* maximum. Rotifers (mainly *Lecane bula*

Gosse, *L. cornuta* Müller, and *L. unguolata* Gosse) dominated the zooplankton community, representing 64% (mean) of total zooplankton abundance. The rotifer genus *Trichotria* occurred only in the phase without *E. najas*.

At the end of *Egeria* dominance, as well as at the end of the low-water period, the proportions of medium-sized filter-feeders were similar to or higher than those of the small filter-feeders (Figure 4). Medium-sized filter-feeders and omnivores–carnivores (cyclopoids) showed the lowest abundances during the higher *Egeria* PVI months (April 2002 and 2003). The main taxa of cladocerans were *Bosminopsis deitersi* Richard, *Ceriodaphnia cornuta* Sars, *Diaphanosoma birgei* Korinek, and *Moina minuta* Hansen; the copepods were *Notodiaptomus amazonicus* Wright and *Mesocyclops longisetus* Thiébaud var. *curvatus* Dussart.

Interactions

The temporal patterns of PVI, phytoplankton biomass and water level were closely correlated (Table 2) with low-water levels and high turbidity and phytoplankton biomass during the phase without *Egeria*.

The temporal pattern of chlorophyll-*a* was also closely linked to variation in the concentrations of N-NH_4^+ and SRP (Table 2). The high phytoplankton biomass coincided with high ratios of small to medium filter-feeders (Table 2). Thus, the periods with the largest proportion (in terms of abundance) of cladocerans and calanoids in the zooplankton community showed the lowest phytoplankton biomass. There was no significant relationship between the temporal pattern of the medium-sized filter-feeders and the PVI.

DISCUSSION

The dominant pattern in the dynamics of the lake ecosystem is obviously the explosive expansion of submerged macrophytes in the high-water period, followed by the collapse of the plants and a strong increase in turbidity as the water level falls again.

At first sight, this annual rise and fall of submerged macrophytes in our tropical system may seem similar to what is observed over the seasonal cycle in temperate lakes. However, irradiation and temperature barely vary during the year, and are therefore unlikely to drive phenomenological cycles as they do in temperate systems. Rather, the behavior of our tropical lake appears to shift between contrasting alternative states driven by hydrology. Water-level change has been identified

as the cause of shifts between a turbid state and a clear, macrophyte-dominated state in several shallow lakes (Wallsten and Forsgren 1989; Engel and Nichols 1994; Sanger 1994; Beklioglu and others 2007). However, the pattern in our tropical lake is opposite to what is typically observed. The studies so far have highlighted cases where an increase in water level caused a collapse of submerged macrophytes, and a decrease in water level caused a shift from turbidity to macrophyte dominance. In contrast, macrophyte dominance in our tropical lake is related to high-water levels. We will first ponder which mechanisms may drive the sharp expansion and the subsequent demise of *Egeria*, and subsequently discuss which mechanisms may explain the large change in water clarity over the season. Finally, we reflect on the question of whether we should interpret the dynamics as shifts between alternative stable states.

The Shift to Macrophyte Dominance

Clearly, the spectacular increase in water clarity as the flooding begins is a likely explanation of the seemingly odd relationship between vegetation cover and water level. Our analysis shows that despite the rise in water level, the water transparency increased markedly just prior to the explosive development of the macrophytes (Figure 2). On the other hand, underwater shade is proportional to the product of the depth and the vertical attenuation coefficient (Scheffer 1998). This metric suggests that the light conditions at the bottom in the middle of the period without *Egeria* (November) were in fact quite similar to those in the period with *Egeria* (Figure 2). Therefore, the improvement in water transparency during the high-water period may not be a crucial condition for the recovery of *Egeria*. Another possibility is that the flooding river water brings new propagules of the plants to the lake. We could find hardly any remains of this plant by the end of the turbid period. Such a recolonization mechanism has also been suggested by Thomaz and others (2006), in their analysis of the effect of drawdown on *Egeria najas* in a large subtropical reservoir (Itaipú, Brazil).

The Collapse of the Submerged Vegetation

As the water level begins to fall in May, underwater light conditions deteriorate slightly. However, this seems unlikely to affect the dense *Egeria* beds, which by that time have grown to the water surface over most of the lake. Once submerged mac-

rophytes form such canopies, light attenuation in the water column has relatively little effect on growth (Van Nes and others 2003). Several other mechanisms might potentially explain the sudden and massive die-off of the weed beds during falling water levels. One possibility is that exposure of the plant mass to direct sunlight and surface desiccation triggers the die-off. It could be that once started, this is a self-catalyzing process, because it causes anoxia in the adjacent plant masses. Very low oxygen levels were observed in station 3 at midday, especially during the period with *E. najas*. Most likely, during night time hypoxic or anoxic conditions occurred throughout the water column. The low oxygen saturation, in combination with the massive decomposition of plant material may also have led to high ammonium concentrations. Although our relatively sparse record suggests a maximum of 0.3 mg l^{-1} higher concentrations may well have occurred. Other studies have shown high ammonium (and sulfide) concentrations to be acutely toxic for aquatic plants, and die-off has been associated with such toxicity for marine as well as freshwater systems (van Katwijk and others 1997; Li and others 2007; Cao and others 2007; van der Heide and others 2008).

On a more general level, other studies have reported that *Egeria* (Thomaz and others 2006) and other submerged plants (Adler 2002) are particularly sensitive to drawdown of the water table, indicating that the observed response to falling water level is not a peculiarity of our lake. Moreover, a similar temporal pattern is observed in the Amazonian floodplain lakes where other growth forms, such as floating and emergent macrophytes, also start to grow at rising water levels and decay during the decreasing water level period (Junk and Piedade 1997). Although the causal mechanisms remain unresolved in those different studies, the fact that different growth forms have comparable dynamics suggests that perhaps toxicity rather than underwater oxygen or light is a key in triggering mortality at falling water levels.

In any case, it seems that although hydrology may be linked to the rise as well as the demise of *Egeria*, quite different mechanisms appear to be involved in both situations.

Drivers of Water Clarity

Much of the work on alternative stable states in shallow lakes emphasizes the role of phytoplankton in determining water clarity. Although chlorophyll-*a* concentrations were indeed higher in our lake during the turbid period, the contribution of

phytoplankton to overall turbidity and underwater light attenuation (estimated by different approaches) was relatively minor in our study lake as well as another lake in the region (Loverde-Oliveira and Huszar 2007). The spectacular increase in clarity as the water level rises seems to result mainly from flushing with river water, which has lost most of its suspended solids during the slow flow over the flooded lands. The steady increase in underwater light attenuation during the dry period seems likely to result from a combination of factors. The concentration effect from evaporation and input of organic matter and nutrients from decomposing plants will add to a situation in which dissolved organic substances, phytoplankton and dead suspended matter accumulate in the water column. Also, increased wave resuspension during the low-water period may play a role. This is especially so because wind intensity increases during the period of low-water level (Mourão 1989; Carvalho and others 1991). In addition to promoting turbidity, waves might hamper colonization and growth of *E. najas* during the low-water period as suggested in another tropical lake study (Bini and Thomaz (2005).

Effects of *Egeria najas* on the Plankton Community

Remarkably, the expansion of *Egeria* seems not to promote water clarity. Reduction of turbidity by submerged macrophytes has been shown in numerous studies, and can be explained by a suite of mechanisms including reduction of resuspension, shading of the water column, reduction of nutrient availability, allelopathic effects, and grazing by large herbivorous zooplankton protected by the plants against fish predation (Jeppesen 1998; Scheffer 1998). However, the increase in clarity in our tropical lake occurs before *Egeria* expands (in March), and neither the chlorophyll-*a* level nor turbidity decrease as the plants expand to their peak in April. Thus, it seems more likely that flushing with clear water has boosted the phytoplankton loss rate. Also, increased light limitation of phytoplankton in deeper water (Scheffer 1998) may have played a role as the lake volume in the wet period increased by approximately 100% (Loverde-Oliveira and others 2007), as seen in many tropical floodplain lakes (García de Emiliani 1997; Huszar and Reynolds 1997; Train and Rodrigues 1998).

Other notable changes in the phytoplankton community as *Egeria* became dominant were the disappearance of N-fixing cyanobacteria and the increased proportion of flagellates. Flagellates do

not need turbulence to prevent sinking, are better adapted to exploit a heterogeneous and structured environment (Sommer 1988) and are often found to be relatively abundant in systems with abundant submerged plants (Balls and others 1989). The presence of N-fixing cyanobacteria during the period without *Egeria* might be associated with the lower DIN:SRP ratios (Smith and Bennett 1999, but see Reynolds 1999).

The zooplankton structure was dominated by small filter-feeders (mainly rotifers) as found for a comparable floodplain lake (Frutos and others 2006). The presence of *Egeria* did not promote an increase in the abundance of medium-sized filter-feeders (cladocerans and calanoids), the classic pattern observed in temperate (Jeppesen 1998; Scheffer 1998) and some subtropical lakes (Mazzeo and others 2003; Iglesias and others 2008). Instead, the share of medium-sized filter-feeders occurred at the lowest *Egeria* densities when phytoplankton biomass was at a minimum too. The key question remaining is why the beds of *E. najas* do not provide a refuge for cladocerans and calanoids and indirectly promote their higher abundance?

Analyses of fish assemblages in tropical reservoirs of Brazil (Pelicice and others 2005) have shown that vegetation of *E. najas* and *E. densa* tends to host a particular fish fauna composed of small-sized individuals (<5 cm) many of which feed almost exclusively on zooplankton (Pelicice and Agostinho 2006). This suggests that planktivory in these submerged plant beds may be high, as found in subtropical areas for the summer periods (Iglesias and others 2008; Meerhoff and others 2007; Teixeira-de-Mello and others 2009). This may explain why the *Egeria* beds do not seem to promote a zooplankton community that has a substantial grazing effect on phytoplankton.

CONCLUSION

It is tempting to interpret the dynamics observed in our lake as recurrent shifts between alternative states. Indeed the data suggest a small hysteresis in the response of the *Egeria* to water depth, in the sense that the tipping point for switching to plant dominance appears to occur at a slightly higher water level than the collapse of plants (Figure 5). This difference could be interpreted to result from the difference between the shade tolerated by small plants starting their growth in the sediment far from the water surface, and the far more modest requirements in terms of water clarity of full-grown canopy-forming plants. However, as argued, the mechanism triggering the die-off of *Egeria* has

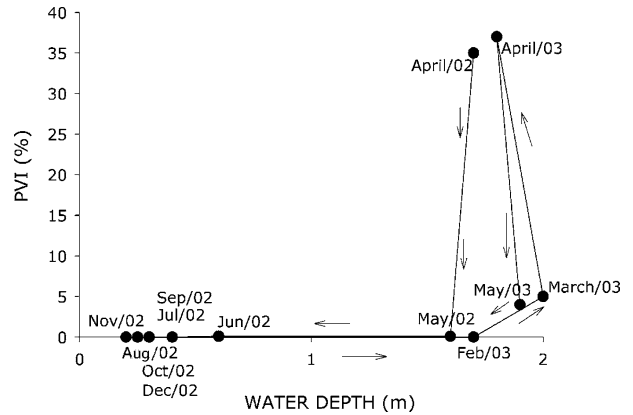


Figure 5. Relationships between the water level (maximum depth) and *Egeria najas* PVI (percentage of volume infested). The graph also shows the temporal sequences of months with and without *E. najas*.

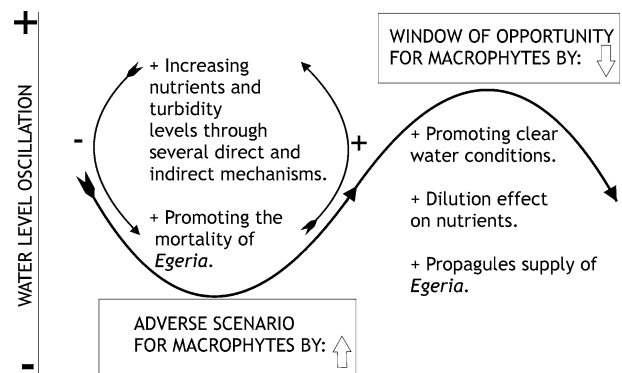


Figure 6. Schematic representation of the possible driver mechanisms of the recurrent clear and turbid regimens caused by the fluctuation in water level.

probably little to do with light limitation. Nonetheless, factors related to water level may be involved in the collapse as well as the recovery of the vegetation (Figure 6). It is obvious, however, that the behavior of this tropical lake is governed by quite different mechanisms than those described in the classical literature on alternative stable states in shallow lakes. Numerous field studies and experimental studies on different scales have provided a good picture of how such temperate lakes work. In contrast, our study highlights the behavior of another type of lake, which appears to be widespread in this region. Experimental work would be needed to unravel what drives the phase shifts in such floodplain lakes. Although this would necessitate a large effort, a better understanding of the effects of hydrological dynamics on these ecosystems is essential if we wish to predict the potential consequences of future modifications of the Pantanal system.

ACKNOWLEDGMENTS

We thank Valdeci Antonio de Oliveira for help with the field collections, and Ibraim Fantin Cruz for help with the work involving the zooplankton community. We also thank FAPEMAT, NEPA/UFMT (Brazil), Conselho Nacional de Desenvolvimento Científico e Tecnológico, CNPq (Brazil), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, CAPES (Brazil), CSIC-UDELAR (Uruguay), and PEDECIBA (Uruguay), SNI-ANII for financial support. We also thank Patricia Mburucuyá and Juancito Carrau for their inspirational comments and suggestions; and finally Dr. Janet W. Reid (JWR Associates) for the revision of the English text.

REFERENCES

- Adler M. 2002. Primärproduktion von Phytoplankton und Periphyton sowie Nährstofflimitation und-konkurrenz mit aquatischen Makrophyten im Pantanal, Mato Grosso (Brasilien), Ph.D Thesis, Universität Hamburg, Hamburg.
- APHA. 1992. Standard methods for examination of waste and wastewater. New York: American Public Health Association.
- Balls H, Moss B, Irvine K. 1989. The loss of submerged plants with eutrophication. I. Experimental design, water chemistry, aquatic plant and phytoplankton biomass in experiments carried out in ponds in the Norfolk Broads. *Freshw Biol* 22:71–87.
- Beklioglu M, Altinayar G, Tan CO. 2007. Water level control over submerged macrophyte development in five shallow lakes of Mediterranean Turkey. *Arch Hydrobiol* 166(4):535–56.
- Bini LM, Thomaz SM. 2005. Prediction of *Egeria najas* and *Egeria densa* occurrence in a large subtropical reservoir (Itaipu Reservoir, Brazil-Paraguay). *Aquat Bot* 83:227–38.
- Blindow I, Andersson G, Hargeby A, Johansson S. 1993. Long-term pattern of alternative stable states in two shallow eutrophic lakes. *Freshw Biol* 30:159–67.
- Canfield DE, Shireman JV, Colle DE, Haller WT, Watkins CE, Maceina MJ. 1984. Prediction of chlorophyll-*a* concentrations in Florida lakes: importance of aquatic macrophytes. *Can J Fish Aquat Sci* 41:497–501.
- Cao T, Xie P, Ni LY, Wu AP, Zhang M, Wu SK, Smolders AJP. 2007. The role of NH_4^+ toxicity in the decline of the submerged macrophyte *Vallisneria spiralis* in lakes of the Yangtze River basin, China. *Mar Freshw Res* 58(6):581–7.
- Carignan R, Neiff JJ. 1992. Nutrient dynamics in the floodplain ponds of the Paraná River (Argentina) dominated by water hyacinth *Eichhornia crassipes*. *Biogeochemistry* 17:85–121.
- Carmouze JP. 1994. O metabolismo dos ecossistemas aquáticos. Fundamentos teóricos, métodos de estudo e análises químicas. São Paulo: Edgard Blücher, FAPESP.
- Carvalho P, Bini LM, Thomaz SM, Oliveira LG, Robertson B, Tavechio WLGD. 1991. Comparative limnology of South-American floodplain lakes and lagoons. *Acta Sci* 23:265–73.
- Edler L. 1979. Recommendations for marine biological studies in the Baltic Sea. Phytoplankton and chlorophyll. Stockholm: UNESCO, Working Group 11, National Swedish Environmental Protection Board, Baltic Marine Biologists.
- Engel S, Nichols SA. 1994. Aquatic macrophyte growth in a turbid windswept lake. *J Freshw Ecol* 9:97–109.
- Fantin-Cruz I, Loverde-Oliveira SM, Girard P. 2008. Caracterização morfológica e suas implicações na limnologia de lagoas do Pantanal Norte. *Acta Sci* 30(2):133–40.
- Frutos SM, Poi de Neiff ASG, Neiff JJ. 2006. Zooplankton of the Paraguay River: a comparison between sections and hydrological phases. *Ann Limnol* 42(2):277–88.
- García de Emiliani MO. 1997. Effects of water level fluctuations on phytoplankton in a riverfloodplain lake system (Paraná River, Argentina). *Hydrobiologia* 357:1–15.
- Golterman HL, Clymo RS, Ohnstad MAM. 1978. Methods for chemical analysis of freshwater. Boston: IBP Handbook 8.
- Hargeby A, Blindow I, Hansson LA. 2004. Shifts between clear and turbid states in a shallow lake: multi-causal stress from climate, nutrients and biotic interactions. *Arch Hydrobiol* 161:433–54.
- Huszar VLM, Reynolds CS. 1997. Phytoplankton periodicity and sequences of dominance in an Amazonian flood-plain lake (Lago Batata, Pará, Brazil). *Hydrobiologia* 346:169–81.
- Iglesias C, Mazzeo N, Goyenola G, Fosalba C, Teixeira-de-Mello F, García S, Jeppesen E. 2008. Field and experimental evidence of the effect of *Jenynsia multidentata*, a small omnivorous-planktivorous fish, on the size distribution of zooplankton in subtropical lakes. *Freshw Biol* 53:1797–807.
- Jeppesen E. 1998. The ecology of shallow lakes. Trophic interactions in the pelagial. Silkeborg: National Environmental Research Institute.
- Jeppesen E, Meerhoff M, Jacobsen BA, Hansen RS, Søndergaard M, Jensen JP, Lauridsen TL, Mazzeo N, Branco CWC. 2007a. Restoration of shallow lakes by nutrient control and biomanipulation: the successful strategy varies with lake size and climate. *Hydrobiologia* 581:269–85.
- Jeppesen E, Søndergaard M, Pedersen AR, Jürgens K, Strzelczak A, Lauridsen TL, Johansson LS. 2007b. Salinity induced regime shift in shallow brackish lagoons. *Ecosystems* 10:47–57.
- Junk WJ. 2005. Flood pulsing and the linkages between terrestrial, aquatic, and wetland systems. *Proc Int Assoc Theor Appl Limnol* 29:11–38.
- Junk WJ, Piedade MTF. 1997. Plant life in the floodplain with special reference to herbaceous plants. In: Junk WJ, Ed. The central Amazonian floodplain: ecology of a pulsing system. Berlin: Springer-Verlag, p 147–85.
- Junk WJ, Bayley PB, Sparks RG. 1989. The flood pulse concept in river floodplain system. *Can Spec Publ Fish Aquat Sci* 106:110–27.
- Junk WJ, Cunha CN, Wantzen KM, Petermann P, Strüssmann C, Marques MI, Adis J. 2006. Biodiversity and its conservation in the Pantanal of Mato Grosso, Brazil. *Aquat Sci* 68:278–309.
- Li H, Cao T, Ni L. 2007. Effects of ammonium on growth, nitrogen and carbohydrate metabolism of *Potamogeton maackianus* A. Benn. *Fundam Appl Limnol* 170(2):141–8.
- Loverde-Oliveira SM. 1999. Variações limnológicas e análise temporal da comunidade fitoplanctônica da baía Sá Mariana, Pantanal de Barão de Melgaço, MT. MSc Dissertation, Universidade Federal de Mato Grosso, Cuiabá.
- Loverde-Oliveira SM. 2005. Implicações da complexidade hidrológica sobre padrões limnológicos na lagoa do Coqueiro, Pantanal de Mato Grosso: alternância de estados estáveis. PhD Thesis, Universidade Federal do Rio de Janeiro, Rio de Janeiro.

- Loverde-Oliveira SM, Huszar VLM. 2007. Phytoplankton ecological responses to the flood pulse in a Pantanal lake, Central Brazil. *Acta Limnol Bras* 19:5–19.
- Loverde-Oliveira SM, Huszar VLM, Fantin-Cruz I. 2007. Implications of the flood pulse on morphometry of a Pantanal lake (Mato Grosso state, Central Brazil). *Acta Limnol Bras* 19(4):1–8.
- Lund JWG, Kipling C, Le Cren ED. 1958. The inverted microscope method of estimating algal number and the statistical basis of estimating by counting. *Hydrobiologia* 11:143–70.
- Machado FA. 2003. História natural de peixes do Pantanal: com destaque em hábitos alimentares e defesas contra predadores. PhD Thesis, Universidade Estadual de Campinas, Campinas.
- Mackereth FJH, Heron J, Talling JF. 1978. Water analysis: some revised methods for limnologists. *Scientific Publications of the Freshwater Biological Association* 6:121p.
- Mazzeo N, Rodríguez-Gallego L, Kruk C, Meerhoff M, Gorga J, Lacerot G, Quintans F, Loureiro M, Larrea D, García-Rodríguez F. 2003. Effects of *Egeria densa* Planch. beds on a shallow lake without piscivorous fish. *Hydrobiologia* 506–509:591–602.
- McBride GB, Vant WN, Cloern JE, Liley JB. 1993. Development of a model of phytoplankton blooms in Manukau Harbour. *NIWA Ecosystems* 3:1–52.
- McKinnon SL, Mitchell SF. 1994. Eutrophication and black swan (*Cygnus atratus* Latham) populations: tests of two simple relationships. *Hydrobiologia* 279–280:163–70.
- Meerhoff M, Clemente JM, Teixeira-de-Mello F, Iglesias C, Pedersen AR, Jeppesen E. 2007. Can warm climate-related structure of littoral predator assemblies weaken the clear water state in shallow lakes? *Glob Chang Biol* 13:1888–97.
- Moss B, Madgewick J, Phillips G. 1996. A guide to the restoration of nutrient-enriched shallow lakes. *Broads Authority/Environment Agency*.
- Mourão GM. 1989. Limnologia comparativa de três lagoas (duas baías e uma salina) do Pantanal da Nhecolândia. MSc. Dissertation, Universidade Federal de São Carlos, São Carlos.
- Neiff JJ. 1990. Ideas for the ecological interpretation of the Paraná river. *Interciencias* 15:424–41.
- Nürnberg GK. 1996. Trophic state of clear and colored, soft and hard water lakes with special consideration of nutrients, anoxia, phytoplankton and fish. *Lake Reservoir Manage* 12:432–47.
- Nusch EA, Palme G. 1975. Biologische Methoden für die Praxis der Gewässeruntersuchung. *GWF-Wasser/Abwasser* 116:562–5.
- PCBAP (Programa Nacional do Meio Ambiente, Projeto Pantanal). 1997. Plano de conservação da bacia do Alto Paraguai. Diagnóstico dos meios físico e biótico. Brasília: MMA/PNMA. v.2.
- Pelicice F, Agostinho A. 2006. Feeding ecology of fish associated with *Egeria* spp. Patches in a tropical reservoir, Brazil. *Ecol Freshw Fish* 15:10–19.
- Pelicice F, Agostinho A, Thomaz S. 2005. Fish assemblages associated with *Egeria* in a tropical reservoir: investigating the effect of plant biomass and diel period. *Acta Oecol* 27:9–16.
- Perrow MR, Moss B, Stansfield J. 1994. Trophic interactions in a shallow lake following a reduction in nutrient loading—a long-term study. *Hydrobiologia* 276:43–52.
- Ponce VM. 1995. Impacto hidrológico e ambiental da hidrovía Paraná-Paraguai no Pantanal Mato-grossense: um estudo de referência. San Diego: San Diego State University.
- Reynolds CS. 1999. Non-determinism to probability, or N:P in the community ecology of phytoplankton. *Arch Hydrobiol* 146:23–35.
- Rip WJ, Ouboter M, Beltman B, Van Nes EH. 2005. Oscillation of a shallow lake ecosystem upon reduction in external phosphorus load. *Arch Hydrobiol* 164:387–409.
- Roopen FCJM, Peeters ETHM, Roijackers R, Wyngaert IVD, Wolters H, De Coninck H, Ibelings BW, Buijse AD, Scheffer M. 2008. Fast response of lake plankton and nutrients to river inundations on floodplain lakes. *River Res Applications* 24:388–406.
- Salas HJ, Martino P. 1991. A simplified phosphorus trophic state model for warm tropical lakes. *Water Res* 25:341–50.
- Sanger AC. 1994. The role of macrophytes in the decline and restoration of Lagoon of Islands. *Lake Reservoir Manage* 9:111–112.
- Scheffer M. 1998. Ecology of shallow lakes. 1st edn. London: Chapman and Hall.
- Scheffer M, Carpenter SR. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol Evol* 18:648–56.
- Scheffer M, Jeppesen E. 2007. Regime shifts in shallow lakes. *Ecosystems* 10:1–3.
- Scheffer M, van Nes EH. 2007. Shallow lakes theory revisited: various alternative regimes driven by climate, nutrients, depth and lake size. *Hydrobiologia* 584:455–66.
- Schelske CL, Carrick HJ, Aldridge FJ. 1995. Can wind-induced resuspension of meroplankton affect phytoplankton dynamics? *J N Am Benthol Soc* 14:616–30.
- Silva RL. 2002. Dinâmica espacial e produção primária do estande de *Eichhornia azurea* na baía do Coqueiro (Pantanal de Mato Grosso, Brasil). MSc. Dissertation, Universidade Federal de Mato Grosso, Cuiabá.
- Smith VH, Bennett SJ. 1999. Nitrogen:phosphorus supply ratios and phytoplankton community structure in lakes. *Arch Hydrobiol* 146:37–53.
- Sommer U. 1988. Some size relationships in phytoflagellated motility. *Hydrobiologia* 161:125–31.
- Teixeira JG, Tundisi JG, Kutner MB. 1965. Plankton studies in mangrove environment. II. The standing stock and some ecological factors. *Bol Inst Oceanogr* 24:23–41.
- Teixeira-de-Mello F, Meerhoff M, Pekcan-hekim Z, Jeppesen E. 2009. Substantial differences in littoral fish community structure and dynamics in subtropical and temperate shallow lakes. *Freshw Biol* 54:1202–15.
- Thomaz S, Pagioro T, Bini L, Murphy K. 2006. Effect of reservoir drawdown of three species of aquatic macrophytes in a large sub-tropical reservoir (Itaipu, Brazil). *Hydrobiologia* 570:53–9.
- Train S, Rodrigues LC. 1998. Temporal fluctuations of the phytoplankton community of the Baía River, in the upper Paraná River floodplain, Mato Grosso do Sul, Brazil. *Hydrobiologia* 361:125–34.
- Uhelinger V. 1964. Étude statistique des méthodes de dénombrement planctonique. *Arch Sci* 17:121–3.
- Utermöhl H. 1958. Zur Vervollkommung der quantitativen Phytoplankton-Methodik. *Mitt Int Ver Theor Angew Limnol* 9:1–38.
- van der Heide T, Smolders AJP, Rijkens BGA, van Nes EH, van Katwijk MM, Roelofs JGM. 2008. Toxicity of reduced nitrogen in eelgrass (*Zostera marina*) is highly dependent on shoot density and pH. *Oecologia* 158:411–9.
- Van Geest GJ, Wolters H, Roopen F, Coops H, Roijackers RMM, Buijse AD, Scheffer M. 2005. Water-level fluctuations affect macrophyte richness in floodplain lakes. *Hydrobiologia* 539:239–48.

-
- Van Geest GJ, Coops H, Scheffer M, van Nes EH. 2007. Long transients near the ghost of a stable state in eutrophic shallow lakes with fluctuating water levels. *Ecosystems* 10:37–47.
- van Katwijk MM, Vergeer LHT, Schmitz GHW, Roelofs JGM. 1997. Ammonium toxicity in eelgrass *Zostera marina*. *Mar Ecol Prog Ser* 157:159–73.
- van Nes EH, Scheffer M, Van den Berg MS, Coops H. 2003. Charisma: a spatial explicit simulation model of submerged macrophytes. *Ecol Modell* 159:103–16.
- Vollenweider RA, Kerekes J. 1980. The loading concept as basis for controlling eutrophication: philosophy and preliminary results of the OECD programme on eutrophication. *Prog Water Technol* 12:5–38.
- Wallsten M, Forsgren PO. 1989. The effects of increased water level on aquatic macrophytes. *J Aquat Plant Manage* 27:32–7.
- Wantzen KM, Junk WJ, Rothhaupt KO. 2008. An extension of the floodpulse concept (FPC) for lakes. *Hydrobiologia* 613:151–70.
- Wetzel RG, Likens GE. 1991. *Limnological analyses*. New York: Springer-Verlag.