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Remote sensing imagery analysis of the lacustrine system of Ibera wetland (Argentina)

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Abstract

The little-known lacustrine ecosystem of Ibera wetland was examined using satellite-measured reflectance to determine several limnological variables (Secchi depth, S_d; nephelometric turbidity, T_n; dissolved organic matter, DOM). The spatial and temporal analysis has shown the main relationships between the local forcing factors and the ecological state of the aquatic ecosystems. The spatial geomorphologic characteristics of the wetland were strongly related to the spatial distribution of the limnological variables. According to this, the macrosystem has been classified into three large regions that enclose lakes that share diverse characteristics. (i) Northwestern region encloses few open water areas, mainly of small size. (ii) Rounded large lakes (probably originated as oxbow floodplain lakes) are characteristics of the Northeastern region. (iii) Elongated large lakes (probably originated as levee floodplain lakes) are characteristics of the Southern region. These lakes showed the highest S_d and DOM values and the lowest T_n. The different water drainage of the regions seems to be the main cause of the limnological differences of the wetland. The described spatial classification agrees also with other ecological characteristics such as the degree of macrophytes development or composition of the fish community. Different disturbed local areas, overlapping the regional classification, were also identified in the borders of the wetland. These areas have been related with the presence of anthropogenic activities, revealing the sensitivity of these shallow lakes. The whole system showed a relatively homogenous seasonal pattern of water transparency related with solar irradiance cycle. The variability of active floodplains lakes of the Upper Paraná was found to be more strongly influenced by the rainfall, presenting a more unpredictable behaviour.

Keywords: Water optical properties; Ibera wetland; Regional classification

1. Introduction

Esteros del Iberá is an internationally important wetland located in the Northeast of Argentina. The vast expanse and accessibility difficulties of this sub-

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tropical wetland hampered the extensive study of the lacustrine system. Limnological studies performed in this macrosystem are scarce (Bonetto et al., 1981; Neiff, 1981, 1999). An intensive study was recently performed in two of the many shallow lakes in the Ibera wetland over a 2 years period (Cózar et al., 2003). To extend this information to the other permanent water bodies in the wetland, researchers, in collaboration with the Argentine space agency (CONAE), obtained a series of satellite images of the wetland region. The recent incorporation of the Argentine SAC-C mission (CONAE) into the International Morning Constellation for Earth observation has greatly facilitated the use of this valuable tool in the study of the Ibera wetland. Available satellites provide a wide range of complementary remote sensed data and enable the observation of vast areas of difficult access like wetlands. Information from the Landsat 5 (TM sensor), Landsat 7 (ETM sensor) and SAC-C (MMRS sensor) satellites has been used in the present study.

The combination of on site measurements with information from the satellite images has been used to study the spatial and temporal characteristics of permanent lakes in the Ibera macrosystem. The objective was to classify the lacustrine system of Ibera wetland into bio-geographic regions. With the term “bio-geographic regions”, we refer to the demarcation of spatial regions that enclose lakes that share similar limnological characteristics and trends. The expanse and number of water bodies of the wetland allow the generation of bio-geographic regions in the lacustrine system in a similar way that those carried out in terrestrial or marine ecosystems (e.g. Santamaría-del-Ángel et al., 1994). In the present work, we use satellite-derived information about lake shape, distribution and optical characteristics (Secchi depth, turbidity and dissolved organic matter) to separate the wetland and its internal lakes into bio-geographical regions. These characteristics were derived from visible radiances measured by the satellite sensors for the water bodies under study. The availability of a series of images from satellites allowed the development of a comparison of the whole lacustrine system related with the temporal co-variation of the limnological variables.

2. Methods

2.1. Study site

Esteros del Iberá is one of the largest pristine inland wetland ecosystems in South America. As a result of its high biodiversity, it has been recently included in the

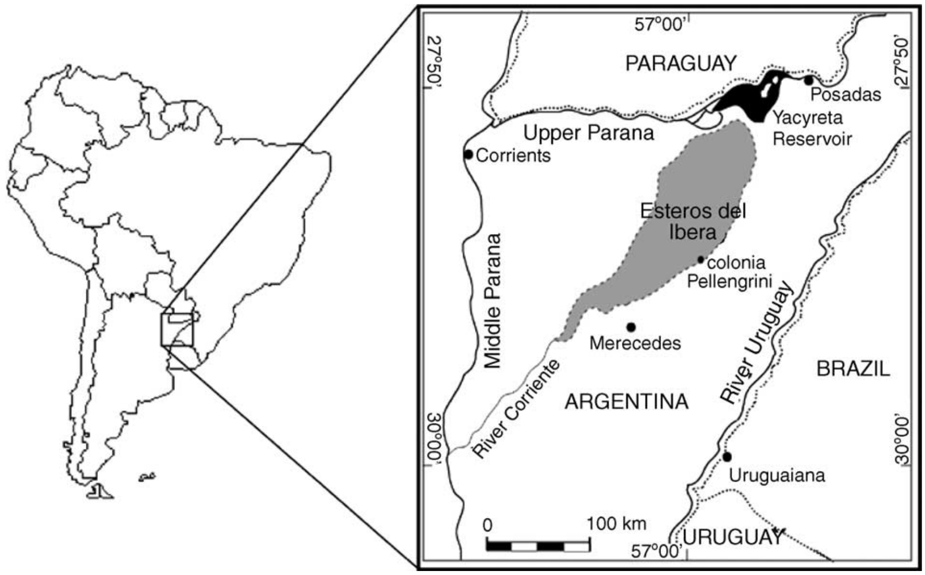

Fig. 1. Location of *Esteros del Iberá* wetland in South America.

Ramsar Convention. *Esteros del Iberá* covers more than 12,000 km^2 that spread between the 30′–28°45′S parallels and the 58°00′–57°30′ O meridians (Fig. 1). The Ibera plain constitutes the ancient bed of the Paraná, which remained connected to the river until the end of the Pleistocene (Neiff, 1999). Currently the basin is mainly fed by rain and drains only through Corriente River in the South.

Ibera wetland consists of a vast mosaic of marshes, swamps and shallow lakes, most of which (60%) remain permanently inundated. Often, characteristic mats of floating vegetation called “embalsados” compose the shores and the surrounding environment of the lakes. These floating mats have relevant impact on the lake waters as a source of humic acids. The wetland is slightly affected by the presence of centers of economic activities (mainly rice farming, forestation and ranching) located on the borders of the macrosystem. Currently, it is also generating a growing tourist demand. The high sensitivity of the Ibera lakes to eutrophication is unavoidably linked to the shallowness, which leads to stronger interactions with the benthos and the surrounding environment (Cózar et al., 2003).

The meteorological, hydrological and land use variability of the vast Ibera macrosystem could cause limnological heterogeneities. Bonetto et al. (1981) separated the wetland into Northern and Southern sections according to the ichthyofauna diversity. The Northern sector is represented by characteristic sedentary fishes of lacustrine waters. The larger carnivores are mainly piranhas (*Serrasalmus* spp.). The Southern sector shows an ichthyofauna more similar to the river ecosystem of the Paraná, to which the Corriente River is attached. The carnivorous species are relatively larger than in the Northern sector (*Salminus maxillosus*, *Prochilodus platensis*).

Table 1
Satellite images used in the analysis of the lacustrine system of *Esteros del Iberá* wetland

Date	Satellite
07-03-1997	Landsat 5
08-04-1997	Landsat 5
10-05-1997	Landsat 5
14-08-1997	Landsat 5
30-08-1997	Landsat 5
18-11-1997	Landsat 5
04-12-1997	Landsat 5
05-01-1998	Landsat 5
13-02-1998	*sim.* SAC-C
22-02-1998	*sim.* SAC-C
26-03-1998	*sim.* SAC-C
20-10-1998	Landsat 5
21-11-1998	Landsat 5
07-12-1998	Landsat 5
08-01-1999	Landsat 5
25-02-1999	Landsat 5
30-04-1999	Landsat 5
01-06-1999	*sim.* SAC-C
04-08-1999	*sim.* SAC-C
20-08-1999	*sim.* SAC-C
21-09-1999	Landsat 5
24-11-1999	*sim.* SAC-C
26-12-1999	*sim.* SAC-C
27-01-2000	*sim.* SAC-C
12-02-2000	*sim.* SAC-C
03-03-2000	*sim.* SAC-C
15-03-2000	*sim.* SAC-C
08-04-2000	Landsat 7
24-04-2000	Landsat 7
05-07-2000	Landsat 5
06-08-2000	Landsat 5
07-09-2000	Landsat 5
01-10-2000	Landsat 7
26-11-2000	Landsat 5
20-12-2000	Landsat 7
05-05-2001	Landsat 5
16-07-2001	Landsat 7
01-08-2001	Landsat 7
05-11-2001	Landsat 7

The simulated SAC-C images (with the same spatial resolution and number of wavebands that the original SAC-C images but built by CONAE from Landsat 5 images) are indicated as *sim.* SAC-C.

2.2. Image processing

The satellite images were processed with ERDAS 8.5 software and using radiometric correction models for each used satellite system (Table 1). Digital numbers were transformed to radiances on the sensor according to the calibration data for each scene. The path irradiance of the measured exo-atmospheric radiance was removed by using the dark object subtraction suggested by Chávez (1996). The reflectance was calculated by determining the sun elevation at the centre of each scene at the time and date of each image.

Lake morphology and lakes distribution were examined through the spectral analysis of the near-infrared band of the MMRS sensor of the SAC-C satellite. A single image of spring 2001 was used to identify all major open water bodies, >0.5 km^2 (Fig. 2). These water

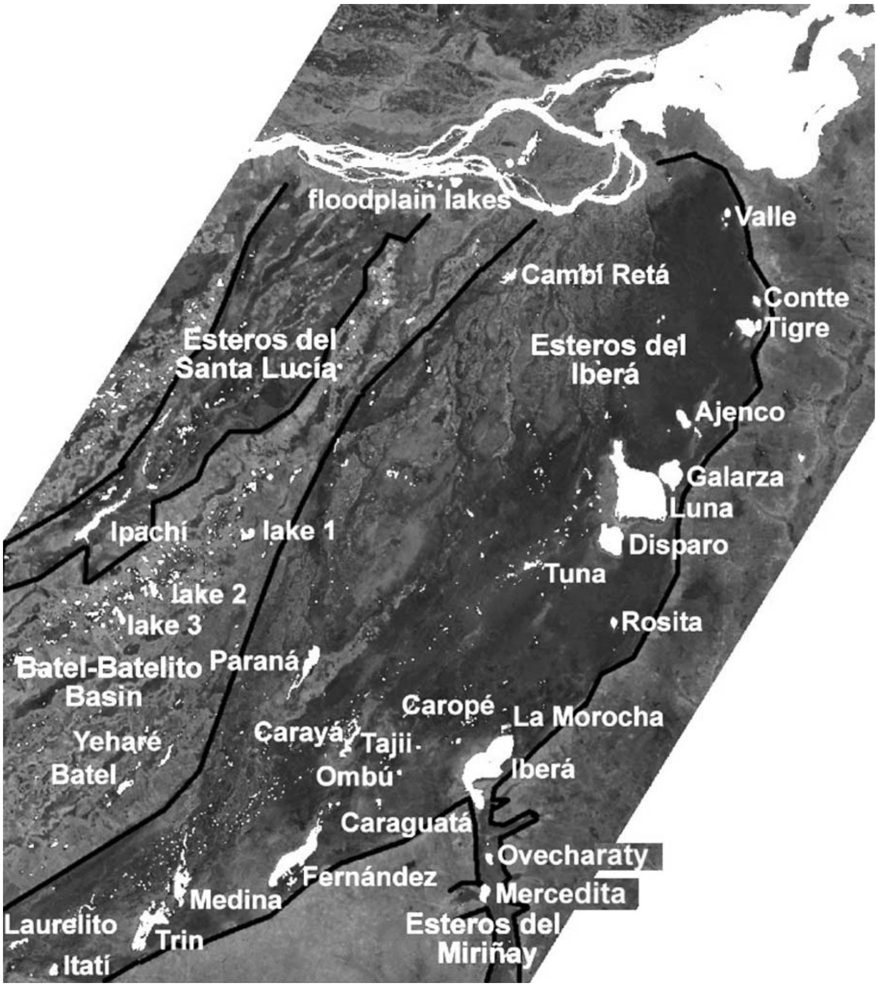

Fig. 2. Open water areas of the *Esteros del Iberá* wetland and the surrounding environment. The location of *Esteros del Miriñay*, *Esteros del Santa Lucía* and *Batel-Batelito* basin is also shown. The open water bodies were highlightened thought the spectral analysis of the near-infrared band of ETM sensor. The lakes with names indicate the water bodies used to the spatial and temporal analyses.

bodies focused the present study. For lakes that were greater than 4 km^2, the lake was sub-divided in sections. These larger lakes were divided into Central, Northeast, Northwest, Southeast and Southwest sections, creating five separate areas in each lake. The reflectance data of each image was then obtained for each lake and each lake subsection. Samples of permanent water bodies just beyond the wetland borders were also included for comparison purposes. A grid of 63 lake sections of a total of 25 water bodies was used (Table 2).

Using the corrected at-surface reflectance of each lake section, the average reflectance for all sections in the visible and infrared wavelengths was recorded for 39 image dates from March 1997 to November 2001 (Table 1). Thus, we build a data matrix for each waveband composed by 63 lake sections (rows) during 39 dates (columns). When clouds covered a particular lake section, a weighted average of the preceding and following images was used to complete the data matrix.

The determination of optical properties of the water bodies by satellite-measured reflectance was made by

Table 2
Studied water bodies in the lacustrine system of Ibera wetland and the surrounding environment

Open water area	Lake-sections
Ajenco	1
Batel	2
Cambí Retá	1
Caraguatá	1
Caropé	1
Conde Contte	1
Disparo	5
Fernández	4
Galarza	5
Ibera (North)	5
Ibera (South)	1
Ipachí	3
Itatí	1
La Morocha	1
Lake 1	1
Lake 2	1
Lake 3	1
Floodplan lake	1
Luna	6
Medina	2
Mercedita	1
Ombú	1
Ovecharaty	1
Paraná	2
Riacho Carayá	2
Riacho Laurelito	1
Rosita	1
Tajii	1
Tigre (eastern basin)	1
Tigre (western basin)	1
Trin	2
Tuna	1
Valle	1
Yacyretá	1
Yeharé	2

The number of lake-sections used into each open water area is also shown. The location and morphology of the water bodies is shown in Fig. 2.

comparing on site measurements with coincident satellite images. The on site measurements were performed during November 2002 in Laguna Iberá (54 km^2) in 71 sites throughout the lake in coincidence to the passage of the Landsat 7 system. Each sampling site was georeferenced and a 3 pixel by 3 pixel area of the satellite-measured reflectance was sampled for the visible wavebands (bands 1–3 on all sensors) and infrared wavebands (bands 4 and 5). The measured water optical properties included Secchi depth, nephelometric turbidity and dissolved organic matter, which consisted mostly of dissolved humic and fulvic acids (Mazzuoli et al., 2004).

Secchi depth (S_d) should relate to the inverse of the beam attenuation and the vertical attenuation coefficients. It will decrease with the increase in the concentration of both dissolved and particulate matter in relation to their scattering and absorption properties. The measurement of nephelometric turbidity (T_n) is a relative approximation of the scattering coefficient (in this case measured at 695 nm) due to particulate matter (Kirk, 1994). Dissolved organic matter (DOM) and in particular humic substances are coloured substances that determine the characteristic dark tea colouring of the water of subtropical and tropical wetlands. This variable was measured through spectrophotometric absorption (Hautala et al., 2000).

Using a least squared approach, a linear combination of three bands was created to estimate the three optical parameters chosen for study (Table 3). Data for chlorophyll *a* concentration (*chl a*) were also compared to satellite-measured reflectance but any significant relationship was obtained. The coloured dissolved organic matter strongly influenced the whole reflectance spectrum of the water bodies. The accepted algorithms ($R > 0.60$) were then applied to the reflectance matrixes. The resulting data were three matrixes (63 lake sections × 39 dates) estimating the calibrated water optical properties (S_d, T_n and DOM). The feasibility of using the obtained calibration algorithms in water bodies disconnected of the Ibera wetland (mainly Paraná floodplain lakes and Yacyretá Reservoir) obviously is lower. When these water bodies showed a very high turbidity, we obtained S_d values above zero. In these cases, we assigned the zero value by default.

Table 3
Calibration algorithms of diverse water optical properties obtained by linear combination of three bands of the ETM sensor ($n = 71$)

Variable (Y)	Algorithms	Pearson
Nephelometric turbidity (NTU)	$Y = -0.333B_1 + 0.774B_3 + 0.0959B_5 + 2.06$	0.79
Humic Acids (mg L^{-1})	$Y = 0.259B_1 + 0.537B_2 - 0.700B_3 + 0.489$	0.63
Secchi depth (m)	$Y = 0.182B_1 - 0.207B_3 - 0.0549B_4 + 0.3903$	0.79

The B_i coefficients are the reflectance for the bands 1–5. The Pearson coefficient of each multiple linear regression is also shown.

The spatial analysis was performed by comparing the studied optical properties (S_d, T_n and DOM) and the morphology and distribution of the lakes. A monthly average of 4 years of satellite data was calculated for each lake section. The spatial distribution of these average characteristics of the water along the wetland was contrasted with geo-morphological classification of the lacustrine system.

The study of the temporal variability on the macroscale level was made using an empirical orthogonal functional analysis (EOF; Kidson, 1975). This approach is often used in meteorological (e.g. Kondragunta and Gruber, 1997) and oceanographical analyses (e.g. Nezlin et al., 2002), but this is the first time that is applied on a large lacustrine system. This analysis was focused on the Secchi depth matrix (63 lake sections × 39 dates). The S_d is indicative of the trophic status of the lakes and, as an estimate of the water transparency, it can also be considered a measurement of the aesthetic aspect of the water. Although S_d integrates diverse water characteristics, seasonal data of S_d and *chl a* of two of the wetland lakes (Cózar et al., 2003) show a strong correlation (ANOVA; $P < 0.01$, $n = 68$). The *chl a* data explained the 51.2% of the S_d variability. To carry out the analysis of the temporal series, a covariance matrix was built through the subtraction and division of the average S_d for each measurement date. Thus, each element was converted into an anomaly or relative deviation from the average. Using the EOF analysis of the covariance matrix, different eigenfunctions were extracted which indicated distinct modes of temporal variability. Additionally, the temporal series of the locally measured meteorological (temperature, photoperiod, rainfall and wind velocity) and hydrodynamic factors (water level) were also compared. These data series were built from the concurrent data obtained in population centers surrounding the wetland (Colonia Pellegrini, Mercedes, Concepción, Galarza, Pay Ubre, Chavarría and Yacyretá). An averaged temporal series of each forcing factor was built from the gross data collection. A general temporal pattern of a relative water temperature of the lacustrine system was also obtained from a EOFs analysis on the effective temperature extracted from the Landsat (TM and ETM) infrared bands (*Landsat Science Data Users Handbook*; http://ltpwww.gsfc.nasa.gov/IAS/handbook/handbook_toc.html).

3. Results

3.1. Spatial analysis

A first structural classification of the wetland was obtained by using topographical information of the wetland (Ferrati and Canziani, this issue) and on site and remote (based on tassel cup indexes) observations of the vegetal colonization and flooding. The wetland was divided into three preliminary regions. (i) The Northwest region is a higher area of the wetland, with herbaceous vegetation and lakes characterized by a generally irregular shape and reduced dimensions ($<0.5\,\mathrm{km}^2$). It is an important sector from the economic viewpoint (farming, ranching, and ecotourism). (ii) The Northeast region contains larger lakes with a rounded morphology, and generally surrounded by floating vegetation mats (embalsados). Open marsh areas are also dominant in this area as the drainage of this basin is poorly defined. (iii) The Southern region is the lowest area of the wetland, where all the water drains before entering into the Corriente River. In this area, the lakes have a similar dimension as the Northeastern region but are characterised by an elongated shape (in a NE–SW direction).

We found a valuable guideline to determine the possible geneses of the large lakes in the general classifications of the floodplain lakes (e.g. Hutchinson, 1957). Two sub-types are usually differenced, which seem to be exemplified in Northeastern and Southern regions. On the one hand, the levee lakes are characterized by an elongated morphology parallel to the river course. Thus, the major axes of the large lakes of the Southern region are parallel to the central longitudinal band where it is hypothesized the location of the old Paraná riverbed. The oxbow lakes are the second large sub-type of floodplain lakes. These lakes are generated when the meanders are cut off from the river course. The lower slope of the Northeastern region could cause a winding course of the ancient Paraná River. Note that the direction of the Southern basin of Laguna Iberá strayed off the general NE–SW direction of the large lakes of the Southern region. The origin of this basin seems to be related with the water outflow into the macrosystem from Río Miriñay (from the east, *Esteros del Miriñay*).

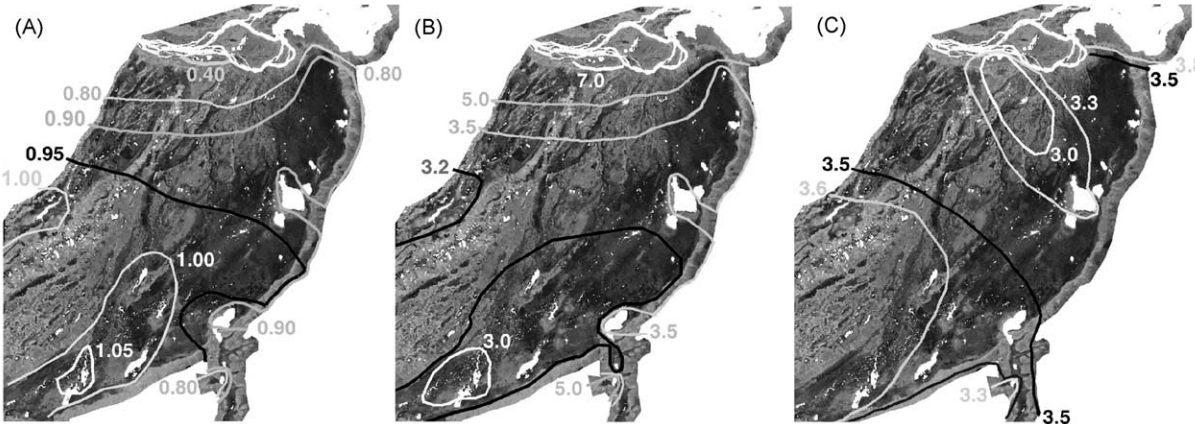

Fig. 3. Spatial distribution of the seasonal average (1997–2001) of several limnological variables in the lacustrine system of Ibera wetland and the surrounding environment. Secchi depth (m^{-1}) (A); nephelometric turbidity (NTU) (B); dissolved organic matter ($mg\,L^{-1}$) (C). Because of the degradation of plant material is also a main source of dissolved organic (humic) matter, the area of lowest DOM could be related with the low ratio of perimeter: area (L. Luna) and with the differences of littoral vegetation in the area of L. Cambí Retá and the Paraná floodplain lakes, where higher anthropic pressure is present.

The spatial distribution of the water optical properties showed strong similarities with the described geomorphological regions. The lacustrine subsystem of the Southern region showed higher S_d values, while the lakes of Northeastern and Northwestern regions showed lower transparency (Fig. 3A). Laguna Luna and Laguna Iberá showed a different behaviour with respect to the "North–South" pattern of transparency in the macrosystem. Lakes selected outside the Ibera wetland (mainly Laguna Mercedita and the active floodplain of the Upper Paraná) showed the lowest transparency of all the sampled water bodies.

The analysis of nephelometric turbidity (T_n) data confirms the characteristics observed in the analysis of S_d (Fig. 3B). The lakes in the Northeastern and Northwestern regions showed higher turbidity than the lakes in the South. Once again, the exceptions to this observation were Laguna Luna and the Northern basin of Laguna Iberá, which showed a higher T_n and lower transparency. The dissolved organic matter also showed a North–South differentiation (Fig. 3C). In this case, the lakes of the Southern region showed higher DOM concentrations. The effect of these substances into the ecosystem mainly depends on its capacity to alter the light penetration along the water column. Bracchini et

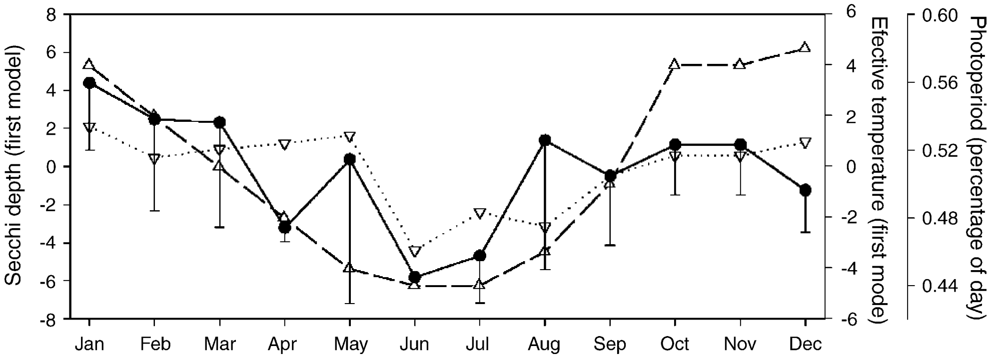

Fig. 4. Seasonal variability of the first EOF mode extracted from the Secchi depth matrix (continuous line). The bars indicate the standard deviation. The first EOF mode extracted from the effective temperature matrix (dotted line) and the weekly photoperiod (dashed line) is also shown.

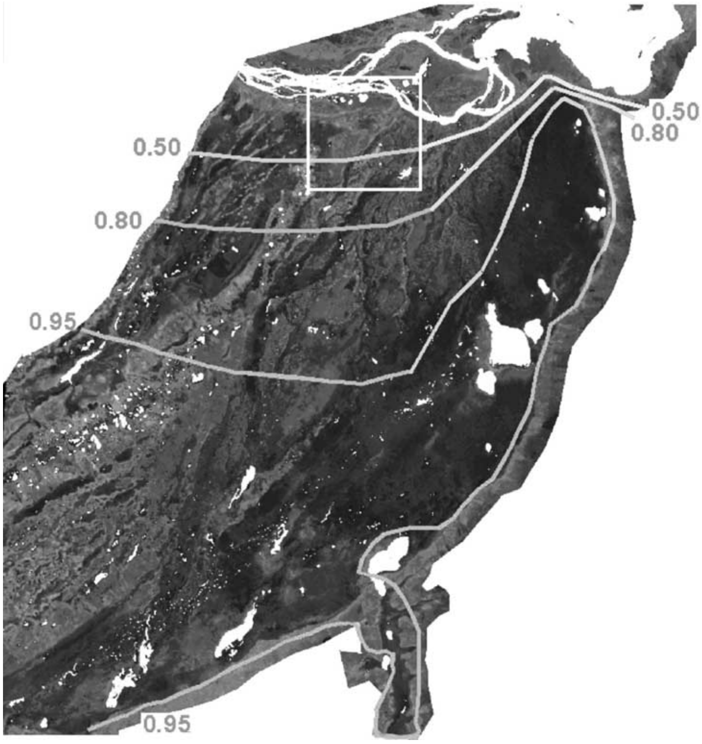

Fig. 5. Pearson coefficient of the linear regression between the first EOF mode extracted from the Secchi depth matrix and the temporal series of Secchi depth in each water sector. The white square indicates the area shown in Fig. 7.

al. (this issue) show the important role that these substances have in the light environment of the lakes of this wetland. Nevertheless, particulate matter fraction (estimated as T_n) seems to control the North–South differences of water transparency (lower S_d in the North). Higher DOM concentrations in the Southern region would contribute to reduce the transparency differences between both regions.

3.2. Temporal analysis

The temporal dynamics of the lacustrine systems within the wetland were analysed using the EOF analysis of the series of Secchi depth. The first EOF mode extracted from the covariance matrix of S_d explained the 56.4% of the variance of the collection of temporal series. The remainder of the modes always explained less 4% of the variability. The first mode showed the seasonal nature of the lacustrine system of the wetland, showing transparency maxima during June and minima during January. This pattern was significantly correlated with the weekly photoperiod (ANOVA, $R = 0.631$, $P < 0.05$) and the relative water temperature (ANOVA, $R = 0.595$, $P < 0.05$). The monthly maxima and minima of effective water temperature respectively coincide with the maxima and minima of S_d (Fig. 4). The correlation between *chl a* and S_d ($R = 0.716$) in the ecosystem seems to be the cause of the described seasonal trend. The remainder studied forcing factors (rainfall, water level and wind velocity) did not show significant correlations with the main seasonal pattern.

To compare the temporal variations of S_d in the whole lacustrine system, the temporal trend in each lake section was compared to the first EOF mode. The Pearson coefficient of the lineal correlation was used to quantify the deviation in the temporal trend of each site when compared to the general seasonal trend. The spatial distribution of the Pearson coefficient in the wetland and bordering lakes is shown in Fig. 5. Within the Southern and Northeastern regions of the wetland,

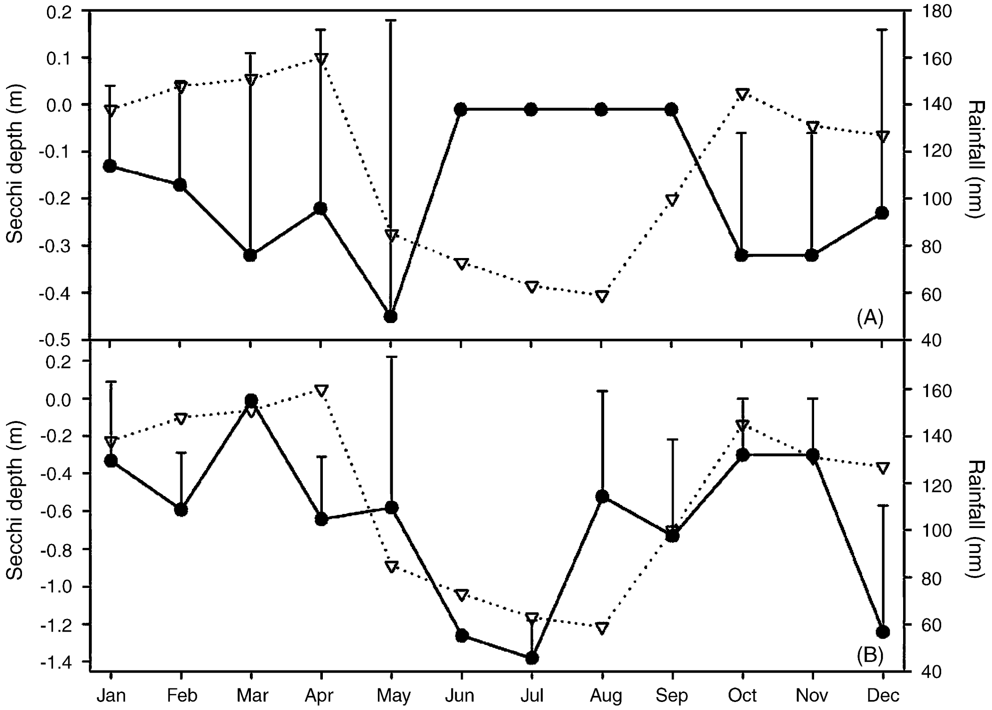

Fig. 6. Averaged seasonal variability (1997–2001) of the satellite-derived Secchi depth in the Upper Paraná floodplain lakes (A) and Yacyretá Reservoir (B). The bars indicate the standard deviation. The dotted line shows the averaged seasonal variability of the rainfall.

the temporal trend was found to closely follow the first EOF mode ($R > 0.95$). The high correlation within these lakes underlies their connectiveness. The lakes connected to agricultural areas (Northern basin of Laguna Iberá and Laguna Mercedita) show a larger deviation from the EOF mode. On site studies are also showing a different temporal evolution of the phytoplankton in the Northern basin of Laguna Iberá compared with the Southern basin and Laguna Galarza (Cózar et al., 2003). The temporal dynamics of the Southern basin of Laguna Iberá is more strongly influenced by the inflow from *Esteros del Miriñay*. Laguna Cambí Retá, in the Northwestern region, shows an even larger deviation ($R < 0.80$). All these areas (Northern basin of Iberá, Mercedita, Cambí Retá) are directly subject to nutrient inflows that may lead to changes in the expected seasonal cycle of phytoplankton. The analysis of the seasonal trend within the artificial reservoir on the Paraná River and the floodplain lakes demonstrated a completely different behaviour ($R < 0.50$). Although the irradiance cycle also plays an appreciable role in the S_d dynamics of these areas (especially in the floodplain lakes), the rainfall showed a higher influence in these areas than in the wetland lakes. The weekly rainfall explained the 26.7% of the S_d variability in the floodplain lakes and the 30.9% in Yacyretá Reservoir (Fig. 6). As water bodies located in areas of high anthropic influence, the Paraná floodplain lakes characteristically show very low values of transparency. The rain periods coincided with an increase in water transparency, apparently as a result of the “washing” of the basin when the Paraná River passes through the floodplain (Fig. 7). Similar observations have been made in Venezuela in the Orinoco floodplain (Castillo, 2000). As part of the Paraná River, rain events have also a higher influence on the water quality of the Yacyretá Reservoir, with the lowest transparency corresponding with the two periods of higher rains (March–April and October–November). This result would be supported by the solids dragging to the reservoir during the period of higher discharges from Paraná.

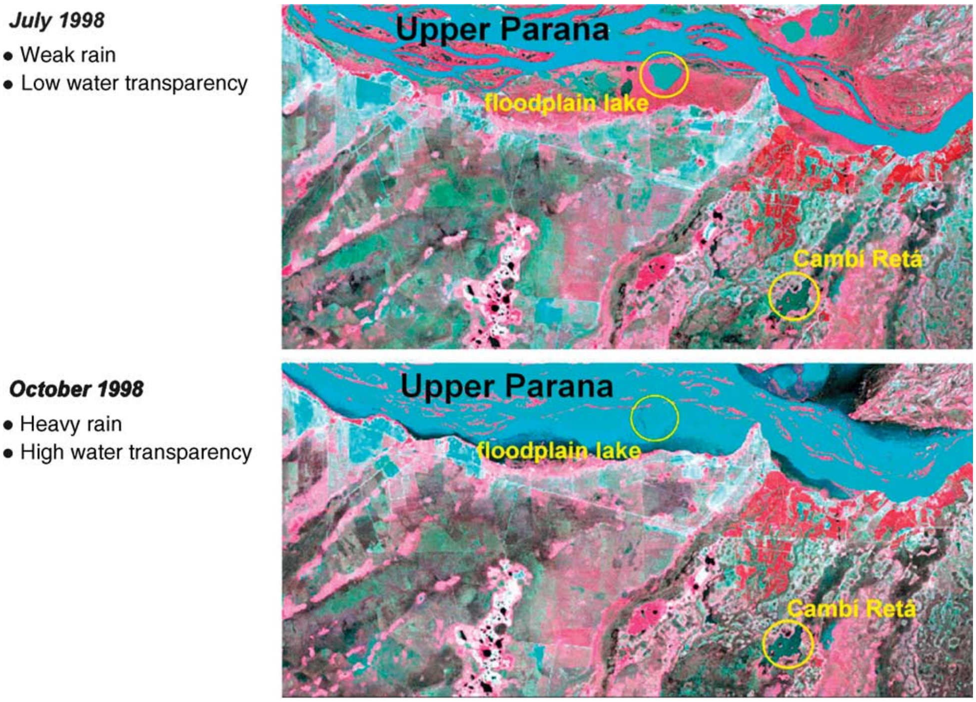

Fig. 7. Comparison of two Landsat images corresponding to the Upper Paraná floodplain lakes during July and October 1998. The location of Laguna Cambí Retá is also shown.

4. Discussion

The proposed geomorphologic regions showed also significant differences in the water optical properties (using the monthly averages of the four years of satellite data). The analysis of the spatial trends of the lacustrine system of the Ibera wetland showed a general North to South gradient of water properties. The Northwestern region is characterised by small lakes (<0.5 km^2) and, probably, it is the region more disconnected of the main drainage of the wetland. The largest lake, Cambí Retá, was characterized by a very high turbidity and very low transparency. The lacustrine subsystem of the Northeastern region shows an average transparency and turbidity of an intermediate range in the wetland. The concentrations of dissolved organic material are relatively low (<3.5 mg L^{-1}). The Southern region contains the lakes with the lowest concentration of particulate matter (as T_n), and the highest transparency. The concentrations of dissolved organic material are highest in the wetland. The most transparent waters were located in the central zone of this region, in particular L. Medina and the Northern section of L. Trin ($S_d = 1.1$ m^{-1}, $T_n = 2.8$ NTU). A general seasonal trend was demonstrated in the lacustrine system of the wetland, significantly related to the irradiance cycle. We have overlapped several “disturbed areas” by deviations from both the general North–South spatial pattern as well as the temporal variability. These wetland lakes were located in border areas of the wetland (Fig. 8). The T_n values in these disturbed areas were 30–75% higher and the S_d values 20–50% higher than the group of most transparent wetland lakes.

Water quality, in particular transparency, is strongly affected by the presence of aquatic macrophytes in shallow lakes (e.g. Madsen et al., 2001). Higher transparency facilitates the macrophytes development. Macrophytes, in turn, establish a positive feedback leading to lower concentrations of particulate matter, both phytoplankton and resuspended matter. Neiff (1981) pointed out interesting differences regarding the development of the submerged vegetation cover in the some large lakes of the Ibera macrosystem. The studied lakes in the Southern region (Fernández, Trin and Med-

Fig. 8. Bio-geographic regions of the lacustrine system of *Esteros del Iberá* wetland based on geo-morphological characteristics and water optical properties.

ina) were characterized by a great development of the submerged vegetation, reaching values of vegetal cover above 50% of the lake surface. More recent airplane flights over the Ibera lakes have confirmed these observations. The remote sensing analysis can also offer valuable information above the floating and emergent vegetation cover. Using remote sensing, we estimated a ratio for floating-emergent vegetation cover to lake area of 1% for L. Luna and L. Galarza (Northeastern region) during summer (maximum vegetation cover). In turn, this relation reached 8% in L. Trin and L. Medina (Southern region). In lakes where anthropogenic disturbances are apparent like Laguna Iberá, this relation only reached 0.05%.

The degradation of plant material is also a main source of dissolved organic (humic) matter, whose concentration was higher in the South. The elevated concentrations of DOM (mostly humic substances) in the Southern region may be also favoured by a concentration of these substances in the water as it flows South. Humic substances have a very slow degradation rate. Therefore, their concentration in the wetland should increase as water flows through areas of degraded vegetation toward the outlet in the South.

Diverse potential causes can be suggested to explain the general "North–South" pattern (S_d, macrophytes development, T_n, DOM). One the one hand, the morphological differences between the lacustrine subsystems of the Southern and Northeastern region could be suggested as a potential factor. Lakes of the Southern region are characterised by a higher perimeter to area ratio (P:A), which would favour the development of macrophytes (higher littoral area). However, no correlation between water optical properties and lake dimension (inversely related with P:A) was found. Another potential factor that could influence the spatial distribution of water quality within the wetland lakes is the possibility of superficial infiltration from the Paraná in the Northeastern region. This possibility is discussed in Ferrati and Canziani (this issue). In this context, we suggest the drainage of the wetland as a main factor to explain the observed "North–South" pattern. The hydrodynamic flow was also suggested as a determining cause in the morphological differences of the lakes. As the water from all the wetland flows South, Southern region shows a larger catchments area. The retention times towards the Southern region lakes would be shorter and shorter. These elongated lakes have a significant flowrate and in many cases (e.g. Itatí, Carayá) are more similar to slow rivers rather than lakes, facilitated by the extended shape along the NE–SW axis. This factor would also explain the low values of T_n and high transparency of L. Ipachí, in the Southern sector of *Esteros del Santa Lucía*.

Laguna Iberá and Luna (disturbed areas) strayed from the general North–South pattern of the wetland lakes. As both lakes are bordered by agricultural areas, it would appear that the presence of agricultural activities has an effect on the water quality and the temporal variability of the phytoplankton community. The presence of channels from the agricultural areas to the lake facilitates the exchange of nutrients and agricultural chemicals. Laguna Iberá and Luna are the two largest lakes of the wetland. The consequent higher residence times would hamper the restoration and conservation of their natural state. Likewise, L. Fernández could also have been affected by the nearby agricultural areas. However, the limnological characteristics of this lake do not differ from the rest of the lacustrine subsystem of the Southern region. The low retention times of L. Fernández may reduce the effect of increased nutrient loads on the ecosystem. Laguna Cambí Retá was also located in an area in which agricultural activities were present. It is also classified as a disturbed lake according to both the water optical characteristics and the temporal variability. In this case, the disconnection from the main drainage of the wetland favours a higher retention time.

The comparison of the wetland lakes with the surrounding water bodies show clear differences resulting from both water optical properties and temporal variability. The surrounding lakes show some indications of being more affected by the anthropogenic pressure (e.g. Laguna Mercedita, Upper Paraná floodplain lakes). Because of the Ibera wetland lakes were active floodplain lakes of the Paraná, it is interesting the comparison with the actual floodplain lakes of the Upper Paraná. The general seasonal trend observed in the both lakes types is related to the irradiance cycle. Aditionally, rainfall (more especifically changes in the river flow) plays also a considerable role in the dynamics of the active floodplain lakes. The incidence of these flood episodes induces a more broken seasonality in these floodplain lakes. The smoother seasonal nature of the Ibera wetland lakes compared to those just adjacent to Paraná River could have facilitated a divergence of the evolutionary process between both ecosystems. Neiff (1999) points out the progressive development of diverse vegetation in Ibera as consequence of a more predictable variability of the environment. Animal species such as the piranhas (*Serrasalmus* spp.), a predominant fish species in the Ibera lakes (Bonetto et al., 1981), are also favoured in environments with a more stable interannual seasonality (Lowe-McConell, 1975).

5. Conclusion

Esteros del Iberá can be defined as a macrosystem of marshes and lakes, whose characteristics follow a clear spatial NE–SW gradient. This gradient, which can be considered as natural, seems to be controlled by the flowrate and retention time of each lake. The seasonal dynamics of water properties is quite regular in the Ibera macrosystem and it is controlled mainly by the irradiance cycle. The effect of the rainfall differentiates the water quality dynamics of the Ibera wetland lakes and the actual Paraná floodplain lakes. The centers of anthropogenic activities in the border of the wetland appreciably influence the nearby lakes, which are strayed from the general spatial gradient and from the expected seasonal dynamics.

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