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Seasonal wetlands in the Pacific coast of Costa Rica and Nicaragua: environmental characterisation and conservation state

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ABSTRACT

Seasonal wetlands in the Pacific coast of Costa Rica and Nicaragua: environmental characterisation and conservation status

On the Pacific coast of Nicaragua and Costa Rica, rainfall patterns and clay-rich soils allow the development of extensive wetlands. These environments constitute unique habitats for the maintenance of aquatic biodiversity and provide significant ecological services to the surrounding seasonal dry forest. Despite these benefits, wetlands have been severely reduced in the last four decades, and little information is available on their biology and current conservation status. Here, we describe the main limnological traits of 30 sites representing different types of wetlands from four distinct physiographic regions: Tempisque River Lower Basin; Tempisque River Middle Basin; Delta del Estero Real River; and the Oriental Region of Nicaragua. At each site, samples were taken at the beginning (infilling phase), middle (maximum flooded areas) and end (desiccation phase) of the 2010 hydrological cycle. We analysed a set of water parameters (depth, temperature, pH, conductivity, dissolved oxygen, major ions and nutrient concentrations) and biological parameters (shoreline vegetation, chlorophyll *a*, macrophyte cover) and assessed the conservation status of wetlands using the Index of the State of Conservation of Shallow Lentic Ecosystems (ECELS). In most sites, the water was relatively clear with near basic pH-values, low conductivity, and low levels of dissolved oxygen, nitrates, nitrites, phosphates and sulphates. Chlorophyll *a* and alkalinity varied through the season and among regions. Ion concentrations were generally low in most wetlands except for those close to estuarine and marine coastal areas. A total of 49 taxa of aquatic plants were found in the study sites, the most common being the emergent *Typha domingensis* and *Thalia geniculata*, and the floating *Pistia stratiotes* and *Eichhornia crassipes*. Wetlands within the same region exhibited great similarity in their aquatic plant communities but not necessarily in their physicochemical attributes. According to the ECELS index, wetlands could be ranked from medium to good quality, although most of them are threatened by anthropogenic impacts, including those protected at Delta del Estero Real Nature Reserve (Nicaragua) and Palo Verde National Park (Costa Rica).

Key words: Palo Verde National Park, Delta Estero Real Natural Reserve, Central America, macrophytes, wetland conservation, tropical limnology, tropical dry forest.

RESUMEN

Humedales estacionales de la costa Pacífica de Costa Rica y Nicaragua. Caracterización ambiental y estado de conservación

En la costa Pacífica de Nicaragua y Costa Rica, el régimen pluvial y los suelos ricos en arcillas permiten el desarrollo de extensos humedales. Estos ambientes constituyen hábitats únicos para el mantenimiento de la biodiversidad acuática y proporcionan servicios ecológicos importantes para el bosque seco estacional circundante. A pesar de estos beneficios, los humedales se han reducido drásticamente en las últimas cuatro décadas y actualmente se dispone de poca información sobre *su biología y estado de conservación. En este trabajo describimos los principales atributos limnológicos de 30 sitios que representan diferentes tipos de humedales de cuatro regiones fisiográficas distintas: la Cuenca Baja del Río Tempisque; la Cuenca Media del Río Tempisque; Delta del Río Estero Real y la Región Oriental de Nicaragua. En cada sitio, se tomaron muestras al inicio (fase de inundación), mitad (máxima inundación) y final (inicio de fase de desecación) del ciclo hidrológico del 2010. Se analizó un conjunto de variables físico-químicas del agua (profundidad, temperatura, pH, conductividad, oxígeno disuelto y concentración de iones principales y nutrientes) y biológicas (cobertura de vegetación litoral y de macrófitos, clorofila-*a*) y evaluamos su estado de conservación mediante el Índice del Estado de Conservación de los Ecosistemas Lénticos Superficiales (ECELS). En la mayoría de sitios, el agua es relativamente clara, con pH casi básico, baja conductividad y bajos niveles de oxígeno disuelto, nitratos, nitritos, fosfatos y sulfatos. La clorofila* a *y la alcalinidad varían a través de las estaciones y entre las regiones. Las concentraciones de iones fueron bajas en todos los humedales a excepción de aquellos situados en lugares cercanos a zonas estuarinas o marinas. Observamos un total de 49 taxones de plantas acuáticas en nuestros muestreos, siendo las más comunes las emergentes* Typha domingensis *y* Thalia geniculata *y las flotantes* Pistia stratiotes *y* Eichhornia crassipes. *Los humedales dentro de la misma región muestran también gran similitud en sus comunidades de plantas acuáticas, pero no necesariamente en sus atributos fisicoquimicos. Según el índice ECELS, los humedales estacionales podrían ser clasificados como de calidad media a buena, aunque la mayoría de ellos están amenazados por impactos antropogénicos, incluyendo humedales protegidos, como la Reserva Natural del Delta Estero Real (Nicaragua) y el Parque Nacional Palo Verde (Costa Rica).*

Palabras clave: *Parque Nacional Palo Verde, Reserva Natural Delta Estero Real, Centro América, macrófitos, conservación de humedales, limnología tropical, bosque seco tropical.*

INTRODUCTION

Wetlands are important habitats for the maintenance of aquatic biodiversity and provide significant services as water reservoirs, groundwater recharge zones, filters for pollutants, and buffer zones in coastal regions that protect inland areas from storms and floods (Leibowitz, 2003; Mitsch & Gosselink, 2007). Coastal wetlands also act as breeding grounds for fishes and other organisms of commercial interest and play a central role in nutrient cycling. They are also known to absorb and gradually release sediments and to act as sinks for carbon dioxide and other greenhouse gases (Boavida, 1999; Mitra *et al*., 2005). Despite these benefits, wetlands are generally undervalued and suffer from over-exploitation and disturbance by drainage, sedimentation, and pollution, factors that threaten their conservation and global functionality (Hollis *et al*., 1992). Consequently, more than 50 % of the original area covered by wetlands in North America has been lost since colonial times (Tiner, 2005); and the reduction reported in European countries might be even higher (Angélibert *et al*., 2004; Airoldi & Beck, 2007). In tropical areas, the situation could be even worse, although there is relatively little information available on the conservation status of wetlands for most countries included in this region (Junk, 2002; Mitra *et al*., 2005).

Along the Pacific coast of Central America, more than 70% of the original area covered by seasonal wetlands has been transformed into lands for agriculture, aquaculture production, or urban development (Jiménez-Ramón, 1999; Ellison, 2004). This region is characterised by a warm climate and a highly seasonal rainfall regime; conditions that allow the development of seasonal dry forest, perhaps the most endangered terrestrial ecosystem in the Tropics (Janzen, 1988). Thus, the reduction of wetlands there represents not only a significant loss of biological diversity but also a noticeable decrease of the flow of materials and biomass from the aquatic to the surrounding dry forest (Mora *et al*., 2012).

The largest and most important wetlands along the Central American Pacific coast are those located in Bahía de Jiquilisco (El Salvador), at the estuary of the Estero Real River in Golfo de Fonseca (Honduras-Nicaragua), in the Región Occidental de Nicaragua (western Nicaragua), and in the Lower Basin of the Tempisque River (northwestern Costa Rica). The hydrology of these wetlands appears to be tightly associated with temporal changes in rainfall and many of them are waterless during the driest months of the year. There is a general lack of knowledge on the limnological characteristics and seasonal dynamics of these systems. Furthermore, there is no adequate diagnosis of the wetlands that remain in the region, although several of them are included under some category of protection. Those in Estero Real and in the lower Tempisque River basin are recognised to be wetlands of international importance under the Ramsar Wetland Convention (http://www.ramsar.org/pdf/sitelist.pdf).

As part of a larger effort to characterise wetlands along the Pacific coast of Nicaragua and Costa Rica and to understand the biotic communities that inhabit them, we here depict their main geographical features, describe seasonal changes in their limnological parameters during the rainy period, and provide a preliminary assessment of their macrophyte flora and conservation status.

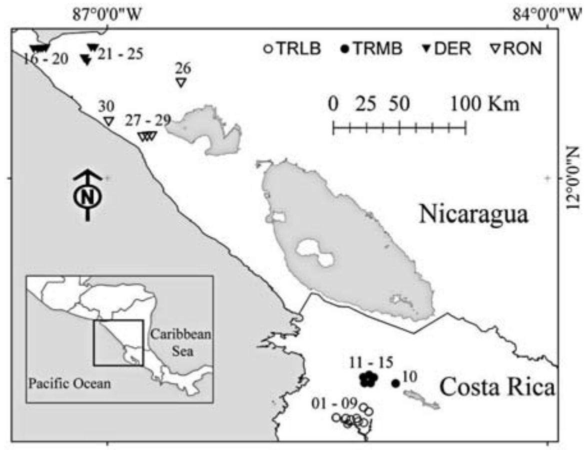

Figure 1. Map of sampled sites according to region in the Pacific coast of Costa Rica and Nicaragua. *Mapa de sitios muestreados por región en la costa Pacífica de Costa Rica y Nicaragua.*

MATERIALS AND METHODS

Study sites

Thirty sites from nineteen water bodies were non-randomly selected to ensure the representation of different sizes, land uses, connectivity, and seasonality in four geographic regions along the dry Pacific coast of Costa Rica and Nicaragua (Fig. 1). A brief description of these regions follows (see also Supplementary information, Fig. S1, available at www.limnetica.net/internet).

1. Tempisque River Lower Basin (TRLB, sites #1-9 in Supplementary information, Table S1/, available at www.limnetica.net/internet). The Tempisque River basin extends over 5406 km^2 from the Cordillera Volcánica de Guanacaste to the Golfo de Nicoya, in northwestern Costa Rica. We sampled four large wetlands in the lower basin (< 50 m elevation), standing ~19 km from the mouth of the river (Table S1, Fig. 1). These wetlands lie on alluvial deposits that are fed mainly by local precipitation and runoff, although in some sporadic years, the Tempisque River overflows during the peak of the rainy season (Trama, 2005). Three of the sampled wetlands lie within Palo Verde National Park: Palo Verde (Table S1), Bocana, and Laguna de Nicaragua. Another wetland, Tamarindo, is located on private property outside the National Park.

2. Tempisque River Middle Basin (TRMB, sites #10-15 in Table S1). The remaining six water bodies sampled in Costa Rica are ponds located at the mid-basin of the Tempisque River at an elevation between 340 and 470 m: Tenorio, Altamira, Sainalosa, Las Brisas, Eneas and Lagarta. Some of these sites are used as water reservoirs for livestock, so they have lost much of their original characteristics. All these sites are established in the stratigraphic formations of Liberia and Bagaces, originated in the Quaternary, and have low permeability (Civelli *et al.,* 2005).

3. Delta del Estero Real (DER, sites #16-25 in Table S1). Six water bodies sampled in Nicaragua are located at the Reserva Natural Delta Estero Real, a protected area some 170 km northwest of the city of Managua (Fig. 1). The Estero Real River Basin covers an area of 1919 km^2 and has characteristics of estuarine and coastal marine wetlands with tidal influence from the Golfo de Fonseca (Herrera

& Almanza, 2007). This complex wetland system includes some 338,000 hectares of mangroves and seasonal marshes and receives its water mainly from local rainfall, although the Estero Real river occasionally floods during the peak of the rainy season. Wetlands in this region have been greatly reduced, especially towards the mouth of the river, where some 39 000 Ha have been transformed into shrimp aquaculture ponds (MARENA, 2006). Pueblo Nuevo and Playones de Caterina (Table S1) lay towards the mouth of the estuary. Tonalá and Puerto Morazán are located in the south shore of the main channel, and finally Estero Real is located ~32 km east of the mouth, within a 3900 hectare floodplain on the north shore of the main channel.

4. Western Region of Nicaragua (RON, sites #26-30 in Table S1). Four ponds were surveyed (Fig. 1): Dos Motes, San Jorge Izapa, Los Corrales, and Palermo. The first three are naturalised ponds that provide water for cattle ranching during part of the dry season. Palermo is a 10 hectare pond that is fed by runoff and a small channel, so water during the dry season lasts longer, and some years it does not dry completely.

Limnological characterisation

Studied wetlands were georeferenced with GPS and mapped over GoogleEarth® images using ArcMap® (ArcGis® version 10.0) to generate coverage polygons for wetlands and associated

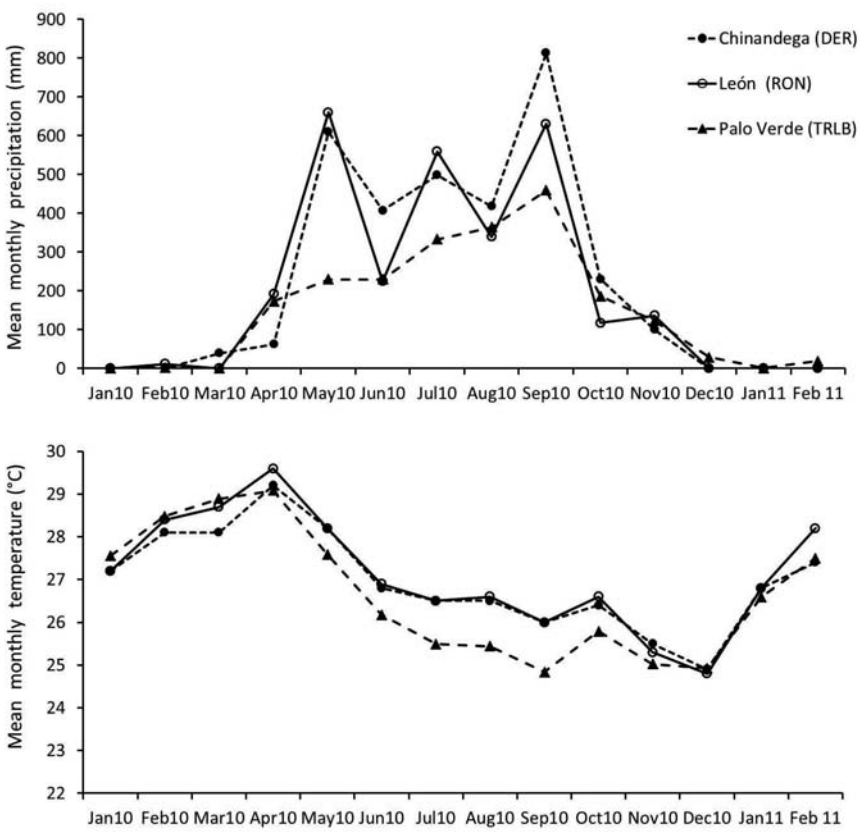

Figure 2. Mean monthly rainfall and mean monthly temperatures in Chinandega (DER), León (RON) and Tempisque Basin (TRLB). *Precipitación media mensual y temperatura media mensual en Chinandega (DER), León (RON) y la Cuenca del Tempisque (TRLB).*

vegetation. With the vector information of each coverage, we proceeded to obtain basic geographic information (area, perimeter and geometry) using the "Utilities: Calculate Areas" of the Spatial Statistics Tools ArcToolBoox® version 10.0.

To characterise the physicochemical and biological attributes of the studied wetlands, we conducted surveys in three different months: June 2010, September 2010, and January 2011, which corresponded to the beginning (infilling period), middle (maximum flooded areas) and end (desiccation period), respectively, of the 2010 hydrological cycle. General information about wetland type, hydrology, connectivity, naturalness (artificial, naturalised, and natural), water source, estimated age of the wetland (recent, historical, and geological), land uses, and impacts were noticed at each sampled site. In addition, general conditions during data acquisition (temperature, cloud cover, and precipitation), wetland morphology, depth and width of the water surface, type of substrate, and dominant species of macrophytes and vegetation cover were recorded. We measured water temperature, pH, and electrical conductivity (mS/cm) *in situ* using portable probes (Hanna® pH/EC meter HI 98130) and estimated dissolved oxygen (mg/L) using an AquaMerck® Winkler test kit. Relative water transparency was measured using a Snell tube. At each site, filtered and unfiltered water samples were collected in polyethylene bottles, transported at 4 °C, and stored in the laboratory at −20 °C for chemical analyses. Chlorophyll-*a* was extracted with acetone from the cellulose filter and analysed using spectrophotometry following Jeffrey & Humphrey (1975). Dissolved nutrients (nitrate, nitrite, ammonium and phosphate), chloride, sulphate and alkalinity were analysed using AquaMerck® and Spectroquant-Merck® test kits and a BioSpec-1601 Shimadzu spectrophotometer (in the case of nutrients and sulphate). A 100 ml water sample fixed in the field with HNO_3 was used for cation (Ca^{+2}, Mg^{+2}, K^{+}, Na^{+}) analyses, using ion chromatography at LASEQ laboratory (Universidad Nacional de Costa Rica).

Macrophytes at each site were identified *in situ* using regional guides (Crow, 2002; Gómez, 1984). When proper identification was not possible in the field, samples were collected and transported to the National Herbarium of Nicaragua (Universidad Nacional Autónoma de Nicaragua, León) for further analysis. Vegetation cover (at the water surface and at the wetlands' shore) was estimated by analysing the proportion of area covered by major species at each site.

Climate data

Monthly precipitation and temperature data for the 2010 hydrological year was estimated from Campbell Scientific weather stations. For the Tempisque River basin, the station is operated by the Organisation of Tropical Studies at Palo Verde marsh (10°20′38″N, 85°20′18″W, http://www.ots.ac.cr/meteoro/default.php?pestacion=1). Climate data for DER and RON were collected by the Nicaraguan Institute for Territorial Studies and Meteorology Directorate (INETER, 2011) from stations located at Chinandega (12°38′00″N, 87°08′00″W) and León (12°25′36″N, 86°54′48″W), respectively.

Wetland Conservation Status

We evaluated the conservation status of the studied wetlands using the *Index of Conservation Status of Shallow Lentic Ecosystems* (ECELS), established by Boix *et al.* (2010), available from http://acaweb.gencat.cat/aca/documents/ca/directiva_marc/Indicadors_Zones%20Humides_2010.pdf. This index is a relative measure of the degree of alteration of wetlands and is based on the sum of five "blocks of information": (1) the slope and presence of buildings or landfills on the shoreline, with a maximum score of 20 pts that is corrected if the shoreline is steep or has constructions; (2) the impact of infrastructure (roads, property) and human uses, with a maximum score of 20 pts that is corrected if the wetland shows signs of pollution or water extraction; (3) the water quality, which is assessed by colour/turbidity and odour and has a maximum score of 10 pts; (4) the diversity and cover of emerging helophytes, extension of the perimeter, and temporality, with a maximum score of 30 pts that is corrected if there is over dominance of one species; and (5) diversity and cover of submerged and floating vegetation, with a maximum score of 20 pts that is corrected if there is dominance of floating algae or aquatic lentil (*Azolla* sp). The highest value on the ECELS index is 100, denoting wetlands with no disturbance. The final score of the ECELS index, obtained from the sum of the blocks, categorizes the quality of the wetland into five quality classes: (a) very good (range 80-100); (b) good (range 60-80); (c) medium (range 40-60); poor (range 20-40); and very poor (range 0-20). Although the index was conceived for wetlands in the Mediterranean

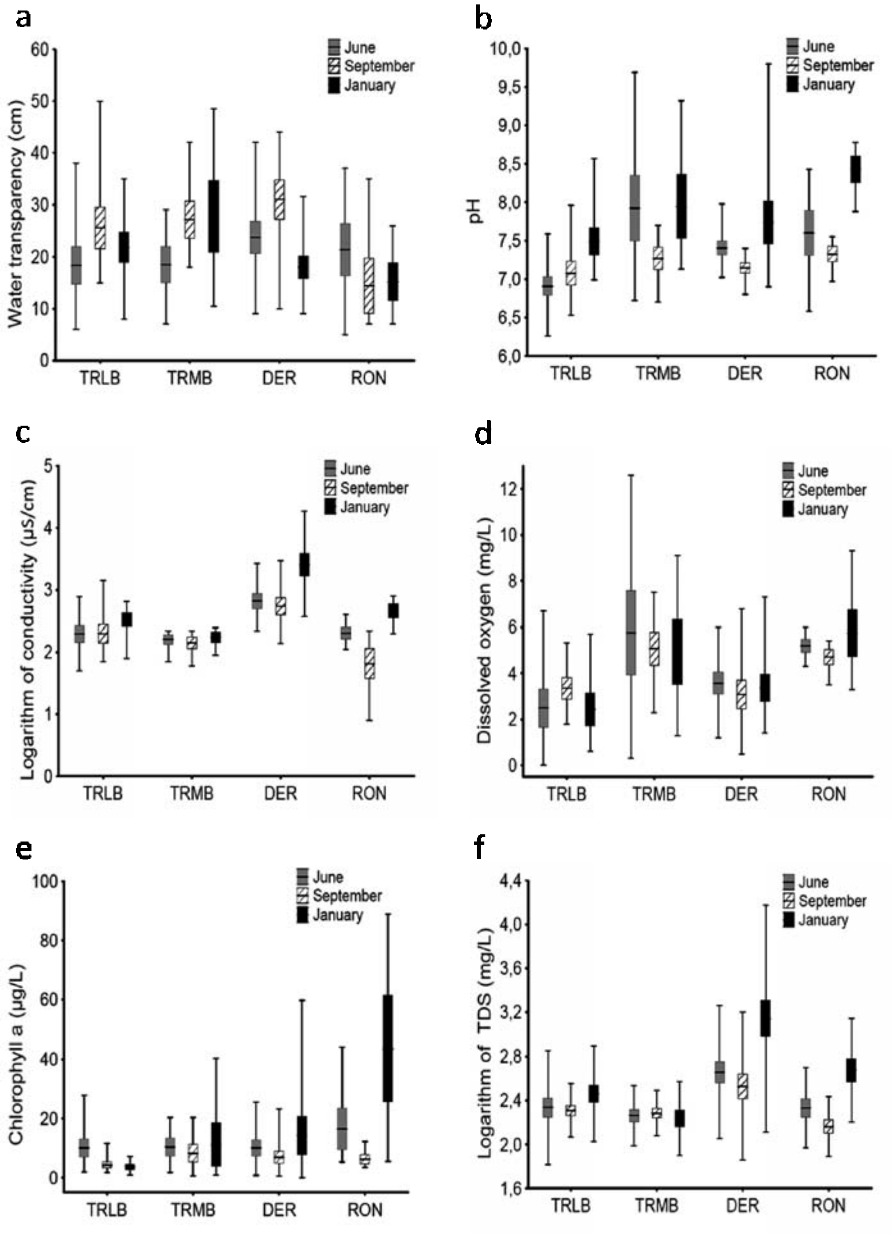

Figure 3. Seasonal change in water attributes of wetlands according to region. (a) Transparency; (b) pH; (c) conductivity; (d) dissolved oxygen; (e) chlorophyll *a*; and (f) total dissolved solids. *Cambio estacional en características del agua en humedales por región. (a) Transparencia; (b) pH; (c) conductividad; (d) oxígeno disuelto; (e) clorofila* a*; (f) solidos totales disueltos.*

region, it is also applicable to the tropical region under study. First, the index evaluates the main anthropogenic impacts on wetland environments and their surrounding areas. The Pacific slope is one of the most disturbed regions in Central America, so most habitats there have been affected by anthropogenic causes. In addition, wetlands in dry environments mainly depend on the marked seasonality in rainfall patterns, which resemble the situation of many Mediterranean wetlands. Both regions are also known for their high biodiversity, which is considered in the fourth and fifth blocks of the index.

Statistical analyses

Descriptive statistics and the comparison of the means of selected continuous variables studied during the sampling periods were performed using analysis of variance for repeated measures, using region as the between subjects' factor and month as the within subject factor. A Mauchly (1940) test was used to evaluate the assumption of sphericity; Greenhouse-Geisser correction on the degrees of freedom was performed if the data violated this assumption. The existence of patterns in physico-chemical data of the studied variables was determined via principal component analysis (PCA) using a correlation matrix. To correct for large deviations from normality, the variables of area, elevation, conductivity, dissolved oxygen, chloride, phosphates, and sulphates were $\log_{10}(x + 1)$-transformed, whereas macrophyte and riparian vegetation covers were transformed using the arcsine of their square root before the PCA. All statistical analyses were implemented in the program SPSS (version 19, IBM Corporation).

RESULTS

Characterisation of wetlands and climate of the area

The prospected wetlands vary in their geographic attributes, although within each region, they tend to share several features (Table S1). Most of the studied wetlands are natural systems or have been naturalised in historical times. An exception is Tenorio, the only artificial reservoir included in the study. The dimensions of these wetlands differ markedly: from small water bodies less than half a hectare (Tamarindo, San Jorge, Dos Motes) to those with a surface of more than a thousand hectares (Palo Verde, Laguna de Nicaragua, and Estero Real, Table S1). Most studied wetlands are temporary and dry completely some months per year, except for Tamarindo, Tenorio, Eneas, Las Brisas, and Sainalosa. The first two are artificially permanent (Table S1).

As with other places along the Pacific coast of Central America, the climate in the study region is warm, isothermal, and with an irregular rainfall pattern. Mean monthly temperatures ranged between 24.8 °C (in December) to 29.6 °C (in April, Fig. 2), and no major differences were observed among regions. However, strong rainfall seasonality, which included a five-month dry season, was recorded during the study (Fig. 2). Overall, the rainy season starts in late April and ends around December. Considerable differences in overall annual rainfall during the studied period were observed among regions: the Tempisque Basin was significantly dryer than Estero Real and the Occidental Region of Nicaragua (Fig. 2).

Limnological characterisation

During our surveys, the water temperature ranged from 23.2 °C at Altamira (TRMB) to 34.0 °C in Playones de Caterina (DER), both measured during January. Despite these differences, the mean water temperatures did not differ significantly among the regions ($F_{3,26} = 3.22$, $p = 0.05$), although some differences were noticed among sampling months ($F_{2,52} = 4.31$, $p = 0.03$).

In most sites, water transparency was relatively high, except in Tamarindo (TRLB), Palermo, and San Jorge (RON). In general, this parameter did not change throughout the year ($F_{2,52} = 2.77$, $p = 0.07$) nor among regions ($F_{3,26} = 1.02$, $p = 0.39$; Fig. 3a).

Most water samples showed neutral or slightly basic pH-values (7.0-8.0), but the mean acidity differed among sampling months ($F_{2,50} = 16.82$,

$p < 0.01$). Thus, for all sites except those in TRLB, the pH-values were lower during the months with the highest precipitation (September) and were higher in January, when the wetlands started to dry (Fig. 3b). The mean pH values also varied among regions (Fig. 3b, $F_{3,24} = 3.86$, $p = 0.02$). The mean electrical conductivity was close to 1 mS/cm, but high variation was observed among regions ($F_{3,26} = 6.64$, $p < 0.01$), with the highest values in sites at DER (Fig. 3c). This parameter also varied seasonally ($F_{2,50} = 4.28$, $p = 0.02$), with the lowest conductivities measured in the middle of the wet season (Fig. 3c). The mean dissolved

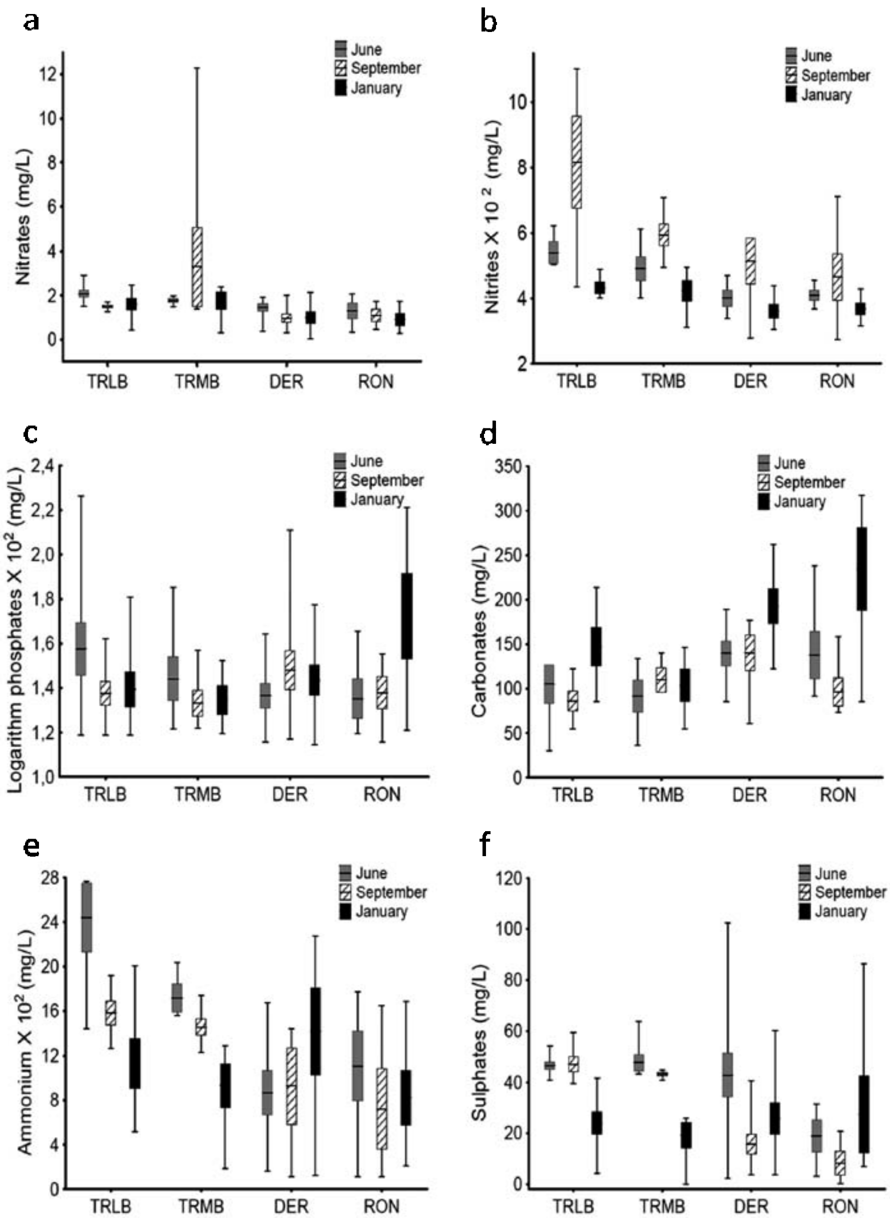

Figure 4. Seasonal change in selected nutrients and ionic concentrations of wetlands according to region. (a) Nitrates; (b) nitrites; (c) phosphates; (d) alkalinity; (e) ammonium; and (f) sulphates. *Cambio estacional en concentraciones de nutrientes e iones en humedales por región. (a) Nitratos; (b) nitritos; (c) fosfatos; (d) alcalinidad; (e) amonio; y (f) sulfatos.*

oxygen concentration was 3.8±2.3 mg/L, with several sites under 1 mg/L, up to a maximum of 12.0 mg/L in Sainalosa (TRMB); regional ($F_{3,25}$ = 3.27, p = 0.03) but not seasonally effects ($F_{2,54}$ = 0.17, p = 0.84) were recorded for this parameter (Fig. 3d). The mean chlorophyll-*a* concentration was 11.0±15.7 µg/L, ranging from 0.1 µg/L to 88.9 µg/L (Fig. 3e). A seasonal effect was noticed ($F_{2,46}$ = 5.87, p < 0.02) showing a minimum in the middle of the rainy season and a maximum by the end of the hydroperiod in three of the four regions (except in TRLB). Variation among regions was only marginally significant ($F_{3,23}$ = 2.98, p = 0.05) with higher concentrations in wetlands at RON (Fig. 3e). In addition, the sampled wetlands showed low levels of total dissolved solids (calculated from the sum of concentrations of all analysed ions); regional ($F_{3,24}$ = 9.84, p < 0.01) and seasonally ($F_{2,48}$ = 10.47, p < 0.01) effects were recorded for this measure (Fig. 3f).

Nitrate concentration was lower than 2 mg/L in most samples, except at Palo Verde and Laguna Nicaragua (2.0-3.0 mg/L), and at Tenorio, which recorded the highest observed value in September (12.3 mg/L). Regional ($F_{3,23}$ = 7.14, p < 0.01) but not seasonal ($F_{2,46}$ = 2.98, p = 0.07) effects were observed in mean nitrate concentration (Fig. 4a). In contrast, nitrite concentrations were lower than 0.2 mg/L, and both seasonal ($F_{2,46}$ = 12.98, p < 0.01) and regional ($F_{3,23}$ = 5.20, p < 0.01) variations were noticed (Fig. 4b). Reduced phosphate concentrations (< 0.50 mg/L) were recorded throughout the rainy season in most samples, with maximum values recorded up to 1.83 mg/L. However, no seasonal ($F_{2,46}$ = 1.04, p = 0.36) or regional ($F_{3,23}$ = 0.90, p = 0.46) effects were noticed for this parameter (Fig. 4c).

Low levels of ion concentrations were observed in all wetlands, although some variation was recorded among samples. Alkalinity ranged between 31 and 329 mg/L (Fig. 4d) and differed among sampling months ($F_{3,46}$ = 8.25, p = 0.01) and regions ($F_{3,23}$ = 12.94, p < 0.01). Observed ammonium levels ranged between 0.01 and 0.24 mg/L. Seasonal ($F_{2,52}$ = 4.36, p = 0.07) but not regional ($F_{3,26}$ = 1.99, p = 0.14) effects in mean ammonium concentration were observed (Fig. 4e). On the other hand, sulphates were lower than 100 mg/L at all sites except Playones de Caterina (DER) at the end of the rainy season (102.4 mg/L). Despite this variation, no seasonal ($F_{2,46}$ = 0.24, p = 0.79) or regional ($F_{3,23}$ = 0.89, p = 0.45) effects were noticed (Fig. 4f). The concentration of chloride was usually lower than 188 mg/L, although during January, it increased to 3600 mg/L at Estero Real. Similarly, the highest concentrations of Ca^{+2} (330 mg/L), Mg^{+2} (620 mg/L), Na^{+} (6500 mg/L) and K^{+} (144 mg/L) were observed at Estero Real at the beginning of the dry sea-

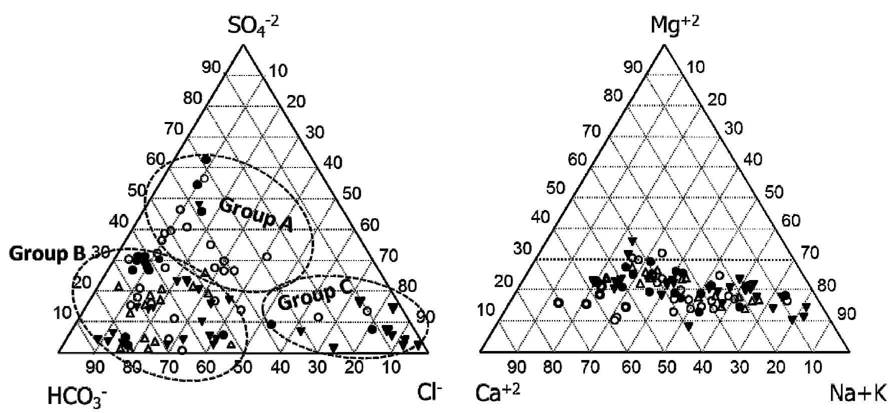

Figure 5. Ternary diagram of the major cations and anions in water of wetlands according to region: TRLB (●), TRMB (▼), DER (○), RON (△). *Diagrama ternario de los cationes y aniones del agua de humedales por región: TRLB (●), TRMB (▼), DER (○), RON (△).*

son. However, seasonal effects were noticed only in Ca^{+2} mean concentrations ($F_{2,46}$ = 6.54, p = 0.014). In contrast, except for Na^{+}, mean concentrations of all other cations vary among regions ($F_{3,23} > 4.02$, $p < 0.02$ in all cases).

Figure 5 shows the position of samples from each region on a Piper ternary diagram according to relative ionic composition. Anionic composition showed three patterns: Group A, which included wetlands with slightly higher levels of SO_4^{-2} ($SO_4^{-2} >$ $HCO_3^{-} > Cl^{-}$), including mainly samples from TRLB and TRMB collected early in the rainy season (June); Group B, which included wetlands dominated by HCO_3^{-} ($HCO_3^{-} >$ $SO_4^{-2} > Cl^{-}$), with samples mostly from DER and RON (and a few from TRMB) collected late in the rainy season (January); and finally Group C, which included wetlands that are dominated by chlorides ($Cl^{-} \gg SO_4^{-2} >$ HCO_3^{-}), mainly those in DER. Cation composition does not allow further differentiation among regions (Fig. 5) and the most frequently observed pattern was $Na^{+} > Ca^{+2} >$ $Mg^{+2} > K^{+}$, although calcium was dominant in wetlands at TRLB and TRMB during September and June, respectively.

A PCA performed over the above physico-chemical parameters together with estimated depth and macrophyte cover allowed discrimination of some of the studied wetlands. The first component accounts for 30.5% of the variance and differentiates mainly DER wetlands from those in other regions (Fig. 6). This component is negatively correlated with conductivity, Cl^{-} and cation concentrations and, to a lower extent, SO_4^{2-} and HCO_3^{-} concentrations, whereas depth, NO_3^{-} and NO_2^{-} are positively related to conductivity. The second component accounts for 13.2% of the variance and separates wetlands with higher oxygenation and chlorophyll-*a* concentration from those with higher macrophyte cover and water transparency regardless of their geographical region. Both components also allow discrimination between the artificial wetland Tenorio (site #10) and all other studied sites (Fig. 6).

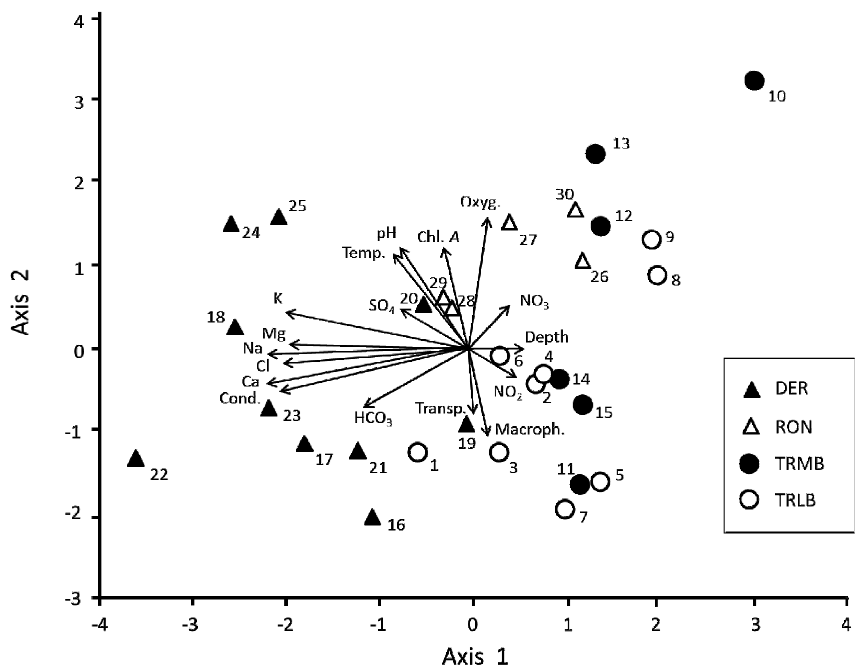

Figure 6. Relative position of sampled sites according to region as determined using the first two components extracted via PCA. The first component accounts for 30% of the variance, and the second component accounts for 13.2% of the variance. Strength and direction of the correlation between physico-chemical variables (and vegetation cover) and the PCA factors are represented by the arrows. *Posición relativa de sitios muestreados por región, determinada por los dos primeros componentes del PCA. El primer componente explica el 30% de la variación, mientras que el segundo el 13.2% de ella. Las flechas representan la dirección y magnitud de la correlación entre variables fisicoquímicas (y de cobertura de vegetación) y los componentes del PCA.*

Aquatic vegetation

A total of 49 species of macrophytes, including 34 families were found (Supplementary information, Table S2, available at www.limnetica.net/internet). This sample comprises one species of algae (*Chara vulgaris*) and five species of ferns (*Acrostichum aureum, Azolla carolinensis, A. microphylla*, *Salvinia minima* and *Thelypteris dentate*). The other 43 species are angiosperms. The most common emergent species were *Typha domingensis* and *Thalia geniculata,* present in 53% and 30% of the sites, respectively; the most common floating macrophytes were the water lettuce *Pistia stratiotes* and the water hyacinth *Eichhornia crassipes*, found in 36% and 33% of the sites, respectively. Other common species include emergent taxa such as *Eleocharis elegans*; submerged species such as *Chara vulgaris* or *Ceratophyllum muricatum;* arbustive species growing around water bodies such as *Gliricidia sepium*, *Cocobola caracassana;* and floating species as *Nymphaea ampla*, *Salvinia minima* and *Azolla microphylla*. These last three species, as well as *Pistia stratiotes* and *Eichhornia crassipes,* can cover huge areas preventing light penetration in the water column. Aquatic vegetation richness varies greatly among the samples: from 2 species in Tenorio (*Chara vulgaris* and *Juncus* sp.) to 29 species in Pueblo Nuevo in DER.

In general, wetlands within the same region exhibit great similarity of aquatic vegetation. A multidimensional scaling ordination of the studied sites using the Jaccard coefficient reveals that aquatic vegetation separates wetlands from each sampled region along the first dimension (Fig. 7).

Wetlands conservation status

Our sites show different levels of disturbance, and the source of impacts and intensity vary among wetlands. The main observed threats were the use of wetlands as water reservoirs for cattle and other domestic animals, the expansion of the agricultural frontier and modifications at the wetland shoreline, the presence of exotic grasses, and the introduction of exotic fishes (Table S1). In a few ponds, human developments and domestic garbage were also visible. Some of these impacts affect wetlands that are located within protected areas, such as Palo Verde, Laguna de Nicaragua, and Bocana in TRLB

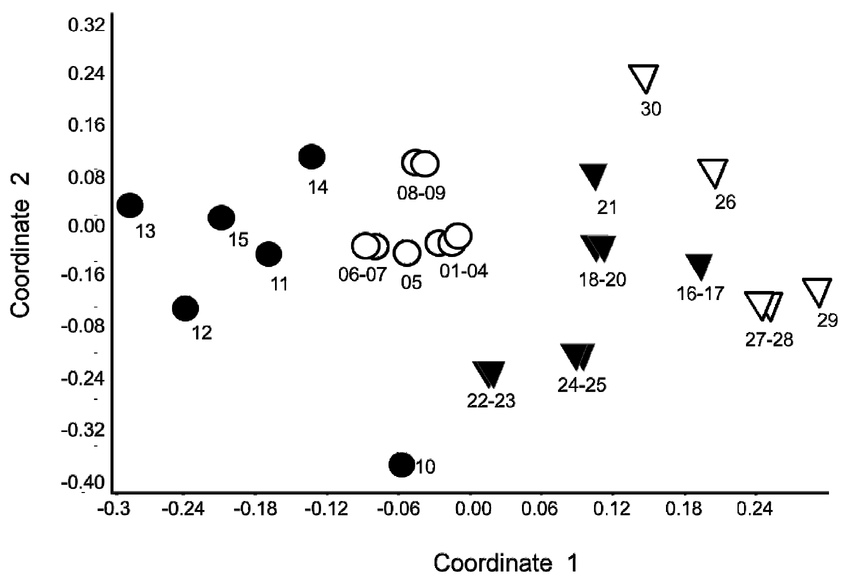

Figure 7. Multidimensional scaling plot showing ordination of sampled sites according to region based on Jaccard similarities of observed macrophytes. Regions as in Figure 5. Reability measured as Kruskal stress = 0.1504. *Ordenamiento de sitios muestreados por región a partir del escalamiento multidimensional basado en similitudes de Jaccard de los macrófitos observados. Regiones como en la Figura 5. Fiabilidad medida con el estrés de Kruskal = 0.1504.*

(Table S1). On the other hand, Estero Real sites were heavily impacted by intensive fishing with trammel nets. Furthermore, several wetlands in DER and most in TRLB are densely covered by emergent vegetation, especially *Typha domingensis*. Consequently, there is an important reduction of spaces with open water, a situation that might alter some of the ecological functions of these wetlands.

Results on the application of the ECELS index (Supplementary information, Table S3, available at www.limnetica.net/internet) allow objective estimation of the degree of disturbance of wetlands. The first block assigns the highest value if the shore has a gradual slope without any infrastructure obstruction, conditions that prevail along Estero Real, Palo Verde and Laguna de Nicaragua but not in the remaining wetlands. For the second block, the two wetlands and Bocana reached the maximum score, whereas scores for the other wetlands were reduced due to the impacts of ranching and wetland use, especially in Dos Motes, Tamarindo, Tenorio and Los Corrales (Table S3). Most wetlands scored high on the third block (water quality), suggesting that most sites have transparent waters with no odours. Notable exceptions were Dos Motes, La Lagarta and San Jorge, where water is stagnant and turbid. The fourth block, which measures the extent and coverage of emergent vegetation was highest in Estero Real, Pueblo Nuevo, Playones de Caterina (DER) and Las Brisas (TRMB), which show high levels of plant richness, although vegetation only partially covers the shoreline even in these sites. Wetlands at TRLB show over-dominance of *Typha domingensis* and *Thalia geniculata*, and their scores were penalised in this block (Table S3). Finally, the fifth block evaluates the diversity and cover of aquatic vegetation. Estero Real, Playones de Caterina, Palo Verde, and Bocana scored higher (range 10-15) than the other wetlands due to the extent of submerged vegetation, although the score of these last two wetlands was penalised due to dominance of *Eichornia crassipes*. Tamarindo, Lagarta, Las Brisas, and Dos Motes scored lower in this block due to low submerged vegetation cover and the dominance of *Azolla microphylla*.

Overall, most sites are classified as showing good or medium quality, whereas only Estero Real is considered very good quality according to the ECELS index. On the other hand, Tenorio, Tamarindo and Dos Motes are classified as poor quality water bodies (Table S3), mainly as a consequence of their relatively low surface area and high degree of anthropogenic impact.

DISCUSSION

Along the Pacific coast of Nicaragua and Costa Rica, clay-rich vertisols, topography, and the climate regime allow for the development of extensive wetlands that are mostly temporary or, if permanent, are subject to a significant reduction in water level during the dry season. These tropical aquatic systems resemble those in the Mediterranean region that are also characterised by a marked dry period, although the latter are influenced by the increase in temperature during the summer. Mediterranean wetlands have been intensely studied in recent years, and seasonal changes in ionic composition (Díaz-Paniagua *et al.*, 2010; Fernández-Aláez & Fernández-Aláez, 2010), nutrient availability (Serrano *et al.* 2003), aquatic plant communities (Fernández-Aláez *et al.*, 2004), plankton (Antón-Pardo & Armengol, 2012; Rojo *et al.*, 2012) and macroinvertebrate dynamics (Neckles *et al.*, 1990; Boix *et al.*, 2001; Florencio *et al.*, 2013) have been well documented.

Like other seasonal pools in semiarid and subhumid climates (Deil, 2005), our studied wetlands exhibit large spatial and temporal variation in morphological and physico-chemical parameters that can be explained in part by the nature of their geological substrate but also by rainfall variation. Rain (and direct runoff) is the major source of water in these systems; therefore, the dynamics of chemical parameters depend largely on the rainfall regime; this association is particularly noticeable in the changes in salt concentrations (but not so much in major nutrients), which tend to fade at the peak of the rainy season. Nevertheless, not only temporal but also large spatial variations in hydrochemistry are observed. In this context, wetlands that have the greatest influence from the marine environment, i.e., those at Delta Estero Real (DER), tend to exhibit brackish waters with slightly higher concentrations of chlorides, sodium, and magnesium. Contrary to the endorheic saline systems in the Mediterranean region (e.g., Rodrigo *et al*., 2002; García-Ferrer *et al*., 2003), we did not observe a higher concentration of dissolved phosphorus in the wetlands at DER than those at the other regions.

In general, nutrient loads in the studied sites were relatively low but comparable to those reported in other Neotropical wetlands (De la Lanza-Espino *et al*., 1998; Díaz-Vargas *et al*., 2005; Mitsch *et al*. 2008; Roldán & Ramirez, 2008). In natural wetlands, dissolved phosphates tend to fluctuate slightly and are usually reported at concentrations less than 0.6 mg/L (Roldán & Ramirez, 2008). Although the levels of nitrates and phosphates recorded here are low, in some sites at RON and TRLB, the slightly higher values observed may reflect contamination from household waste and livestock. This is further supported by site differences in algae biomass, as inferred from chlorophyll *a* concentrations (Fig. 3e). Although the majority of sites show low levels of algal biomass, those in RON and TRLB show evidence of eutrophic and hypertrophic systems (OCDE, 1982).

Among the variables measured to assess water quality, dissolved oxygen is perhaps the most important to understand chemical dynamics in aquatic systems as it affects most chemical processes and is fundamental for aquatic life. Gas exchange across the water surface is an important source of oxygen, as dissolved levels are relatively low in warm tropical wetlands (Esteves, 1998). As emergent vegetation and floating plants do not provide oxygen to the water, compete for nutrients, and interfere with light penetration into the water column affecting photosynthetic activity, it is not surprising that those sites dominated by *Typha domingensis, Pistia striatiotes* and *Salvinia minima* (Table S2) show the lowest dissolved oxygen levels. In tropical regions, oxygen concentrations in wetlands at sea level are often reported at values lower than 10 mg/L, although the measure depends on temperature (Pérez-Castillo, 2004). At low concentrations (< 5 mg/L), several studies have shown negative effects in aquatic communities, reducing foraging, growth and reproductive activities (Breitburg *et al*., 1997; Connolly *et al*., 2004). Nevertheless, low oxygen concentrations seem to be the norm rather than the exception in the studied seasonal wetlands, so their aquatic communities might be somehow tolerant to these hypoxic conditions or are adapted to the thin oxygen layer localised around the roots of floating plants among the pleustal (Por & Rocha, 1998).

In our study, it is clear that we underestimated the actual macrophyte diversity in these wetlands. Palo Verde marsh provides a good example. Ten species were found in our surveys, but sixty-four more are known for this locality (Crow, 2002), including few terrestrial species that can be observed in stagnant waters. Despite they represent only such a small fraction, our samples are representative of the dominant aquatic flora at each site, as denoted by the ordination analysis that groups them by region. This pattern of close resemblance among wetlands within the same geographical region is not so clearly supported by limnological variables, as revealed by the principal component analysis. Hence, even if sites in some areas (e.g., DER) show higher average ion and conductivity levels, others (e.g., RON sites) hold higher amounts of phytoplankton (as inferred from higher levels of chlorophyll-*a*, greater amounts of dissolved oxygen and lower transparency). Other sites (mostly at TRMB and TRLB) are dominated by emergent and floating vegetation and show more transparent and less oxygenated waters, whereas the overlap in the ordination of samples according to limnological parameters is too large to allow a clear-cut differentiation of samples according to their geographic regions.

The wetland conservation strategy of Costa Rica and Nicaragua has provided some protection to their Pacific wetlands. However, it is estimated that less than 30% of the original area covered by these aquatic ecosystems currently remains in the region (Jiménez-Ramón, 1999). From our analysis, it is clear that the vast majority of seasonal wetlands that exist in both countries can be preliminarily described as medium to good quality, although even those included in the latter category suffer from anthropogenic impacts.

For sites within the Tempisque River Lower Basin, some information is available on the pollution levels of surface water. Total phosphorus concentrations are high in the drainage canals of the irrigation district surrounding the wetlands at Palo Verde National Park (Pérez-Castillo, 2004). The waters at the irrigation district are also contaminated with agrochemicals at doses that exceed levels acceptable to protect aquatic life (Pérez-Castillo, 2004). The situation in the other regions is less known, although wetlands at Delta Estero Real face similar threats (MARENA, 2006). A major challenge in these aquatic systems is the overgrowth of aquatic emergent vegetation: since the mid-1980s, wetlands along the Tempisque River Lower Basin (including those at Palo Verde) experienced the expansion of the herbaceous cattail *Typha domingensis* and the woody species palo verde *Parkinsonia aculeata* and zarza-bush *Mimosa pigra*. The explosion of these species resulted in a significant reduction of open spaces in the wetlands (Trama, 2005), which in turn has affected various taxonomic groups that require open water bodies for their survival. For example, the loss of open space has alienated waterfowl, forcing them to seek non-protected environments, a situation that disagrees with the national parks' goal of protecting aquatic species and the wetland environment (McCoy & Rodriguez, 1994; McCoy, 1996). This condition has forced the government to perform active management of wetlands to ensure open water spaces and proper functionality. The challenge in the near future is to incorporate the remaining seasonal wetlands into some category of protection and to provide support to those that require intervention.

This study should be considered a first approach to understand the limnology of seasonal wetlands that remain in the Pacific coast of Central America, environments that have been neglected from the scientific mainstream. Our work has shown the importance of seasonal variation and macrophyte composition for proper characterisation of these temporary systems and provides a limnological description of a very broad set of wetlands in an area of dry tropical forest intensely threatened by anthropic pressure. However, further characterisation of the plankton community and its dynamics, as well as the aquatic fauna associated with these environments is required to complete the baseline information needed for the protection and proper management of these ecosystems.

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