Effects of Changing Rainfall on the Limnology of a Mediterranean, Flowthrough-Seepage Chain of Lakes

key words: geographical setting, groundwater, nutrients, planktonic biomass, surface water flux

Abstract

Relationships between groundwater and lake ecology are often overlooked, but they may be strong, particularly in seepage lakes. As a result, the nature and degree of groundwater effects on lakes are usually neglected. In this study interactions among rainfall, groundwater and surface water and their limnological effects were traced seasonally for two years of changing rainfall in a Spanish flowthrough, seepage lake complex. Cumulative rainfall dictated recharge of groundwater with delays of nine months. Groundwater discharge, in turn, increased surface discharge downstream. Mediated by the geographical setting of lakes, both fluxes impinged on lake water renewal time, but effects of the latter on limnological variables were much stronger at the district scale than at the single lake scale. These water-renewal effects included the following: decreasing salinity, total phosphorus concentration and phytoplankton biomass and increasing water transparency and total nitrogen concentration as water renewal shortened, the nitrogen effect arising because of nitrate-rich water entering the lakes as groundwater levels rose. This complex response of a Mediterranean lake district to water availability may also be expected in cold temperate lakes as climate change effects become stronger.

1. Introduction

Lakes are subject to many scales of environmental variability (IMBODEN and WÜEST, 1995). The seasonal one is perhaps the more often studied, but diel, daily, weekly, yearly and interannual variability of lakes have been examined as well (O’SULLIVAN and REYNOLDS, 2003; WETZEL, 2001). Sources of lake variability are mostly of climatic origin, but man-made impacts are also common (HARPER, 1992). Irradiance, air temperature, heat exchange and wind experience their own internal variabilities that impinge on lake dynamics resulting in ecological effects at many temporal scales (IMBODEN and WÜEST, 1995).

Variability of water inputs and their changing impacts on lake functioning have seldom been reported (TOWNLEY et al., 1993). Since most limnological studies have been carried out in latitudes where water is rarely limiting, the scarcity of limnological studies addressing the effects of low water inputs on lake dynamics is not surprising. However, studies of this kind should be fostered in view of the shortages of water that many areas of the world will experience in the near future as a result of climate change (ARNELL et al., 1996; ALVAREZ-
COBELAS et al., 2005a). Such studies may aid in environmental mitigation of climate change effects on lakes.

With regards to their water supply, lakes are usually described as either “drainage” or “seepage” lakes (WETZEL, 2001). Drainage lakes are those where input and output water occurs mainly by surface flow, whereas in seepage lakes it enters/exits mainly through groundwater exchange. Some lakes comply with both types of water supply, such as the Croatian Plitvice lakes (EMILI, 1958) and the Wisconsin lake district (KRATZ et al., 1997). Very often, groundwater and surface waters interact to render complex patterns of water supply to lakes whose water availability changes accordingly (NIELD et al., 1994). However, the effects of such a complex process on lake features have seldom been explored. More specifically, the ecological effects of changing hydraulic renewal time of surface origin have been studied (DICKMAN, 1969; WALZ and WELKER, 1998; KÖHLER et al., 2005), but nutrient and biota responses to changes in water availability, mediated by complex interactions between groundwater and surface water, have scarcely been dealt with.

Some studies have already reported that drought can affect the chemical content of lakes, particularly of those being fed by seepage (WEBSTER et al., 1996). However, few studies have considered the interactions among rainfall, groundwater, stream flow and lake dynamics at the scale of months. That water renewal time is a key factor in lake ecology is a well known topic in limnology (PIONTELLI and TONOLLI, 1964) but, despite this acknowledgement and its extensive use in early eutrophication models (VOLLWEIDER, 1976), it has been a somewhat neglected topic in the study of freshwaters, maybe because most lakes and wetlands have long residence times. It has been more often tackled in wastewater treatment (UHLMANN and HORN, 2001).

Here we report on how rainfall variability dictates groundwater supply to streams and lakes, and how this supply acts upon water residence time, and hence on lake dynamics, in a hydrologically-connected chain of lakes in Central Spain. We also show that these effects take place at a rarely studied scale because rainfall, surface and groundwater interactions result in delayed inputs of water availability to that lake system.

2. Methods

2.1. Study Site

The Ruidera lakes are situated in the Campo de Montiel area of Central Spain (Fig. 1). The entire surface catchment of all these lakes collectively covers 800 km², an area that lies between the mountain fringe of Sierra de Alcaraz in the South and La Mancha Plain to the North. Water drains to three major watersheds, but that of the Guadiana is by far the most important. Ruidera lakes are located within a Natural Park that comprises 37.72 km² (Fig. 1). They comprise 18 natural basins and a man-made reservoir (Fig. 2). These water bodies are chain-connected, small (0.1–103 ha), shallow or moderately deep (0.5–10.4 m of average depth; Table 1), SE-NW flowthrough, groundwater- and riverine-fed lakes. The lake system drains towards Peñarroya reservoir, which also stores water drained from the underlying aquifer and is used for irrigation purposes.

Ruidera lakes are basins where the Guadiana River has been dammed by natural travertine barrages. The build-up of those barrages is a mixed chemical-biological process, whereby carbonate-rich groundwater is degassed and hence the resulting bicarbonate is used by benthic plants (Charophytes and cyanobacteria). Plant photosynthesis increases water pH and carbonate precipitates upon those plants, thus slowly building a travertine barrage in the steeper areas of the riverine environment. Given enough time, barrages form chain-like lakes. This process has started 235,000 years ago and has been repeated at least four times, because barrages have also broken periodically and hence the process has started again (ORDÓÑEZ et al., 2005).

The order of the lakes from upstream to downstream is as follows: Blanca, Conceja, Tomilla, Tinaja, San Pedra, Redondilla, Lengua, Salvadora, Santos Morcillo, Batana, Colgada, Rey, Cueva Morenil- lla, Coladilla, Cenagosa and Peñarroya reservoir. All lakes, except Blanca and Cenagosa lakes, are warm
monomictic and usually stratify from May to October (Table 1). Most lakes are very similar hypsographically, being convex, except the shallower ones that are more concave. So slight changes in lake levels result in strong changes in lake volume in the deeper ones, but this is not so in shallow lakes. No islands occur in the lakes with the exception of a small one in Colgada lake. Wind fetch is short, but mixing dynamics of lakes is very rapid because of their small extension. The number of basins of all lakes is 1–3, but maximal depths of all basins of a given lake are not very different and are usually located on the main riverine axis. Groundwater inputs feed all lakes, but such a feeding may take place through point-source (e.g. subaquatic springs) and/or diffuse flows (Table 1), and hence this could be another source of among-lake variability.

The aquifer of Campo de Montiel, upon which Ruidera lakes are located, is a subhorizontal plain with undulated topography, whose thickness is very variable, reaching 300 m at either its eastern area or north Ossa de Montiel. Its average thickness ranges 75–100 m, lying on Triassic (Keuper facies) impermeable materials. It is a 2,575 km², unconfined aquifer, whose only source of recharge is direct rainfall, its discharge taking place through springs. Those located at the Southern borders of the aquifer are associated with the contact area between carbonated, permeable, Jurassic materials and the underlying impermeable Triassic materials. The remaining springs appear when topography intersects with phreatic levels. In addition to Ruidera lakes, springs also feed all streams. Regional groundwater preferentially flows in the SEE-NWW direction. Hydrologic dynamics of Ruidera lakes as related to groundwater dynamics are complex, depending upon bottom topography and its surrounding geology, but four distinct groups of lakes can be envisaged. The upper lakes (Blanca, Conceja and Tomilla lakes) respond to changes in hydraulic head very rapidly; only if the reduction of hydraulic head is very strong surface exports downstream are interrupted. The next group of basins (Tinaja, San Pedra, Redondilla, Lengua, Salvadora, Santos Morcillo and Batana lakes) is fed mostly by surface inputs from upper lakes, but some subterranean inflows can be important sometimes (Fig. 2); thus the water volume of these lakes diminishes easily when surface inflows decrease and so lake basins can even dry. Colgada and Rey lakes comprise the third lake complex, having surface and groundwater (Colgada lake only) inputs; impermeable Triassic materials at their walls and bottoms reduce water losses and hence their water levels hardly change. The lower group is embraced by Cueva Morenilla, Coladilla and Cenagosas lakes and is fed by surface inflows and small groundwater exports through the semipermeable travertine barrage of Rey lake. In addition to the regional flow sensu TOTH (1963), some local flow has been proved, connecting Redondilla with Salvadora lakes, on the one hand, and San Pedra with Batana and Colgada lakes, on the other (Fig. 2).
Table 1. Morphometric and some physical features of the studied Ruidera lakes.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Elevation (m.a.s.l.)</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Surface area (Ha)</th>
<th>Volume (Hm³)</th>
<th>Maximum depth (m)</th>
<th>Average depth (m)</th>
<th>Stratifying?</th>
<th>Relative epilimnetic volume (%)</th>
<th>Relative hypolimnetic volume (%)</th>
<th>Groundwater inputs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conceja</td>
<td>863</td>
<td>38°55′ N</td>
<td>2°48′ W</td>
<td>29.35</td>
<td>2.45</td>
<td>14</td>
<td>8.37</td>
<td>yes</td>
<td>53</td>
<td>13</td>
<td>Diffuse</td>
</tr>
<tr>
<td>Tomilla</td>
<td>863</td>
<td>38°55′ N</td>
<td>2°49′ W</td>
<td>8.76</td>
<td>0.69</td>
<td>14</td>
<td>7.91</td>
<td>yes</td>
<td>53</td>
<td>14</td>
<td>Diffuse</td>
</tr>
<tr>
<td>Tinaja</td>
<td>842</td>
<td>38°56′ N</td>
<td>2°50′ W</td>
<td>8.04</td>
<td>0.65</td>
<td>17</td>
<td>8.06</td>
<td>yes</td>
<td>52</td>
<td>15</td>
<td>Point and diffuse</td>
</tr>
<tr>
<td>San Pedra</td>
<td>836</td>
<td>38°57′ N</td>
<td>2°50′ W</td>
<td>28.61</td>
<td>2.97</td>
<td>21</td>
<td>10.39</td>
<td>yes</td>
<td>42</td>
<td>27</td>
<td>Diffuse</td>
</tr>
<tr>
<td>Lengua</td>
<td>821</td>
<td>38°57′ N</td>
<td>2°51′ W</td>
<td>20.09</td>
<td>1.36</td>
<td>14</td>
<td>6.75</td>
<td>yes</td>
<td>59</td>
<td>8</td>
<td>Diffuse</td>
</tr>
<tr>
<td>Salvador</td>
<td>814</td>
<td>38°57′ N</td>
<td>2°51′ W</td>
<td>8.73</td>
<td>0.66</td>
<td>12</td>
<td>7.55</td>
<td>yes</td>
<td>62</td>
<td>8</td>
<td>Point and diffuse</td>
</tr>
<tr>
<td>Santos Morcillo</td>
<td>812</td>
<td>38°57′ N</td>
<td>2°52′ W</td>
<td>11.71</td>
<td>0.91</td>
<td>14</td>
<td>7.8</td>
<td>yes</td>
<td>55</td>
<td>11</td>
<td>Diffuse</td>
</tr>
<tr>
<td>Batana</td>
<td>803</td>
<td>38°57′ N</td>
<td>2°52′ W</td>
<td>6.54</td>
<td>0.29</td>
<td>8</td>
<td>4.48</td>
<td>yes</td>
<td>78</td>
<td>12</td>
<td>Point and diffuse</td>
</tr>
<tr>
<td>Colgada</td>
<td>799</td>
<td>38°58′ N</td>
<td>2°53′ W</td>
<td>103</td>
<td>8.65</td>
<td>18</td>
<td>8.39</td>
<td>yes</td>
<td>51</td>
<td>20</td>
<td>Point and diffuse</td>
</tr>
<tr>
<td>Rey</td>
<td>799</td>
<td>38°58′ N</td>
<td>2°53′ W</td>
<td>37.85</td>
<td>3.67</td>
<td>20</td>
<td>9.83</td>
<td>yes</td>
<td>44</td>
<td>29</td>
<td>Diffuse</td>
</tr>
<tr>
<td>Cueva Morenilla</td>
<td>772</td>
<td>38°59′ N</td>
<td>2°54′ W</td>
<td>7.14</td>
<td>0.39</td>
<td>8</td>
<td>5.53</td>
<td>yes</td>
<td>62</td>
<td>14</td>
<td>Point and diffuse</td>
</tr>
</tbody>
</table>
The Ruidera lakes are heavily polluted by nitrate inputs through groundwater, whose main origin is irrigation agriculture at the Southern area of the catchment. The lakes have total nitrogen concentrations of 7–17 mg N L$^{-1}$, 75–90% of which is nitrate. Towns in the area are small, with less than 3,000 inhabitants. However, San Pedra lake receives treated wastewaters from Ossa de Montiel, whereas Cueva Morenilla and Coladilla lakes receive important phosphorus inputs through septic tank leakage of surrounding cottages and direct inputs from Ruidera town. Except those aforementioned lakes, the remaining ones are oligo-mesotrophic. Further data on the lakes and the underlying aquifer can be found in ALVAREZ-COBELAS et al. (2006), where all previous studies are reported.

2.2. Sampling Programme and Procedures

2.2.1. Rainfall and Groundwater and Lake Levels

Rainfall was recorded daily at a meteorological station, run by the Spanish National Meteorological Institute, located near Fuenllana, a town in the centre of the Campo de Montiel aquifer. Groundwater level was followed every third month using a network of piezometers run by the Guadiana Water Authority, the closer of which to Ruidera lakes was one located near Blanca lake. Water levels of nine lakes were recorded monthly by the Natural Park staff and their data were used to calculate lake volume changes which in turn enabled us to estimate the water renewal time of lakes. For those lakes lacking water level recording devices, changes in water level were traced periodically by discharge measurements at their inlet and outlet, using a flowprobe. A single gauge whose data were recorded monthly by the Guadiana Water Authority was operating downstream of Rey lake since 1973. Although this study covered 2000–2001 events in Ruidera lakes, 1999 data will also be reported here to provide starting points for rainfall and discharge trends. Also, interannual rates of rainfall-driven groundwater recharge were explored regressing cumulative October–June rainfall vs. piezometric level close to Blanca lake for the period when those data were available (1992–2001).
2.2.2. Limnological Sampling and Analysis

The effects of changing water fluxes on the Ruidera lakes were tested on water transparency, salinity, total nitrogen (TN hereafter), total phosphorus (TP hereafter) and bacterial, phytoplankton and zooplankton biomass. Eleven lakes were monitored (Concejilla, Tomilla, Tinaja, San Pedro, Lengua, Salvador, Santos Morcillo, Batana, Colgada, Rey and Cueva Morenilla lakes) in 2000 and 2001. The remaining lakes either were intermittent waterbodies or had their access restricted at times. Sampling was undertaken every third month in the central area of each lake. Transparency was measured with a Secchi disc whereas surface water conductivity was measured with a Crison probe. Water was collected using a Niskin bottle at 1-m intervals and an integrated sample for the mixed layer was compounded, that layer being defined following the methods by CORNETT and RIGLER (1980). Shortly after collection, TN and TP concentrations were measured in integrated samples. APHA (1989) and BACHMANN and CANFIELD (1996) procedures were followed for TN and TP analyses, respectively. Phytoplankton chlorophyll “a” was measured “in situ” with a 10–005R Turner fluorometer calibrated against chlorophyll standards.

Bacterioplankton and phytoplankton were sampled at each meter and then gently mixed to provide a mixed layer aliquot, fixed according to standard procedures, and then their populations were measured and counted on aliquots by fluorescence- (HOBIE et al., 1977) and inverted microscopy (ROTT, 1981), respectively. Phytoplankton biomass was estimated by the ROTT (1981) approach.

In 2001 at least 30 litres of water of the mixed layer were filtered seasonally through a 53 µm mesh to retain rotifer and crustacean zooplankton in each lake. Preliminary tests did not show statistically significant differences (p > 0.05) among zooplankton biomass of different depth layers of Ruidera lakes. Each sample was fixed immediately with sucrose-formalin (HANEY and HALL, 1973). Identification and counting of all zooplankton specimens were carried out by inverted microscopy (MCCAULEY, 1984). In every sample, all crustaceans and rotifers, including copepodites and nauplii, were counted. Fresh weight biomass of rotifers was calculated after biovolume estimations, assigning a well known geometrical body to each species (MCCAULEY, 1984). Relative biomass of ciliate and heterotrophic flagellate was negligible (ROJO, unpublished data). Individual biomass was ascertained on a dry weight basis for all identified forms of crustaceans. Cladoceran and copepod dry biomass was obtained from MCCAULEY (1984, Table 7.2) equations, which used animal length to arrive at animal biomass through least-squares equations. Later, dry weight biomass of cladocerans and copepods was converted into fresh weight biomass assuming different FW: DW ratios (MCCAULEY, 1984). Overall biomass of a given species on a given day was the result of individual biomass times individual density on that specific day. Since we lacked zooplankton data for 2000 and PETERS (1986) reported strong relationships between TP and zooplankton biomass, we estimated zooplankton biomass for that year using our 2000 TP data as the independent variable, the explained variability of zooplankton biomass by phosphorus being 78% in 2001 (p < 0.05).

3. Results

3.1. Rainfall, Groundwater Levels and Lake Responses

Yearly rainfall experienced many fluctuations in the area (Fig. 3 upper panel), averaging 481 ± 139 mm for the 1963–2001 recording period. Rainfall was lower in 1999 and 2000 (353 and 409 mm, respectively) than the long term average, rising from October 2000 and reaching 494 mm in 2001 (Fig. 3 lower panel). Rainfall was strongly seasonal, with spring and autumn maxima, but the magnitude of those maxima varied and those changes were very influential on groundwater recharge (see below).

Piezometric levels at the SE lake chain, near Blanca lake, steadily declined from 1999 until October 2000 (Fig. 4, upper panel) with minimal and maximal values attaining 11.5 and 4 m, respectively. From October 2000 onwards, it increased until early 1999 values were reached around June 2001. Those changes could be followed throughout the aquifer (Fig. 4, middle panel), rainfall inputs in late 2000 and early 2001 increasing piezometric levels somewhat farther than in the early 1999 peak. Cumulative rainfall for the period October-June of 1992–2001 showed a strong, positive and statistically significant relationship with
Figure 3. 1963–2001 yearly rainfall (upper panel) and monthly rainfall from January 1999 to December 2001 (lower panel) in Fuenllana meteorological station, SW Lagunas de Ruidera Natural Park. The straight line represents the yearly average.

Figure 4. Upper panel. Piezometric level from January 1999 to December 2001 at a piezometer close to Blanca lake, the southeasternmost area of the Ruidera lake complex. Groundwater usually discharges to Blanca lake when hydraulic head is shallower than 4 m. Data gathered by the Guadiana Water Authority.

Middle panel. Average piezometric level in Campo de Montiel aquifer (meters above sea level) from March 1999 to October 2001. Standard deviations are roughly the same (44–47 m) and therefore have not been plotted in order not to obscure the pattern. More than 20 piezometers are routinely surveyed by the Guadiana Water Authority and have been used to plot this picture.

Lower panel. October-June cumulative rainfall at Fuenllana meteorological station vs. piezometric level in late spring at the closest Blanca lake piezometer from 1992 to 2001.
Effects of Rainfall on Chain of Lakes

Piezometric level (m)


0 | 2 | 4 | 6 | 8 | 10 | 12

Piezometric level (m.a.s.l.)


854 | 855 | 856 | 857 | 858 | 859

Cumulative rainfall (mm)

Cumulative rainfall (mm)

PL = -0.036*R + 21.945

R² = 0.89
piezometric level ($p < 0.05$; Fig. 4, lower panel). Providing that piezometric levels were not too deep to recover in a normal way (e.g. not after a heavy drought), significant groundwater delivery to lakes usually started once that cumulative October–June rainfall exceeded 420 mm (Fig. 4, lower panel).

Rainfall increase in October 2000–June 2001 resulted in groundwater recharge, its level rising 0.5–4 m in the upper, SE area of the Natural Park from May 2000 to June 2001 (Fig. 5). This in turn enhanced groundwater discharge to lakes, whose surface connection had been discontinued from early 1999 to June 2001. By summer 2001 all lakes were connected by surface streams and groundwater delivery to the lower lakes began, increasing further by autumn 2001.

Water exports at the single existing gauge dropped from early 1999 to late 2000, increasing afterwards, but they had still not reached early 1999 values by the end of the study period (Fig. 6). Lake water levels changed more in upper and middle than in lower lakes (Fig. 7),
Figure 6. Monthly water discharge at the gauge downstream Rey lake from January 1999 to December 2001. Data gathered by the Guadiana Water Authority.

Figure 7. Water levels of selected Ruidera lakes from January 1999 to December 2001. Data gathered by the Lagunas de Ruidera Natural Park staff. Tomilla is a more mountain lake (863 m above sea level) than Cueva Morenilla lake (772 m above sea level), whereas Santos Morcillo lake is located in-between (812 m above sea level).
Figure 8. Average and standard deviations of water transparency (upper plot) and electric conductivity (lower plot) in surface water of Ruidera lakes in 2000 (white bars) and 2001 (grey bars). Lake data are plotted on a downstream order from the left of the picture. The number of observations was 4 in any year.

Table 2. Water renewal time (in years) of Ruidera lakes in 2000 and 2001. Data for Salvador and Batana lakes are unavailable because they lack water scales to measure lake level.

<table>
<thead>
<tr>
<th>Lake</th>
<th>2000</th>
<th>2001</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conceja</td>
<td>9.14</td>
<td>4.08</td>
</tr>
<tr>
<td>Tomilla</td>
<td>10.30</td>
<td>4.60</td>
</tr>
<tr>
<td>Tinaja</td>
<td>11.19</td>
<td>5.00</td>
</tr>
<tr>
<td>San Pedra</td>
<td>12.38</td>
<td>3.91</td>
</tr>
<tr>
<td>Lengua</td>
<td>14.47</td>
<td>2.00</td>
</tr>
<tr>
<td>Santos Morcillo</td>
<td>32.50</td>
<td>3.96</td>
</tr>
<tr>
<td>Colgada</td>
<td>18.40</td>
<td>18.43</td>
</tr>
<tr>
<td>Rey</td>
<td>11.21</td>
<td>11.47</td>
</tr>
<tr>
<td>Cueva Morenilla</td>
<td>13.01</td>
<td>13.56</td>
</tr>
</tbody>
</table>
those changes being influenced by lithological features of the area (see the Study Site description above). In some lakes, such as Lengua lake, there could be stronger water level changes on account of the rock fissurable environment. On average, water level changes in upper and middle lakes ranged 3–4 m, whereas those in lower lakes fluctuated less than one meter. Water renewal time was clearly different in 2000 and 2001 for most lakes (Table 2), being shorter for the Conceja-Santos Morcillo chain than for the lower lakes, whose water renewal time remained almost unchanged.

### 3.2. Limnological Responses

For the whole lake chain, transparency was lower in 2000 than in 2001 (5.41 ± 2.74 vs. 6.72 ± 2.80 m in 2000 and 2001, respectively; U-test, \( p < 0.05 \); Fig. 8, upper panel). Differences between both years were statistically significant for most upper lakes and Cueva Morenilla lake (\( p < 0.05 \); Table 3). The opposite was true for conductivity, being used as a proxy of salinity. That variable was statistically higher in all lakes (U-test; \( p < 0.05 \); Table 3) in 2000 than in 2001 (Fig. 8, lower panel), suggesting an important dilution effect of salt-poor, higher groundwater inputs on lake waters in 2001.

TN and TP concentrations in the mixed layer of all lakes experienced opposite patterns in 2000 and 2001. TN increased in 2001 as a result of higher groundwater inputs of nitrate-rich water in that year (8.59 ± 2.01 vs. 8.71 ± 3.42 mg N L\(^{-1}\) in 2000 and 2001, respectively; U-test, \( p < 0.05 \); Fig. 9 upper panel), whereas TP decreased in 2001 by a diluting process (0.011 ± 0.004 vs. 0.009 ± 0.004 mg P L\(^{-1}\) in 2000 and 2001, respectively; U-test, \( p < 0.05 \); Fig. 9 lower panel). In individual lakes only Lengua lake for TN and Tomilla, Lengua, Rey and Cueva Morenilla lakes for TP showed statistically significant differences between 2000 and 2001 (Table 3). It was noteworthy that TN variability appeared to be higher in 2001 whereas that of phosphorus was in 2000 (Fig. 9). Yearly-averaged total phosphorus did not show any statistically significant relationship with water renewal time for all lakes (\( p > 0.05 \)). However, if the lower lakes of the complex were removed from the analysis (those lakes also having the longer retention times), then a good fraction of the TP variability was explained by water renewal time (\( R^2 = 0.59, p < 0.05; TP = 0.0003*Water Renewal Time + 0.0064 \)).
The variability of phytoplankton chlorophyll “a” was higher in 2001 (CV 0.31–1.20 in 2001 vs. 0.15–0.85 in 2000) when water renewal time was higher in most lakes, but it did not statistically change between 2000 and 2001 (2.20 ± 1.86 vs. 2.31 ± 2.69 µg L⁻¹ in 2000 and 2001, respectively; U-test, p > 0.05; Fig. 10). Chlorophyll “a” and phytoplankton biomass were not statistically significantly related in any year (p > 0.05). The plot of summer epilimnetic TP vs. summer epilimnetic chlorophyll “a” of all lakes, albeit weak, was statistically significant for both years (R² = 0.33; p < 0.05).

Bacterial biomass did not statistically change between years (0.14 ± 0.12 vs. 0.16 ± 0.09 mg FW L⁻¹ in 2000 and 2001, respectively; U-test, p > 0.05), their variability also being higher when renewal time was longer. Conceja, Tomilla, Salvador, Santos Morcillo and Batana lakes had statistically higher bacterial biomasses in 2000 (Table 3). Phytoplankton biomass was statistically higher in 2000 along with lower water renewal for the whole lake chain (2.95 ± 2.02 vs. 1.50 ± 1.01 mg FW L⁻¹ in 2000 and 2001, respectively; U-test, p < 0.05; Fig. 11), with higher variability as water renewal increased. For individual...
lakes, only Tomilla, Tinaja, Santos Morcillo and Colgada lakes showed statistically higher phytoplankton biomass in 2000 (Table 3). Finally, our lack of zooplankton observational data for 2000 precluded meaningful comparisons between years, but average data in 2001 appeared to be much lower than calculated data in 2000 (1.04 vs. 0.25 mg FW L\(^{-1}\) in 2000 and 2001, respectively).

The lakes shared the dominant phytoplankton species in both years (a mixed assemblage of diatoms, cryptophytes and green algae in all lakes, with a few Cyanobacterial species in eutrophic lakes), but the number of rare, fugitive species increased in 2001, along with water renewal time. Changes in plankton species will be published elsewhere.

Figure 10. Average and standard deviations of phytoplankton chlorophyll “a” in the mixed layer of Ruidera lakes in 2000 (white bars) and 2001 (grey bars). Lake data are plotted on a downstream order from the left of the picture. The number of observations was 4 in any year.

Figure 11. Average and standard deviations of phytoplankton biomass in the mixed layer of Ruidera lakes in 2000 (white bars) and 2001 (grey bars). Lake data are plotted on a downstream order from the left of the picture. The number of observations was 4 per year.
4. Discussion

Our study suggests that: 1) cumulative rainfall dictates groundwater recharge of the aquifer on which the Ruidera lakes are located (Fig. 4); 2) groundwater discharge, in turn, increases surface discharge downstream (Fig. 6); 3) both processes affect lake water renewal (Table 2); and 4) the effect of rainfall on water fluxes is delayed up to nine months (Fig. 4). However, such water renewal impinges on limnological variables differently, depending on the geographical scale involved. At the lake district scale, significant differences in transparency, salinity, TN, TP and phytoplankton biomass emerge as water renewal decreases (Figs. 8, 9, 11). At the single lake scale, there are differences between years of contrasting water renewal in some lakes only, and those lakes are never the same for all limnological variables (Table 3). Therefore, it appears that there is some idiosyncracy in lakes of the Ruidera chain that react differently to individual changes in water renewal time. Such an idiosyncracy may arise from the geological setting of lakes, the nature (e.g. diffuse and/or definite springs) and volume of groundwater inputs and the volume variability of stratifying layers (Table 1). Hence, control mechanisms of lake performance happen to operate at a variety of scales, as other studies on riverscapes have demonstrated (ALLAN, 2004). Idiosyncrasy of limnological variables can be a negative proxy of temporal coherence, i.e. the higher the idiosyncrasy of any lake the lower the temporal coherence among lakes. Salinity appears to be more coherent among lakes in the setting chain than other chemical (TN, TP) or biological variables (plankton biomass), as other studies (KRATZ et al. 1998; GEORGE et al., 2000) have suggested.

Clearly, groundwater regional flow sensu TÓTH (1963) must explain some variability in the patterns observed, but lake idiosyncrasy is still a remarkable feature of the Ruidera flowthrough lake complex. Such a lake specificity could be related with the interaction between topographic setting of a given lake and local forcing of water fluxes in and near that lake (SMITH and TOWNLEY, 2002), which, in turn, are the outcome of local and regional groundwater fields. However, these processes have not been explored as yet, but, if studied, they may certainly throw some light on the idiosyncrasy of each Ruidera lake.

This study also suggests that groundwater flux into lakes located in the lowest position of the chain is more stable than that for lakes farther upgradient, and that fact is shown by the strong changes in levels of upper and middle lakes, as opposed to those in lower lakes (Fig. 7). Also, periods of intense groundwater recharge increase surface flow to lower lakes (Fig. 6). This is what is expected for seepage chain lakes as suggested by the CHENG and ANDERSON (1994) model. However, impermeable rock substrata underlying lower lakes and the high variability in water discharge of Mediterranean environments (ÁLVAREZ-COBELAS et al., 2005b), which can also be seen in interannual patterns of rainfall and piezometric level, around Ruidera lakes (Fig. 4), may result in more complex patterns of lake volume changes, particularly in lower rainfall periods. Hence, water renewal, partly associated with groundwater flux, and landscape position help explain divergences in ecosystem responses (WEBSTER et al., 1996) and groundwater flux changes may vary on a seasonal, albeit delayed, scale. However, long-term behaviour of lake functioning, partly driven by groundwater flux dynamics, cannot be discarded because a ten year cycle in drought is obvious in the area (ÁLVAREZ-COBELAS et al., 2006) and so long term changes in groundwater supply to lakes are expected.

Concerning the effects of water renewal time on limnological variables, our study indicates a remarkable one on TP concentration in lakes with water residence time lower than 33 years, but most responses lack a common pattern if lakes are considered individually. An explanation to this fact could be that changes in water renewal time between 2000 and 2001 were still not strong enough to trigger more dramatic limnological effects. All reported effects of water renewal occur when that period is greatly shortened, so they are occurring more often than monthly (DICKMAN, 1969; WALZ and WELKER, 1998; ÁLVAREZ-COBELAS, unpublished results). However, our study has demonstrated that some effects of water renew-
al on lake dynamics can be envisaged at the lake district scale and some might also occur at the lake scale. Thus, water renewal as a key process on lake functioning depicts a more complex behaviour than previously reported (SCHINDLER, 2006; WINTER, 2003).

To conclude, this study reports an infrequent scale of rainfall forcing on water flux of a flowthrough, seepage lake complex. Such a forcing is common in Mediterranean environments where water availability is highly variable and often scarce. That availability impinges on water renewal time, which affects limnological variables at a regional scale, but not at the local scale, maybe because lake idiosyncracy prevails when water renewal time is not very short. However, rainfall forecasts for the forthcoming decades in Northern Europe as climate change takes place may result in a Mediterranean behaviour of its limnosystems (PARRY, 2000) and hence responses like those reported here will be more frequent in higher latitude limnosystems in the future.

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6. References


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