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Effect of Drought Conditions on Plankton Community and on Nutrient Availability in an Oligotrophic High Mountain Lake

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Abstract

Natural water level fluctuations (WLFs) are an inherent characteristic of Mediterranean inland waters, which are projected to be amplified by global climate change. La Caldera (Sierra Nevada National Park, Spain) is an oligotrophic high mountain lake (3050 m a.s.l.) that has experienced large fluctuations in water volume (13–100%) during the past 20 years due to irregular annual precipitation patterns (371–1816 mm). Because of the lake's cold and dilute abiotic environment, it is likely susceptible to projected increases in global temperature and represents an ideal sentinel of global change. We analyze the effect of WLFs on water quality and on plankton community in La Caldera to better understand the potential effects of recurrent droughts (3 droughts in a 20-year period) on lake ecology. We have found significantly positive effects of WLFs on total phosphorus (TP) concentrations. There was extreme variability in TP concentrations during three recurrent droughts (1995, 1999, and 2005) reflecting sediment resuspension. However, the data also suggest that this was not the only source of phosphorus. Extremely high P-enriched atmospheric dust inputs could have maintained the abnormally high TP in-lake concentrations measured during 2005. The data indicate that recurrent droughts have reduced lake resistance to TP changes but have increased lake resistance to total nitrogen (TN) changes, which supports the idea that a P-enriched atmospheric dust inputs during 2005. An increase in dissolved inorganic nitrogen (DIN):TP mass ratio after 2005 was observed, revealing a higher ecosystem homeostasis of this ratio.

Introduction

Climatic warming is expected to increase water temperatures and length of ice-free periods in lakes at high altitudes (Thompson et al., 2005). However, global change factors are complex, acting at different temporal and spatial scales (Bullejos et al., 2010). Although Mediterranean water bodies are characterized by extreme natural water level fluctuations (WLFs) in response to irregular precipitation patterns (Álvarez-Cobelas et al., 2005), global climate change is projected to amplify this pattern by shorting precipitation seasons and increasing the incidence of summer droughts in this area (Coops et al., 2003). WLFs linked to climate change are most pronounced in closed-basin lakes, where waters levels are controlled by the balance between precipitation and evaporation (Marsh and Lesack, 1996). Although it should be stressed that WLFs are natural variations that are necessary for the survival of many species (i.e. Gafny et al., 1992), extreme or untimely floods and droughts generally have deleterious effects for lake biota (Wantzen et al., 2008). Despite the increasing relevance of WLFs on lentic ecosystems, detailed relationships between WLFs and ecosystem response are not well understood (Coops et al., 2003). The majority of the literature, and our understanding of WLFs, stems from controlled whole lake manipulations focused on macrophyte diversity and biomass (i.e. Cooke et al., 1993). More recently, Turner et al. (2005) and White et al. (2008) have found contrasting effects of WLFs on water quality, community structure, and biodiversity. While Turner et al. (2005) did not find significant change in either nutrient (N and P) concentrations or phytoplankton biomass, White et al. (2008) observed significant effects on water quality parameters such as dissolved organic carbon and major ions concentrations in addition to macrophyte species richness.

Among inland waters, high mountain lakes are considered to be sentinels of global change because of their cold and dilute abiotic environment, low biodiversity, poor functional redundancy, and relative lack of local human perturbations (Battarbee et al., 2002; Psenner et al., 2002; Vinebrooke and Leavitt, 2005). As a consequence of their remoteness, even since industrialization they have traditionally been considered pristine ecosystems (Battarbee, 2005). In contrast, recent research has evinced that even the most remote lakes in Europe are suffering impacts due to land use and climatic changes (e.g. Battarbee et al., 2001; Agustí-Panareda and Thompson, 2002; Catalán et al., 2002; Rognerud et al., 2002; Rose et al., 2002). Land use intensification is likely responsible for greater dust emissions from source areas (Field et al., 2009). In fact, scientists are recognizing dust as a major environmental driver and a source of uncertainty to climate models (Tanaka and Chiba, 2006; Neff et al., 2008). This effect is certainly relevant in Sierra Nevada, the southernmost mountain range in Europe with elevations above 3000 m a.s.l., which contains numerous oligotrophic mountain lakes. Geographic location (altitude and latitude) of Sierra Nevada lakes makes them especially vulnerable to atmospheric deposition as they are within 1000 km of the Sahara Desert (Löye-Pilot et al., 1986; Bergametti et al., 1992). It is accepted that 70% of Saharan dust is deposited within 2000 km (Schütz et al., 1981). In addition, dry deposition of Saharan dust is rich in phosphorus (Morales-Baquero et al., 2006a).

Accordingly, it is important to gain more knowledge about the effect of WLFs and dust on water quality and on plankton community in these relatively simple high mountain lakes. The ability of ecosystems to absorb disturbances, to be changed, and then to re-organize and still have the same identity, retaining the same basic structure and ways of functioning is the definition of resilience and is one of the key concepts in modern ecology (Holling, 1986; Gil-Romera et al., 2010).

In this paper, we hypothesize that lake exposure to 3 recurrent droughts in a 20-year period may have affected lake resistance and resilience. Both higher resistance and resilience in water quality parameters would reflect higher lake stability to drought conditions. In particular, our specific objectives were: (i) the monitoring of nutrient availability and biological structure during two contrasting years (2005 and 2006) to evaluate the recovery (resilience) of lake water quality after an extreme drought year, and (ii) the assessment of long-term effects (20 years) of WLFs on lake water quality and on plankton community by using both our data and those reported in the literature to evaluate long-term changes in lake resistance and resilience.

Methods

STUDY LAKE

La Caldera is located in the Sierra Nevada mountains in southern Spain (36°10′N, 2°70′W) at 3050 m a.s.l. The lake is 2 ha in area with a maximum depth of 14 m. It occupies a glacial cirque basin comprised mainly of impermeable siliceous bedrock and has no visible surface inlets or outlets (Villar-Argáiz et al., 2001). The lake is ice-free for about 5 months (May–June to October–November) of the year. Terrestrial nutrient inputs are restricted to the ice-melt period and atmospheric nutrient deposition has been shown to support P-demand during the ice-free season (Villar-Argáiz et al., 2001).

La Caldera is oligotrophic and total phosphorus concentrations are 4–7 µg L^{-1}; light penetrates to nearly the maximum depth. Macrophytes, littoral vegetation, and fish are absent. The plankton community of La Caldera is characterized by lower species richness (Morales-Baquero et al., 1992) when compared with other Mediterranean aquatic ecosystems (i.e. Alonso, 1998). Phytoplankton is dominated by flagellates (Chrysophyceae and Dinophyceae) and by Cyanophyceae species (Cruz-Pizarro et al., 1998). The main zooplankton taxa are the calanoid copepod *Mixodiaptomus laciniatus* and the cladocera *Daphnia pulicaria* (Carrillo et al., 1996).

FIELD SAMPLING

From June to October 2005 water temperature was monitored at 0.5 m intervals and at 1 m intervals in 2006, using thermistor chains (HOBO H20-001) placed at five different locations in the lake. Each month, depth-integrated water samples were collected for chemistry, bacteria, and phytoplankton at 0.5 m intervals from the deepest point of the lake with a 2 L Van Dorn bottle. Measurements of pH, conductivity, and dissolved oxygen were taken at 1 m intervals with a multiparametric probe (YSI-556MPS). *In situ* fluorescence was measured at 1 m intervals with a field fluorometer (Aquafluor Turner Design Handheld). Chlorophyll-*a* (Chl-*a*) concentrations were later calculated using a previously obtained calibration curve determined by fluorometry. Calibration samples were filtered through Whatman GF/C glass microfiber filters (1.2 µm pore-size), and extracted in 90% acetone for 24 h at 4 °C (Strickland and Parsons, 1968).

Zooplankton was collected by performing vertical net hauls (63 µm mesh, 27.5 cm diameter).

CHEMICAL ANALYSIS

In the laboratory, unfiltered lake water was analyzed for total phosphorus (TP) and total nitrogen (TN; APHA, 1995). Detection limits are 1 µg P L^{-1} and 40 µg N L^{-1} for TP and TN, respectively. Lake water filtered through 0.45 µm pore-size glass fiber filters (Whatman GF/F) was analyzed for dissolved phosphate (SRP; Murphy and Riley, 1962), nitrate (NO$_3^-$; ultraviolet method, APHA, 1995), nitrite (NO$_2^-$; Shinn, 1941), ammonia (NH$_4^+$; blue indophenol method, Rodier, 1989), and total alkalinity (titration method; APHA, 1995). Detection limits are 1 µg P L^{-1}, 45 µg N L^{-1}, 6 µg N L^{-1}, and 10 µg N L^{-1} for SRP, NO$_3^-$, NO$_2^-$, and NH$_4^+$, respectively.

BACTERIA, PHYTOPLANKTON, CILIATES, AND ZOOPLANKTON

Bacterial and heterotrophic nanoflagellate (HNF) samples were preserved with glutaraldehyde (2%), stained with DAPI (0.1 µg mL^{-1}), filtered onto 0.2 µm pore-size polycarbonate filters (Porter and Feig, 1980), and counted using epifluorescence microscopy (Leica DM2000) equipped with a digital camera (Leica DFC350FX). Five digital photographic images were taken per sample and analyzed using image processing software (Image Tool version 3.00, University of Texas Health Science Center in San Antonio, UTHSCSA). Cellular biovolume was calculated using the equation proposed by Massana et al. (1997):

$$V = \pi/4 \, W^2(L - W/3), \qquad (1)$$

where V is the cellular biovolume that is calculated from the two-dimensional parameters obtained by image analysis, length (L) and width (W). Bacteria are considered to be cylinders with two hemispherical caps. Biovolume of autotrophic pico-nanoplankton was determined from cryogenized and unstained subsamples that were processed with a flow cytometer Coulter Epics Elite.

Phytoplankton and ciliates (>10 µm) were preserved with Lugol solution (2%), concentrated in settling chambers for 24 h (Utermöhl, 1958) and enumerated using an inverted microscope (Leica DMIL). Cell biovolume was determined for 100 individuals of each taxa using VIDS-IV (Analytical Measuring System), a semi-automatic image analysis system that estimates simple geometric shapes (Echevarría and Rodríguez, 1994; Ruiz et al., 1996). Zooplankton was preserved in formaldehyde (4%), identified and enumerated under 100 times magnification with a stereo-microscope (Leica MZ 12.5) equipped with a digital camera (Leica DC150). Zooplankton biovolume was estimated for 20 individuals of each taxa in each sample from two-dimensional parameters obtained by image analysis of the recorded length (L) and width (W), and the volume was approximated to cylindrical, elliptical, or spherical forms. Zooplankton was identified to species level, according to Dussart (1967, 1969), Dussart and Defaye (1995), and Ranga (1994) for copepods and Alonso (1996) for branchiopods.

LONG-TERM MONITORING

Data of accumulated annual precipitation, from 1986 to 2006, were obtained from CETURSA Sierra Nevada, S.A. (management

company of Sierra Nevada Ski Resort). Maximum water depth values, nutrient concentrations [TN, TP, and dissolved inorganic nitrogen (DIN)], and biological data (bacteria, HNF, phytoplankton, and zooplankton abundance) were obtained from the literature (see Table 1). All data obtained from the literature used the same methodology as we have used during the study period, making data comparison possible.

Winter North Atlantic oscillation (NAO) index was obtained for each year (1986–2006) from the website http://www.cgd.ucar.edu/cas/jhurrell/indices.data.html#naostatmon. Winter index value is based on the difference of normalized sea level pressures between Lisbon (Portugal) and Stykkisholmur/Reykjavik (Iceland; Hurrell, 1995). The index value of an individual year, n, contains the average December of year n − 1 and January, February, and March of year n.

Differences from the long term mean (DLTM) were estimated as proposed by White et al. (2008). In brief, DLTM for water depth ($DLTM_{depth}$) and for all water quality variables were calculated by determining the mean value of each variable from 1986 to 2006 and then subtracting the mean value for each particular year. Hence, DLTM resulted in positive values when long-term mean was over the value of each particular year (i.e. a reduction in water depth), and negative ones when long-term mean was lower than the value of each particular year (i.e. an increase in water depth). Finally, the long-term effect of WLFs on water quality parameters was assessed by relating DLTM for each variable to $DLTM_{depth}$.

Resistance and resilience, as components of stability, were calculated for each drought period according to Tilman and Downing (1994). Resistance was calculated as the neperian logarithm of the ratio between values of water quality variables in dry and pre-drought years, while resilience was calculated by comparing post- and pre-drought years. Values close to zero means no change for each variable during drought conditions, and therefore the resistance and resilience would be maximum.

STATISTICAL ANALYSIS

Differences in physical, chemical, and biotic variables (abundance and biovolume) between 2005 and 2006 were analyzed with a t-test ($p < 0.05$). In addition, t-test comparisons were used to evaluate differences and relationships among physical, chemical, and biological variables between time periods and between drought years ($p < 0.05$). Median tests were used to analyze intra-annual differences of nutrient concentrations ($p < 0.05$). Relationships between DLTM of depth and DLTM of other water quality variables were explored through Pearson's correlation.

All data were tested for homogeneity of the variance and normalized by logarithmic transformation when it was necessary. All statistical analyses were performed using the software program STATISTICA (version 7.0).

Results

Strong differences in annual accumulated precipitation and hydrological (maximum water depth) data were observed during 2005 and 2006. Precipitation during 2006 (786 mm) was similar to the 20-year average (813 mm) and twofold higher than 2005 (391 mm). As a consequence, maximum water depth was 1.6-fold higher in 2006 (6.6 m) than in 2005 (4.0 m). Data from thermistors always showed changes in water column temperature less than 1 $°C\ m^{-1}$, and no thermal stratification during either 2005 and 2006

(t-test, $p = 0.196$ and $p = 0.193$, respectively; Fig. 1). No significant temperature differences were found between 2005 and 2006 for either the surface (t-test, $p = 0.361$) or bottom (t-test, $p = 0.724$).

No significant intra-annual variations were found in nutrient concentrations (Median test, $p = 0.320$). However, inter-annual variations were observed with significantly higher TP during 2005 than during 2006 (t-test, $p = 0.018$; Fig. 2). By contrast, there was no corresponding difference in TN (t-test, $p = 0.350$), in DIN (t-test, $p = 0.117$), and in SRP concentrations (t-test, $p = 0.478$; Fig. 2, parts a and b). Annual mean TN:TP (by weight) values were significantly higher (t-test, $p = 0.041$; Fig. 2, part c) during 2006 (TN:TP = 56 ± 19) than in 2005 (TN:TP = 28 ± 10). Similarly, the DIN:TP ratio experienced significantly higher mean values (t-test, $p = 0.043$) in 2006 (DIN:TP = 37 ± 24) than in 2005 (DIN:TP = 5 ± 7), showing a possible N limitation during 2005. Mass ratio of the dissolved inorganic forms (DIN:SRP) experienced no significant differences between both study years (17 ± 27 and 69 ± 51, respectively; t-test, $p = 0.123$).

Annual mean chlorophyll-*a* concentrations showed neither spatial (vertical) nor temporal differences (t-test, $p = 0.357$; Table 2). No significant inter-annual variations in abundance and biovolume of bacterioplankton, phytoplankton, HNF, and zooplankton were registered (Fig. 3, parts a–c), but for ciliates significantly lower abundances (t-test, $p = 0.004$) and higher biovolumes (t-test, $p = 0.045$) were measured during 2005 than during 2006 (Fig. 3, parts a and b). No significant inter-annual differences (t-test, $p = 0.106$) in the ratio of total biovolume of autotrophic to heterotrophic organisms (A:H) were found (Table 2). The main heterotrophic and autotrophic components were zooplankton and phytoplankton, respectively (Fig. 3).

During the 20-year monitoring period (1986–2006), La Caldera has experienced large fluctuations in maximum water depth (14–100%; Fig. 4, part a), water volume (13–100%), and precipitation variability (371–1816 mm; Fig. 4, part b). Maximum water depth and precipitation were significantly and positively related during this period ($r = 0.70$; $p = 0.0006$; Fig. 4, part c). Three different time periods can be distinguished based on the annual accumulated precipitation (Table 1; Fig. 4, parts b and c): years with annual accumulated precipitation higher than the average plus standard deviation (period I; >1200 mm), lower than the average minus standard deviation (period III; <425 mm), and intermediate values (period II; 425–1200 mm). Strong differences in maximum water depth were also observed among periods. Periods I and III were characterized by depths >10 m (1996, 1997, and 2001) and <4 m (1995, 1999, and 2005), respectively, while during period II intermediate values were recorded. As expected, the winter NAO index was significantly higher during the driest period III (1.93 ± 1.93) than during the wetter period I (−1.95 ± 1.80; t-test, $p = 0.042$; Fig. 5).

DIN:TP mass ratio, DIN, and TN concentrations showed no significant tendencies among periods (t-test, $p > 0.05$), although TP increased with a reduction in the maximum water depth (from Period I to Period III; t-test, $p = 0.017$; Fig. 6, part a). No significant differences in bacteria and zooplankton abundances were observed among periods (t-test, $p = 0.125$ and 0.09, respectively). By contrast, HNF abundances were significantly higher in Period III than in Period I (t-test, $p = 0.001$; Fig. 6, part b), and phytoplankton abundances were significantly higher in Period III than in Periods I (t-test, $p = 0.0027$; Fig. 6, part b) and II (t-test, $p = 0.029$; Fig. 6, part b).

The long-term effect of WLFs on water quality parameters was assessed by relating DLTM for each variable to $DLTM_{depth}$. While $DLTM_{TP}$, $DLTM_{zoo}$, and $DLTM_{HNF}$ were significant

TABLE 1

Data compiled in previous studies in La Caldera Lake. TP: total phosphorus, DIN: dissolved inorganic nitrogen, TN: total nitrogen, DIN:TP (mass ratio), Phy: phytoplankton abundance, B: bacterial abundance, HNF: heterotrophic nanoflagellates abundance, Zoo: zooplankton abundance.

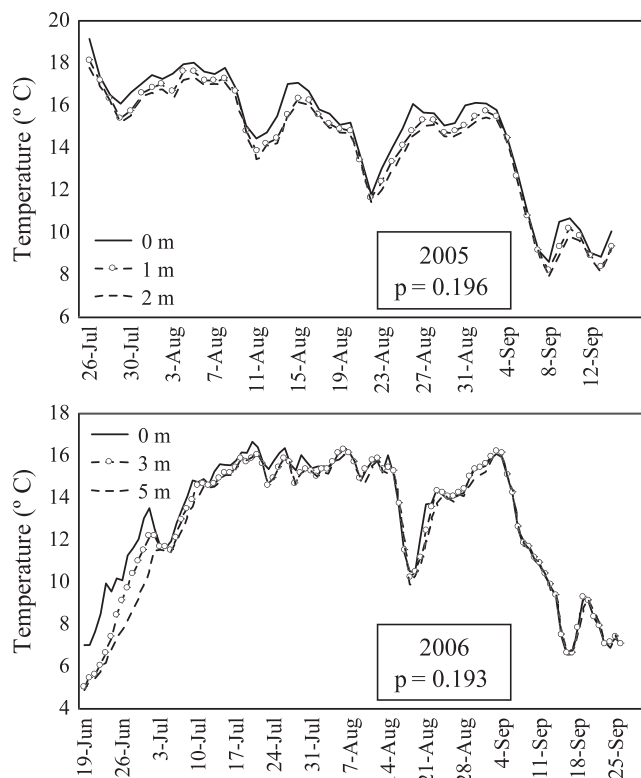| Periods	Date	Annual Precipitation (mm)	Maximum Depth (m)	TP (μg L^{-1})	DIN (μg L^{-1})	TN (μg L^{-1})	DIN:TP	Phy (cells mL^{-1} 10^3)	B (cells mL^{-1} 10^5)	HNF (cell mL^{-1} 10^2)	Zoo (ind L^{-1})	References
II	1986	823	12.5	5.1	310.0		60.8	2.6			17.0	Morales-Baquero et al. (1995, 2006a, 2006b)
II	1987	611	12.5	3.9			62.0					Echevarría et al. (1990); Carrillo et al. (1995)
II	1991	657	7.0	7.0	101.0	315.0						Morales-Baquero et al. (1999)
II	1992	570	5.5	4.4	202.4	441.0	48.3	5.1	13.0		40.0	Carrillo et al. (1996)
II	1993	526	4.5	7.6	171.3	240.0	24.2	8.0	12.5		33.3	Carrillo et al. (1996)
III	1995	371	1.8	7.1	236.6	477.0	36.9	17.2	10.7	97.5	29.0	Medina-Sánchez et al. (1999); Villar-Argáiz et al. (2001, 2002); Medina-Sánchez et al. (1999); Carrillo et al. (2002); Villar-Argáiz et al. (2001, 2002);
I	1996	1816	14.0	4.7	285.9	505.0	65.9	9.1	4.8	0.3	1.0	Morales-Baquero et al. (2006a, 2006b); Medina-Sánchez et al. (1999, 2002); Carrillo et al. (2002);
I	1997	1755	14.0	4.4	160.9	309.0	46.4	7.3	2.0	0.0	20.0	Villar-Argáiz et al. (2001, 2002); Morales-Baquero et al. (2006b)
III	1999	376	3.0	9.1			51.1					Pulido-Villena and Reche (2003); Medina-Sánchez et al. (2004)
I	2001	1351	10.0	6.2		431.2			10.0			Pulido-Villena (2004); Morales-Baquero et al. (2006b)
II	2002	781							8.0			Pulido-Villena et al. (2005)
II	2003	824	12.0	4.9	124.0	339.5	25.0	5.4	2.1	0.1		Medina-Sánchez et al. (2006)
III	2005	391	4.0	14.5	89.0	345.0	5.0	11.4	20.9	167.0	49.1	This study
II	2006	786	6.6	7.8	205.0	398.0	37.0	10.2	36.1	98.0	33.9	This study

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FIGURE 1. Lake thermal response to 24-hour variations in meteorological conditions during the ice-free period in La Caldera (from June to October of 2005 and 2006). Solid line: temperature registered by a thermistor placed at surface, broken line: temperature registered by a thermistor placed at the bottom. p-values corresponding to differences between surface and bottom temperatures are shown for each year.

FIGURE 2. Mean water column concentrations of nutrients. (a) Total phosphorus (TP; $\mu g\ L^{-1}$) and soluble reactive phosphorus (SRP; $\mu g\ L^{-1}$); (b) total nitrogen (TN; $mg\ L^{-1}$) and dissolved inorganic nitrogen (DIN; $mg\ L^{-1}$); and (c) Nitrogen:Phosphorus mass ratio in summer of 2005 and 2006. Broken line in (c) indicates zones of nutrient limitation for the DIN:TP from Morris and Lewis (1988). Above the line, DIN:TP values indicate P-limitation and below the line indicate N-limitation. Significant differences at $p < 0.05$ between years are indicated with letters. Error bars represent ± standard deviation (SD) of the mean.

and inversely related to $DLTM_{depth}$, no significant relationship was observed for $DLTM_{TN}$, $DLTM_{Phy}$, and $DLTM_{B}$ (Fig. 7). Differences between the three droughts (1995, 1999, and 2005) comprising Period III emerge, when considering the shift in maximum water depth between the pre-drought and the drought year. Accordingly, while during 1999 and 2005 a drastic reduction in maximum water depth (>65%) occurred compared to previous years, La Caldera experienced a much more extended and continuous drought in the early 1990s that peaked in 1995.

Differences and similarities in biotic and abiotic variables were more pronounced during the more contrasting droughts (between 1995 and 2005; Table 1). TP and SRP concentrations were significantly higher during 2005 than 1995 (t-test, $p = 0.016$ and 0.011, respectively). No significant differences were observed in TN concentrations (t-test, $p = 0.075$), but DIN was significantly higher in 1995 compared to 2005 (t-test, $p = 0.042$). The DIN:TP ratio was higher (t-test, $p = 0.087$) during 1995 compared to 2005, which reflects a shift in P-limitation (1995) towards a slight N-limitation (2005). During summer 2005, HNF abundances were significantly higher (t-test, $p = 0.006$) than those measured during 1995. However, no significant differences in bacterial, phytoplankton, and zooplankton abundances were observed (t-test, $p = 0.35$, $p = 0.59$, and $p = 0.32$, respectively). TP concentrations were 1.6-fold higher in 2005 than 1999 (Table 1), and as a consequence, DIN:TP mass ratio was 6.6-fold lower in 1999 than in 2005.

The analysis of lake stability to recurrent droughts evinced no clear patterns in either lake resistance or lake resilience. TP and ba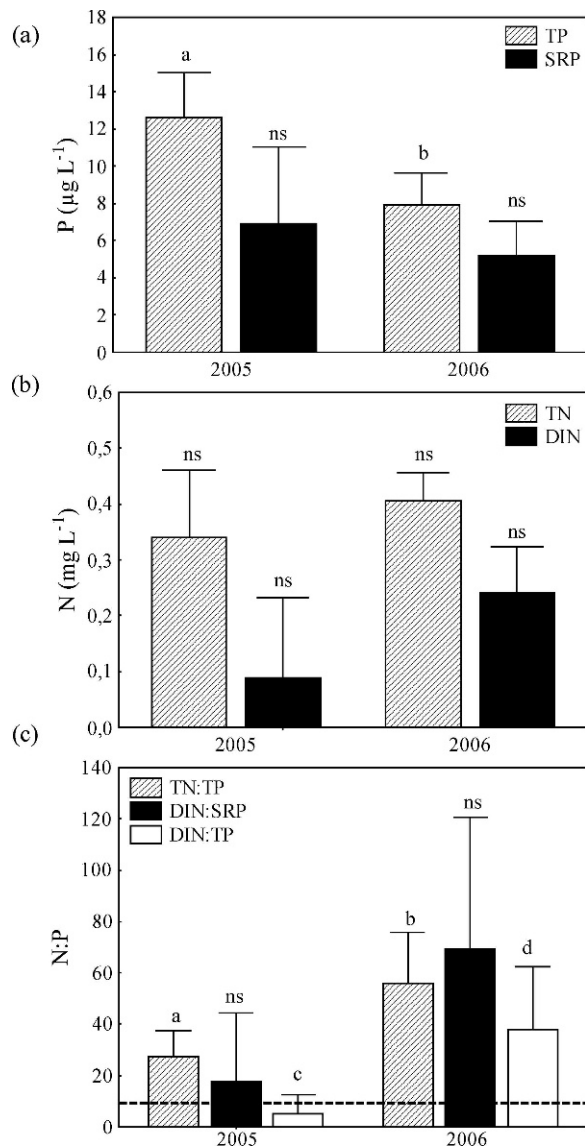cterioplankton abundance were more resistant (−0.1 and −0.2, respectively) during the first drought (1995) but lower resistance (1.1 and 2.3, respectively) was observed during the 2005 drought. By contrast, highest TN and phytoplankton abundance resistance were observed during the 2005 drought (0 and 0.7, respectively). During the 1999 drought, highest resistance was observed for DIN:TP mass ratio and for zooplankton abundance (0.1 and 0, respectively). Similarly to lake resistance, no clear pattern was observed for lake resilience to different drought conditions. Lake resilience was highest for TN and DIN:TP during the 2005 drought (0.2 and 0.1, respectively) while phytoplankton and bacterioplankton abundance experienced highest resilience during the 1995 drought (0.1 and −1.0, respectively). Highest resilience for TP was measured during 1999 (0.3).

TABLE 2

Chlorophyll *a* concentrations (Chl-*a*, μg L^{-1}) and Autotrophic:Heterotrophic ratio (A:H).

	Chl-*a*	A:H
Jun-05	—	5.4 ± 0.8
Jul-05	0.15 ± 0.06	0.3 ± 0.1
Sep-05	0.19 ± 0.03	0.2 ± 0.5
Oct-05	0.14 ± 0.01	5.6 ± 4.0
Mean ± SD	0.16 ± 0.03	2.9 ± 3.0
Jun-06	0.18 ± 0.04	6.4 ± 3.8
Jul-06	0.18 ± 0.01	7.6 ± 2.5
Aug-06	0.19 ± 0.01	3.5 ± 0.5
Sep-06	0.16 ± 0.02	12.6 ± 0.8
Mean ± SD	0.18 ± 0.01	7.5 ± 3.8

Discussion

DROUGHT-INDUCED EFFECTS AND RECOVERY

Although inter-annual changes in precipitation patterns were responsible for maximum water depth during 2005–2006, no changes in thermal structure in La Caldera were observed between both study years, indicating a well-mixed water column. By contrast, drastic changes in nutrient availability were observed. The low DIN:TP ratio of 2005 (DIN:TP = 5 ± 7), compared to previous studies (Carrillo et al., 1995; Reche et al., 1997; Medina-Sánchez et al., 1999; Morales-Baquero et al., 2006a) was caused by a combination of extremely low DIN concentrations (50% of the mean value recorded from 1986 to 2006) and atypically high TP concentrations (more than twofold the mean value measured from 1986 to 2006), never previously registered in this pristine ecosystem. The existence of lower DIN concentration during 2005 could be a consequence of higher primary production linked to higher P availability, which ultimately caused an increase in DIN consumption. Indeed, La Caldera typically undergoes a natural reduction in DIN concentrations during summer, which has been similarly explained by an enhanced primary production due to summer P-external inputs (Morales-Baquero et al., 2006b).

Higher TP concentrations during the 2005 drought compared to 2006 are likely a consequence of both a reduction in maximum water depth (as reflected by the inverse relationship between DLTM$_{depth}$ and DLTM$_{TP}$) and exceptionally high atmospheric P deposition rates. In fact, twofold higher TP atmospheric deposition rates were measured in the study area during 2005 (Morales-Baquero, personal communication) compared to previous years (Morales-Baquero et al., 2006a). The difference in the winter NAO index between 2005 and 2006, which may approximate a Saharan aerosol input to the Mediterranean region (Moulin et al., 1997), confirm the strong differences in the magnitude of atmospheric dust inputs during both study years. It is well known that during high-NAO years (2005; 0.13) precipitation is lower over the Mediterranean Sea and therefore drier conditions cause higher intensity of uptake and transport of desert dust (Moulin et al., 1997). By contrast, during low-NAO years (2006; −1.09) precipitation is likely to be greater over the Mediterranean area, limiting the intensity of dust-transporting atmospheric winds. Similarly, tropospheric content of UV absorbing aerosols measured by an Aerosol Index (AI) using a Total Ozone Mapping Spectrometroscopy (TOMS) instrument have confirmed this increasing dust deposition temporal pattern. Aerosol data have been previously used to study Saharan dust deposition, since positive correlations of TOMS AI with TP and particulate matter of dry atmospheric deposition have been found in this aquatic
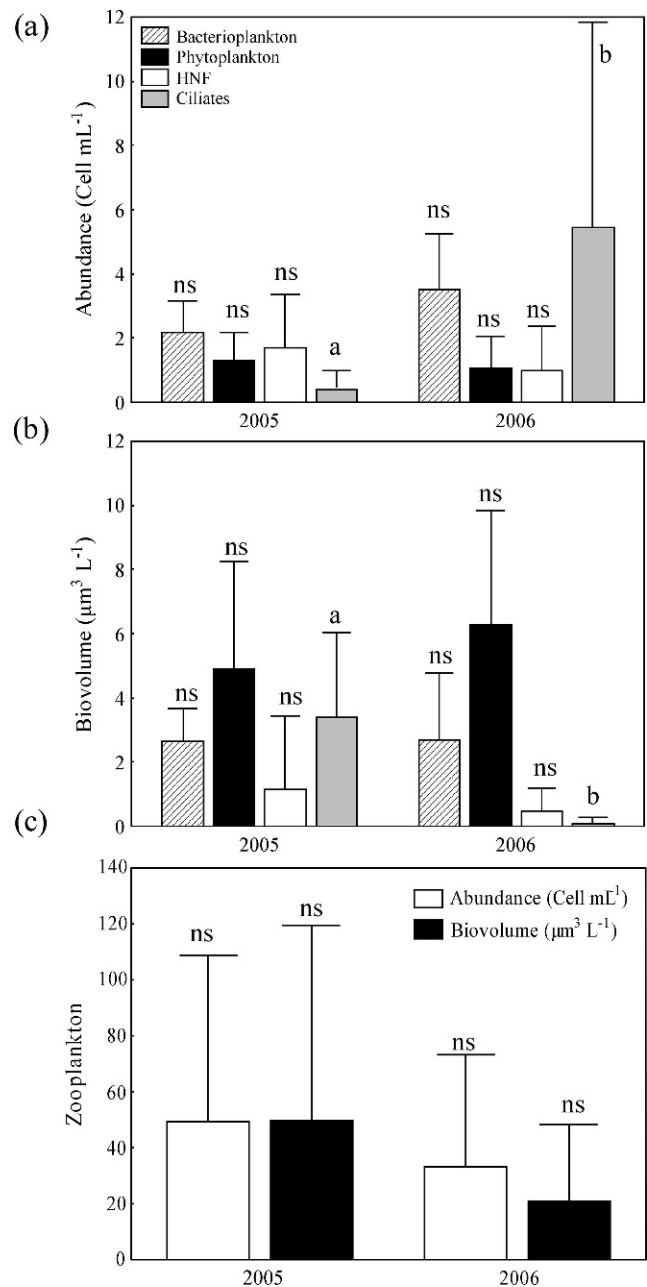

FIGURE 3. Within-year and year-to-year variations in the abundance (a, c) and biovolume (b, c) of bacteria (abundance: 10^9 cell mL^{-1}; biovolume: 10^9 μm^3 L^{-1}), phytoplankton (abundance: 10^7 cell mL^{-1}; biovolume: 10^9 μm^3 L^{-1}), HNF (abundance: 10^7 cell mL^{-1}; biovolume: 10^8 μm^3 L^{-1}), ciliates (abundance: 10^3 cell mL^{-1}; biovolume: 10^8 μm^3 L^{-1}), and zooplankton (abundance: ind L^{-1}; biovolume: 10^8 μm^3 L^{-1}) in La Caldera in summers of 2005 and 2006. Significant differences at $p < 0.05$ between years are indicated with letters. Error bars represent standard deviation (SD).

ecosystem (Morales-Baquero et al., 2006a). More recently, Bullejos et al. (2010) have found, over the past three decades, a tendency for an increase in the magnitude and occurrence of these events in the study area, especially after 1990. Over this period, there was a more than fivefold increase in TOMS AI and a more than threefold increase in the annual frequency of aerosol deposition events (Bullejos et al. 2010).

Apart from external forcing, internal nutrient recycling also plays an important role in nutrient dynamics for extreme oligotrophic lakes where external inputs are likely to be limited
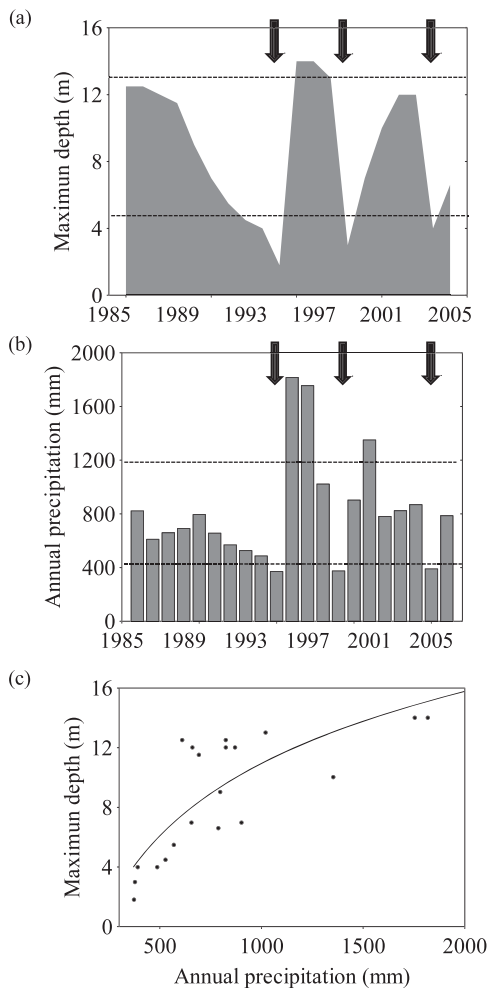
FIGURE 4. Inter-annual variability of (a) maximum depth, (b) accumulated annual rainfall of La Caldera, and (c) relationship between maximum depth and accumulated annual rainfall during the last 20 years. Vertical arrows in (a) and (b) indicate the occurrence of severe droughts (1995, 1999, and 2005), and broken lines in (b) indicate the mean values ± standard deviation of annual precipitation of 1985–2006 period. Data of accumulated annual rainfall were obtained from CETURSA Sierra Nevada, S.A. (management company of Sierra Nevada ski resort).
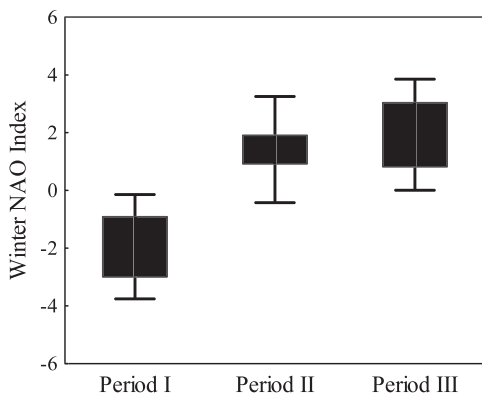

FIGURE 5. Winter North Atlantic Oscillation (NAO) index for each period. Boxes = standard errors. Whiskers = min.–max.
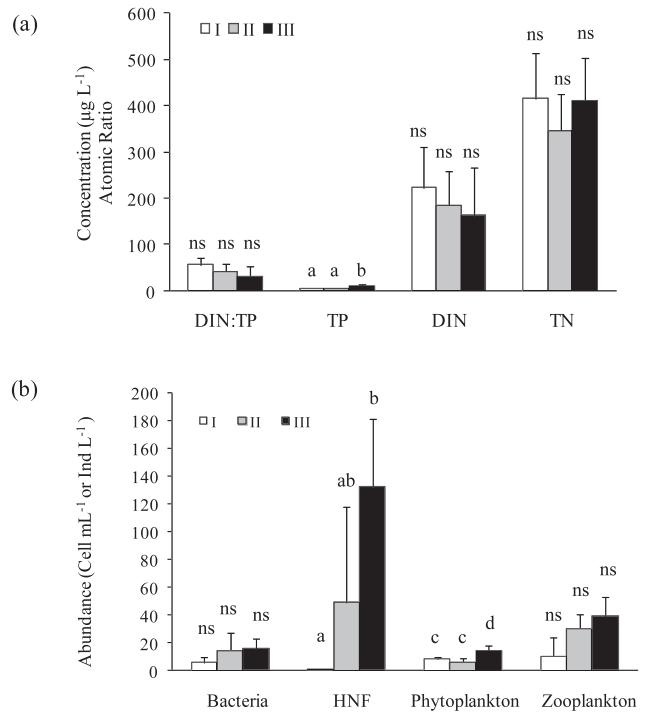

FIGURE 6. Long-term evolution of (a) DIN:TP mass ratio; TP, DIN, and TN concentrations (μg L^{-1}) and (b) bacteria ($\times$ 10^5 cell mL^{-1}), phytoplankton ($\times$ 10^3 cell mL^{-1}), zooplankton (ind L^{-1}), and HNF abundances ($\times$ 10^2 cell mL^{-1}). Error bars represent ± standard deviation (SD) of the mean. Period I: maximum depth > 10 m; Period II: maximum depth ranging from 4 to 10 m, Period III: maximum depth < 4 m. Significant differences at $p < 0.05$ between periods are indicated with letters.

(Baron and Caine, 2000; Webster et al., 2000; Morales-Baquero et al., 2006b). In this sense, zooplankton composition may drastically affect nutrient availability for phytoplankton production through consumer-driven nutrient recycling (CNR; Sterner et al., 1992; Sterner and Elser, 2002). The high N:P ratio of calanoids copepods would cause a proportionally higher P release (Cruz-Pizarro and Carrillo, 1991). Accordingly, the existence of higher abundances of calanoid copepod adults of *M. laciniatus* and *D. cyaneus* during 2005 (80% of the total zooplankton density, data not shown) than during 2006 (65%, data not shown) also support higher TP concentrations during the drought year. Comparing 2005 and 2006, ciliates were the only group having statistically significant differences in abundance and biovolume. Nutrient excretion of ciliates has been related to size (Dolan, 1997). In particular, under laboratory conditions, this author obtained a positive relationship between SRP maximum excretion rates and body size (as reflected by dry weight). By using this equation (in biovolume), SRP excretion rates were notably higher in 2005 than in 2006 as a result of the significantly higher biovolume of ciliates. Despite the differences in the potential contribution of ciliates to SRP concentrations between both study years, significant differences were observed for TP only and not for SRP concentrations.

Contrary to expectation, no concomitant increase in phytoplankton abundance was observed during the 2005 drought compared to 2006. One likely explanation is the increase in grazing pressure as a consequence of higher but not significant zooplankton abundance. In fact, zooplankton abundances reached highest values during summer 2005 compared to a 20-year data base. Our results confirm those obtained by Bullejos et al. (2010) in
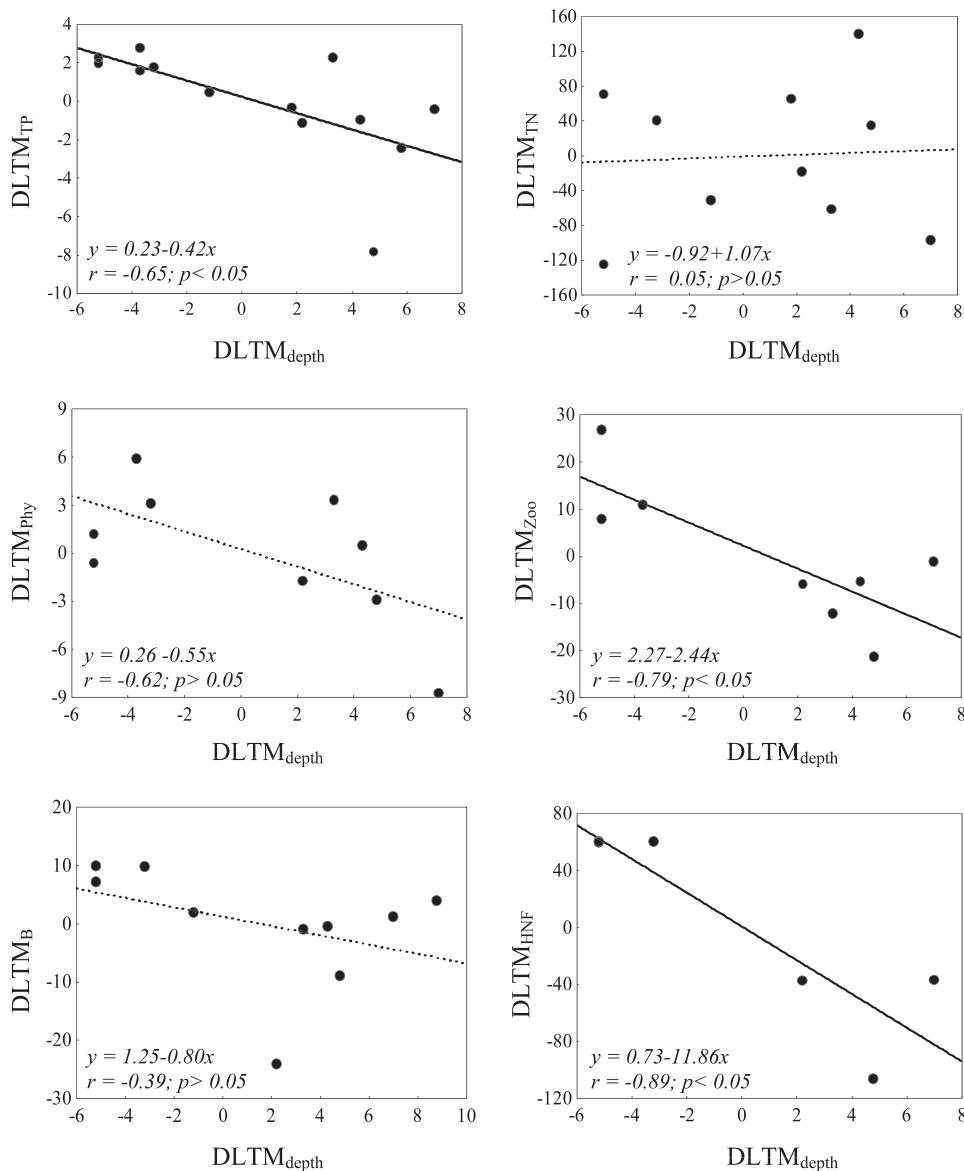
FIGURE 7. Scatterplots between DLTM$_{depth}$ and DLTM for each water quality parameter (TP, TN, Phytoplankton, Zooplankton, Bacteria, and HNF). Solid regression lines are shown for significant relationships while dashed lines are shown for non-significant relationships.

P-enriched experiments carried out in mesocosms in La Caldera, who found a unimodal response of zooplankton biomass to the TP gradient reaching highest zooplankton abundances for TP concentrations close to those measured during 2005. Additionally, HNF abundance was notably higher during the driest year (2005) relative to the post-drought year. Similarly, previous studies (Medina-Sánchez et al., 1999) have recognized the appearance of high HNF abundances during dry conditions (1995), supporting the hypothesis of higher functional diversification of plankton communities during drought.

It is commonly accepted that phytoplankton dominates the food base in more productive eutrophic lakes, whereas heterotrophic biomass dominates in less productive lakes (del Giorgio and Gasol, 1995; Gasol et al., 1997). Our results, however, confirm previous studies (Reche et al., 1996) about the autotrophy of La Caldera (A:H > 1) owing to the negligible input of allochthonous organic carbon into the lake. Despite this general pattern, we measured values of the A:H ratio lower than 1 during extremely dry conditions. Indeed, and similarly to the drought of 1995, during mid-summer 2005, the A:H ratio was below 1, reflecting a well-developed grazing and microbial food web. A rapid recovery

of plankton community was observed after the drought of 1995 and 2005, and shifts in A:H ratio may suggest that during especially dry conditions there is a predominantly top-down regulation of primary production (A:H < 1). During wet years, there is a bottom-up control of nutrients on primary producers (A:H > 1). A possible explanation for the predominance of top-down control (A:H < 1) under drought conditions could be the development of ciliates characterized by higher biovolume. Ciliates can act as a link between pico- and nanoplankton and macrozooplankton (i.e. Cruz-Pizarro et al., 1994). In particular, ciliates allow the maintenance of a high heterotrophic biomass by feeding on size particles not efficiently grazed by large zooplankton and serving as easily assimilated prey for grazers (Porter et al., 1979; Beaver and Crisman, 1982).

Analysis of the speed of recovery to drought conditions (resilience) shows that, despite relatively low resilience in TP concentrations after the 2005 drought, a fast recovery was observed for the TN and DIN:TP mass ratio, revealing a higher ecosystem homeostasis for these variables. In other words, the unusually low DIN:TP characterizing 2005 rapidly increased in 2006 to values close to those measured during the pre-drought year.

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WATER LEVEL EFFECTS ON CHEMICAL AND BIOLOGICAL VARIABLES

La Caldera shows a tight coupling between meteorological and hydrological variables reflected in significant and positive correlations between maximum water depth and precipitation for a 20-year period. Although there is a large body of literature concerning the response of abiotic and biotic variables of La Caldera to contrasting climate conditions (see among others, Medina-Sánchez et al., 1999; Villar-Argáiz et al., 2002; Morales-Baquero et al., 2006b), we compiled long-term data to provide insights about the effect of WLFs on lake ecology.

We have identified three different time periods during a 20-year data base (1986–2006) that differ in average values of winter NAO index. High-NAO years are characterized by drier years (Period III), while low-NAO years by wetter years (Period I). In general, an increasing and significant tendency of TP concentrations and of phytoplankton abundance occurs concomitantly with a reduction in water depth, that is, from Period I to Period III. However, the extreme within-years variability in other variables masks this year-to-year pattern.

WLFs affect the ecological processes and patterns of lakes in several ways (Wantzen et al., 2008), yet a controversy exists about the effect of climatic change on nutrient availability in lakes. Analyzing a long-term data base (1983–2001) in Sierra Nevada lakes (California), Sickman et al. (2003) found increasing P inputs and a concomitant shift from P toward more frequent N limitation on phytoplankton abundance. Similarly, more recently, García-Jurado et al. (2011) found a reduction in the DIN:SRP ratio during a dry year in a high mountain lake in Sierra Nevada (Spain). By contrast, Parker et al. (2008) reported in alpine lakes of the Canadian Rockies, a decreasing tendency in TP concentrations in the 2000s, characterized by dryer summers, relative to the 1990s. Flanagan et al. (2009), when studying for a 6-year period an alpine lake in the Rocky Mountain region, found higher concentrations of major ions during the driest year, while no clear tendency in NO_3^- and SRP concentrations was observed. These contradictory results suggest that changes in nutrient concentrations during drought conditions are more closely related to site-specific physical, chemical, and biological processes.

This assessment of the long-term effect of WLFs on water quality parameters in La Caldera has shown that WLFs significantly affect TP concentrations as well as zooplankton and HNF abundances. There exist several explanations for the higher P availability in the water column during low versus high water-level years. First, because of the reduction in the water volume, sediment resuspension is expected to increase. It is well known that in shallow lakes, sediments are subjected to the continuous physical action of wind waves that cause erosion and resuspension of particulate matter (e.g. Weyhenmeyer and Bloesch, 2001). The effect of sediment resuspension on nutrient dynamics is of particular concern for the oligotrophic high mountain lakes (Cruz-Pizarro and Carrillo, 1996; Villar-Argáiz et al., 2001; de Vicente et al., 2010) where any change in sediment and water interactions is likely to impact nutrient dynamics.

Second, a water volume reduction leads to an increase in the watershed area to lake area ratio and, hence, promotes a more pronounced impact of external nutrient sources (i.e. atmospheric deposition) on the whole lake metabolism. Indeed, dry deposition is relatively P-enriched, based on the slope of the TN:TP relationship compared with the Redfield ratio, while wet deposition is relatively N-enriched (Morales-Baquero et al., 2006a). As has been stated above, it has been observed that data on aerosol deposition, as a proxy of P deposition (Morales-Baquero et al., 2006a) over

the past three decades in Sierra Nevada (Spain), reveal a tendency for an increase in the magnitude and occurrence of these events, especially after 1990 (Bullejos et al., 2010).

Despite of the general increasing tendency for TP concentrations, when water level decreases, strong differences in P concentrations between droughts occurred with higher TP concentrations in 2005 compared to previous droughts in 1995 and 1999 that were characterized by similar maximum water depths. Accordingly, the hypothesis of more intense sediment resuspension during drier years is not supported by our results. The more likely explanation appears to be a concomitant increase in P-enriched atmospheric dust inputs. However, the increase in TP availability linked to a decrease in water level was not followed by enhanced phytoplankton, which was constrained by a more intense grazing pressure (higher zooplankton abundances), resulting in a decoupling of long-term dynamics. Despite these year-to-year patterns, previous studies have found a significant and positive effect of P atmospheric inputs on Chl-a concentrations (Morales-Baquero et al., 2006a) and on bacterial abundances (Reche et al., 2009) in La Caldera during the ice-free period of 2001.

LAKE RESISTANCE AND RESILIENCE TO RECURRENT DROUGHT CONDITIONS

Stability is a useful concept for evaluating the effects of disturbances on ecosystem properties (Díaz-Delgado et al., 2002) and can be applied to investigate environmental controls on ecosystem response to disturbances and changes in disturbance frequency. An emergent theme is that the longer and more severe the drought, the longer that recovery will take (Bond et al., 2008). Our working hypothesis was that lake exposure to recurrent droughts (3 droughts in a 20-year period) would affect lake resistance and resilience. Our results have shown the existence of lower resistance in TP concentrations concomitantly with a higher resistance in TN concentrations after the third drought (2005), which may confirm that concurrent P-enrichment by atmospheric dust inputs are responsible for the increase in lake water TP concentrations. Lake resilience was highest during the last drought for TN while similar resilience was observed for TP during the first (1995) and the last (2005) droughts. Despite these differences, a fast recovery after the 2005 drought was observed for DIN:TP mass ratio, revealing a higher ecosystem homeostasis for this ratio. These results support the idea that lakes with short food chains have faster return rates (Carpenter et al., 1992) but that they are less capable of assimilating P pulses (Carpenter and Cottingham, 1997).

This study has found significantly positive effects of WLFs on TP concentrations in La Caldera. The extreme variability in TP concentrations during three recurrent droughts (characterized by similar maximum water depths) suggests that sediment resuspension was not the only source for increased phosphorus, and that high P-enriched atmospheric dust inputs could have maintained the abnormally high TP in-lake concentrations measured during the 2005 drought. The decoupling between TP and phytoplankton abundance linked to WLFs may have been caused by an intensification of grazing pressure by zooplankton under drought conditions. Lake exposure to recurrent droughts has reduced lake resistance to TP changes but it has increased lake resistance to TN changes. These observations support the idea of an increasing P external forcing represented by P-enriched atmospheric dust inputs. Strong differences in lake resilience for TP and TN concentrations were observed. Despite of these differences, there was a faster recovery after the last drought and an increase in the DIN:TP mass ratio revealed a higher ecosystem homeostasis.

Acknowledgments

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