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WETLANDS BIODIVERSITY AND PROCESSES

Hydrology-driven macrophyte dynamics determines the ecological functioning of a model Mediterranean temporary lake

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Abstract The community composition and metabolism of Mediterranean temporary lakes are sensitive to meteorology, determining the length of the flooded period and water depth. We studied the biological communities and metabolism of Laguna de Talayuelas, a Mediterranean temporary lake selected as a model to disentangle key ecological processes. The development and activity of hydrophytes were determined by hydrology. Water depth favoured differential development of emerged-floating versus submerged species. Rooted macrophytes, especially *Ranunculus*, extracted nutrients from the sediments, making them bioavailable for phytoplankton after senescence. During the studied period the lake showed three functional phases. The first period, with low water depth, was governed by autotrophic processes and coincided with the development of submerged macrophytes. These accounted for most lake's productivity, and a highly diverse community was maintained. A second phase occurred by late spring, coinciding with a sudden increase of the water depth after strong rainfalls; then submerged macrophytes decayed and decomposed, and respiration increased. The lake had a net heterotrophic behaviour and biodiversity decreased. During the third period, in summer, nutrients released from macrophytes decomposition favoured phytoplankton blooms. The system turned to net autotrophy but now based on phytoplankton photosynthesis. Floating macrophytes developed, though the benthic component maintained net heterotrophy.

Keywords Mediterranean temporary lakes · Hydrology · Macrophytes · Nutrient cycling · Primary production · Respiration

Introduction

The composition of the biological community and the metabolic balances of main processes, namely primary production and respiration, are key factors for the ecological functioning of any aquatic ecosystem (Staehr et al., 2012). Small Mediterranean temporary ponds and lakes have often been neglected as relevant ecosystems, though they offer a series of important ecosystem services such as nutrient retention, rainfall interception, or carbon sequestration (Cereghino et al., 2008, 2014). These ecosystems show an ecological behaviour that is largely determined by the specificity of the highly fluctuating Mediterranean climate, and

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its functioning primarily depends upon the intermittent hydrology. Key processes and events are, among others, desiccation, and rewetting; turbidity variations regulated by sediment suspension (regulated by the macrophytes cover) and by phytoplankton growth, as well as sudden depth changes promoted by heavy rainfalls. Overall, its water level depends on the balance between precipitation and evaporation, as they commonly have very small catchments and can even be endorheic. All these determine varying periods of flooding, the most common with filling within fall to spring, then summer desiccation (Fernández-Aláez & Fernández-Aláez, 2010). However, wet spring seasons, such as the case of our study, can allow a positive hydrological balance avoiding summer desiccation.

Among the different components of the aquatic communities inhabiting Mediterranean temporary ponds and lakes, macrophytes can be determinant for the lake metabolism. They also physically structure the ecosystem, and shape the rest of the biological community (Jeppesen et al., 1998). In temporary waters, factors such as the hydroperiod length and lake depth are key for structuring the macrophyte community (Della Bella et al., 2008). Macrophytes can regulate nutrient cycles, preventing excess nutrient availability for phytoplankton when they are healthy growing (Barko & James, 1998; López Archilla et al., 2012). Rooted vascular aquatic plants can obtain nutrients from the sediments, and they are favoured against phytoplankton when external nutrient supply is limited. Then the internal load mostly sustains lake productivity. Increased depths and turbidity, which decrease light availability for submerged plants promoting senescence, are among factors that can drive macrophyte succession, favouring floating-leaved species that escape light limitation (Weisner et al., 1997). Senescent macrophytes can then become a source of nutrients when decomposing. This nutrient release could in turn be profited by other components of the primary producers guild (Søndergaard & Moss, 1998; Asaeda et al., 2000), mostly by phytoplankton that can dominate autotrophic processes over submerged macrophytes. Since temporary lakes and ponds usually lack fishes, consumers span from zooplankton to macroinvertebrates, as well as amphibians, snakes, and waterfowl. All of them are somewhat depending on macrophytes, which can regulate nutrient cycles, serve as food sources, act as a refuge for small animals, and contribute to build-up the physical structure of the ecosystem (Jeppesen et al., 1998).

Mediterranean lakes and ponds have marked seasonal patterns that determine their ecological functioning. The Mediterranean area, and more specifically the Iberian Peninsula, is the part of Europe where the predicted changes on the rainfall patterns and its total amount are stronger, and the occurrence of extreme events of heavy rainfall episodes and long dry periods is likely to increase (IPCC, 2013). Overall, the predicted reduction of the total amount of precipitation and of its temporal distribution, together with the increase of several degrees in temperature, would drive Mediterranean lakes and ponds to deep ecological shifts, including strong changes in the hydrological patterns. Therefore, the knowledge of how these ecosystems function when the normal patterns of seasonal flooding and drying are altered by extreme events, such as in our study, results of paramount importance to establish management modes that enhance its conservation.

In this work we present a study of the communities and the main metabolic traits of Laguna de Talayuelas, that we selected as a representative model of this type of Mediterranean ecosystems. The meteorological pattern and hydrology of the studied period contrasted with the normal seasonal flooding/desiccation pattern of this kind of ecosystems. Our study aims to illustrate how extreme events, like heavy rainfalls, can deeply modify the typical flood–drought succession and the inherent ecological features and functioning of this kind of lakes. We also hypothesize that sudden and abrupt flooding events, caused by strong rainfalls, can trigger the macrophyte development, which drives the community succession and its effects on the ecosystem metabolism.

Materials and methods

Study site

Laguna de Talayuelas is a small (5.6 ha), shallow (max depth <2 m) fluctuating temporary freshwater lake (conductivity 0.18–0.8 mS cm^{-1}) lying on siliceous bedrock. It is situated at 895 m.a.s.l. in East Spain (39°48′59.8″ N, 1°14′24.73″ W), in an area of transition between Mediterranean and Continental climates. Its catchment is mostly covered by pine forest. The lake is within the Site of Community Interest ES4230002—"Sierras de Talayuelas y Aliaguilla", and is considered by the Spanish Water Administration as a water body within the European Water Framework Directive.

Hydrology and meteorology

Meteorological data from the meteorological station nearest to Laguna de Talayuelas were provided by the National Institute for Meteorology of Spain (http://www.aemet.es). A reconstruction of the flooding series and measurements of the dimensions of the macro- and microbasin of Laguna de Talayuelas for the period 2007–2011 (Fig. 1) were performed with the environment for visualizing images software from satellite Landsat 5 TM and Landsat 7 TM images (http://glovis.usgs.gov). From these images, band 5 (1.55–1.75 µm) separates the water body (dark tone) from barren lands, croplands, and grass lands (lighter tone) (Doña et al., 2014). The surface outlet is active only when water level is >2 m. Therefore, the lake is mainly endorheic.

Sampling and physical, chemical, and biochemical analyses

Sampling in Laguna de Talayuelas was done monthly during the flooding period of the 2007–2008

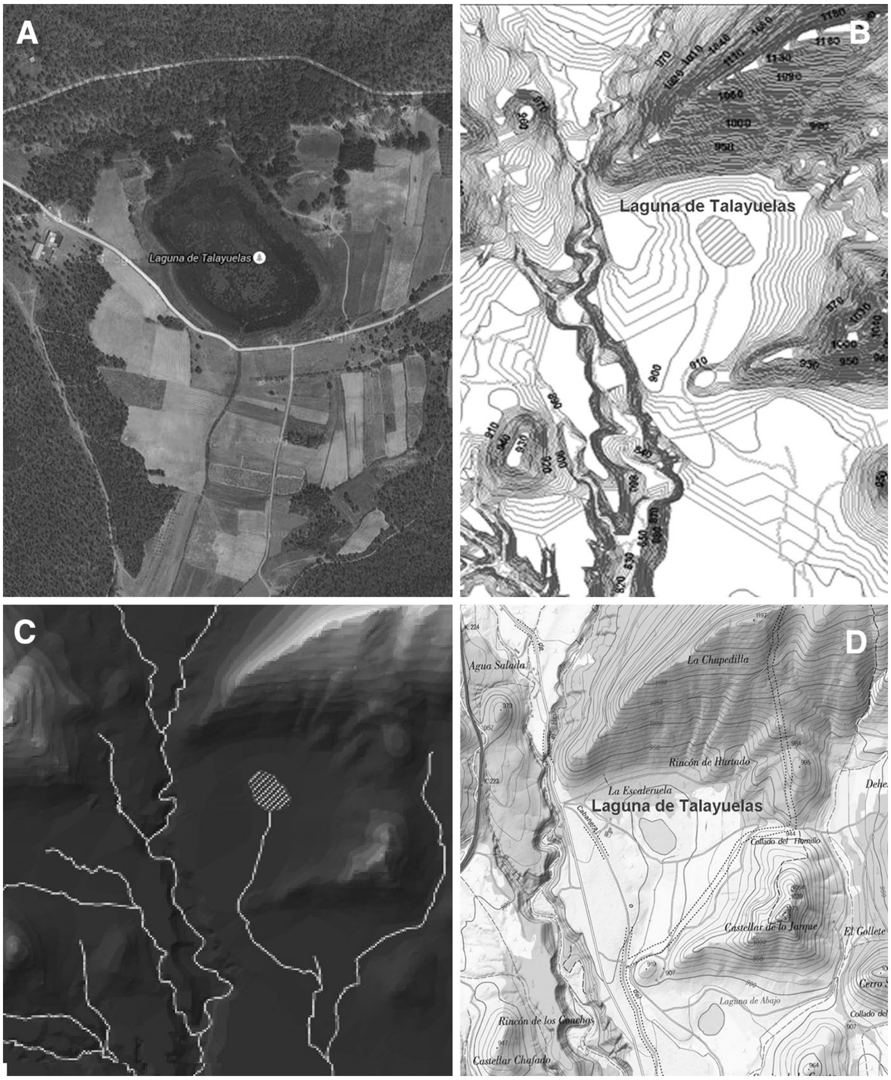

Fig. 1 **A** Aerial view of Laguna de Talayuelas, **B** topography of the catchment, **C** macrobasin, and **D** microbasin of Laguna de Talayuelas

hydrological cycle, from March to August 2008. The water sampling was performed in the central part of the lake, were the maximum depth is attained. Sampling was done from boat with depth >1 m. Concurrently, the coverage analyses and biomass sampling of macrophytes was performed by divers. Dissolved oxygen and temperature (WTA OXI-91), conductivity (Hanna 330i) and pH (WTW 3110) were measured on site. The water transparency was measured as Secchi depth.

Physical and chemical laboratory analyses were performed following Standard methods for water analyses (APHA–AWWA–WPCF, 2005). All samples were preserved in the dark and refrigerated until analyses were performed within not more than 6 h from sampling. Soluble inorganic nitrogen and phosphorus forms were measured from in situ filtered water (GF/F filters). Nitrate plus nitrite was measured spectrometrically after reduction of nitrate to nitrite ammonia was analysed using the phenol–hypochlorite method. Total nitrogen (TN) was measured after double digestion of unfiltered samples to nitrate following Golterman (2004). Soluble reactive phosphorus (SRP) was determined by the phosphomolybdic acid–ascorbic method. Unfiltered samples for total phosphorus (TP) determinations were digested through an acid persulfatic digestion (Ameel et al., 1993). Nitrogen–phosphorus ratios (N/P ratios) refer to TN–TP ratios. Suspended solids and organic matter analyses were performed gravimetrically after filtration of the samples on glass fibre filters (Whatman 934-AH), then incubating at 2 h at 105°C for total suspended solids and 6 h at 460°C for burning of organic matter. Chlorophyll-*a* concentrations were determined by spectrophotometry as described by Picazo et al. (2013). Fluorescence excitation–emission matrices of the water samples were also obtained to quantify the chromophoric dissolved organic matter (CDOM). Humic acids (autochthonous and allochthonous), and protein-like (tryptophan) CDOM were separately estimated according to Stedmon & Markager (2005). Measurements were performed on an F-7000 Hitachi fluorescence spectrophotometer, using standards prepared with quinine sulphate and bovine serum albumin (BSA), respectively.

Total bacterial counts (HPP) and autotrophic picoplankton (APP) abundance were determined by epifluorescence microscopy (Kemp et al., 1993) using a Zeiss III fluorescence microscope at 1250 (G 365 exciting filter, LP 420 suppression filter). For the determination 2 ml of sample was filtered on a 0.2 μm black membrane filter (Isopore GTBP, Millipore) and stained with 4,6-diamidino-2-phenylindole at a final concentration of 0.02 mg ml^{-1} for 5 min. APP was distinguished by its autofluorescence. A minimum of 5000 cells were counted per sample.

For phytoplankton, phytobenthos, zooplankton, and macroinvertebrates, estimates of abundance, richness (number of species) and diversity (Shannon index) were made. Phytoplankton abundance was determined from lugol-fixed samples using the Utermöhl (1958) sedimentation method. Phytobenthos samples were collected by scraping the surface of submerged stones, then fixed with formaldehyde to 2% final concentration, and its abundance was determined microscopically following Streble & Krauter (1987). A total of 500 individuals (or colonies or filaments) per sample were identified both for phytoplankton and phytobenthos as described in Morata et al. (2003). Zooplankton counts were performed microscopically on formalin fixed samples as described by Armengol et al. (2001), following the keys of Dussart (1969) and Koste (1978). Macroinvertebrate samples were taken with a hand strainer in all different environments trying to sample all taxa, then fixed with 70% ethanol and identified in the laboratory using a binocular microscope. Relative abundance and frequency data were obtained after classification following Tachet et al. (1987) and Puig (1999).

The biomass of macrophytes was estimated per unit area at 10 sampling points randomly chosen. Macrophytes were collected within a 30 × 30 cm frame, placed on the sediment surface. In the laboratory macrophytes were cleaned, sorted according to Olivares (1998) and Cirujano et al. (2008), and weighed. Then, the biomass of each taxon was separately dried for 2 h at 105°C to obtain dry weight.

Metabolic rates: primary production and respiration

Planktonic primary production and respiration rates were determined using the oxygen method (Bahamonde & Cabrera, 1984). For the planktonic system, four light and four dark Winkler-type bottles were incubated for 3 h. The variation of oxygen in the light corresponded to the net community production (NCP), this is, the balance between photosynthesis (GPP) and community respiration (CR). CR was calculated from the consumption of oxygen in the dark bottles. Then, GPP was calculated by the summa of NCP plus CR. To also measure the rates of these processes in the benthic system, that embraces macrophytes and the associated benthos including sediments, the bell-jar method (Kemp et al., 1993) was used. Four light and four dark jars were incubated for 3 h. Since bell-jars also included plankton, benthic rates were calculated by subtracting those of the plankton included in the jars. In both cases, plankton and benthos, results given are an average for each four replicates. Transformation of oxygen production/consumption into carbon was performed by considering the stoichiometry of the measured processes. Both planktonic and benthic GPP and CR were referred to lake surface units.

Statistical analyses

A multivariate analysis was carried out by applying a canonical correspondence analysis (CCA; Gauch, 1982; Kovach, 1998) to biotic and abiotic variables. Variables were square root transformed. ANOVA tests were additionally performed to compare among macrophytes' taxa dominance under the three differentially marked hydrological situations (early spring, late spring, and summer). Statistical analyses of CCA and ANOVA were performed using the MVSP 3.0 and SPSS 12.0 software packages, respectively.

Results

Hydrology and water chemistry

The ecological features and metabolism of Laguna de Talayuelas, which we selected as a model temporary Mediterranean lake, were intensively studied during the hydrological 2007–2008 cycle once the lake was flooded in March 2008 (Table 1). As recorded for previous years (data not shown), the flooding pattern of Laguna de Talayuelas is quite variable and depends very much on the rainfall regime. The normal pattern, with summer desiccation, was not followed the studied hydrological year. Though the macrobasin represents a drainage network of up to 157 km^2, this epigenetic lake only receives surface waters coming from a very small catchment area of 3.5 km^2 (Fig. 1). Maximum correlation between series of lake water volume and rainfall covering a period of ca. 5 years shows a quick response of lake hydrology to rainfall, with a lag time of just a few days (data not shown). In the hydrological year when this study was performed (2007–2008), the lake got dry in the previous summer, but did not start again to accumulate water until the end of February 2008, when some late winter precipitations occurred (Table 1; Fig. 2A). In a first flooding phase the lake remained with relatively low depth (around 0.30 m maximum) until middle May. Later on, strong rainfall events, which repeated through late spring, brought the lake to its maximum depth of 1.8 m by June, representing a second hydrological phase. This extraordinary rainfall supply allowed the lake to maintain its flooding during summer, contrasting with other years when it presented summer desiccation. Though decreasing the water level, it maintained more than 1 m depth during this third hydrological period. Overall, average depth during the studied period was 0.97 ± 0.63 m.

Sudden changes of water levels caused anomalous temperature variations, which increased in early spring and were below the typical values in May–June during the rainy phase. Concurrently, the water volume increase caused a dilution of the lake waters, evidenced by the marked conductivity and pH decrease (Table 1). However, pH remained slightly alkaline, due to the bicarbonate availability (data not shown). Water salt content followed the cationic series Ca > Mg > Na > K and anionic series $HCO_3^- > Cl^- = SO_4^{2-}$. Dissolved oxygen concentrations were oversaturated in early spring, coinciding with the development of a submerged macrophytes meadow. Instead, they became very low, down the hypoxia level, in summer, linked to the unbalanced respiration–photosynthesis ratio. The dissolved oxygen concentrations were related to the presence and persistence of the benthic vegetation, as shown also by the water transparency. The latter was clearly affected by the water depth and the development/decay of macrophytes and phytoplankton.

The increases in water supply during late spring also determined a dilution of the lake waters, and dissolved salt concentrations dropped to less than one third of the values found in the initial flooding steps, as shown by the conductivity values (Table 1). Average conductivity values of 447 ± 181 µS cm^{-1} were recorded during the studied year, and, though not very abundant, the dominance of calcium bicarbonate determined a slightly alkaline pH, with values of

Table 1 In situ measured variables during the studied period in Laguna de Talayuelas

Sampling dates	Maximum depth (cm)	Rainfall (mm m^{-2})	Dissolved oxygen (mg L^{-1})	Dissolved oxygen (%)	Temperature (°C)	Conductivity (µS cm^{-1})	pH	Secchi (cm)
11 March 2008	36	52.7	10.1	115	12.6	756	8.08	Bottom
14 April 2008	31	12.1	16.3	202	20.7	489	7.48	Bottom
7 May 2008	31	76.8	11	126	17.6	596	7.13	Bottom
29 May 2008	140	109.8	5.7	75	18.4	236	7.22	60
24 June 2008	180	104.3	1.7	23	27.7	360	7.18	30
21 July 2008	150	1.2	3.3	37	27	302	7.36	50
26 August 2008	110	2.2	5.4	70	25.7	389	7.90	45

Rainfall refers to the accumulated amount between two sampling dates

7.5 ± 0.4. Even though there was a clear seasonal water temperature pattern, high water temperatures were also recorded during favourable spring periods when lake depth was not high (e.g. April), because the high surface–volume ratios allow a strong daily heating of the lake waters. This determined relatively high water temperatures during the day, with averages during the studied period of 21.4 ± 5.6°C. Dissolved oxygen concentrations were oversaturated during early spring, coinciding with the development of a prairie of submerged macrophytes, whereas undersaturated concentrations appeared from middle spring through summer, determined by the higher rates of respiration compared to photosynthesis. Average values for the whole studied period were 7.6 ± 5.1 mg $O_2\,L^{-1}$ and oxygen saturation of 93 ± 61%. Water transparency was also evaluated through the measurement of the Secchi disk depth, which arrived to the bottom in the period of low waters until middle spring, but latter averaged 0.40 ± 0.12 m, showing the decrease in transparency in the hydrological periods 2 and 3.

The inorganic nutrient and OM dynamics in water also showed marked differences through the studied period. Nitrate was always very low <2 µM, whereas ammonia concentrations were also low but slightly higher during the first period after flooding, and later decreased (Fig. 2B). Soluble inorganic nitrogen compounds were relatively scarce compared to other nitrogen forms, as TN varied from 92 to 159 µM (data not shown). TP also peaked at the beginning of the flooding period, but quickly dropped, then progressively increasing (Fig. 2C). Remarkably, although soluble phosphorus concentrations were almost constantly low, they peaked in the second part of spring, coinciding with the decay phase of submerged macrophytes. TN/TP ratios oscillated from 25 to more than 200, a variation through the studied period also occurred in the percent of OM, whose contribution to total suspended solids increased especially during summer (Fig. 2D). Both humic and protein-like CDOM were low in the initial phase of the flooding period but soon peaked during the first half of spring, then slightly decreased during the rest of the studied period (Fig. 2F).

Biological communities: description and dynamics

The most remarkable biological feature of Laguna de Talayuelas was the early spring development of a bilayered carpet of submerged macrophytes formed by a lower stratum of macroalgae (*Chara* sp.) overlaid by the vascular plant *Ranunculus peltatus*, and accompanied by emerged common tules (*Scirpus lacustris*). The macrophyte biomass increased during the low water phase, then declined after flooding from May

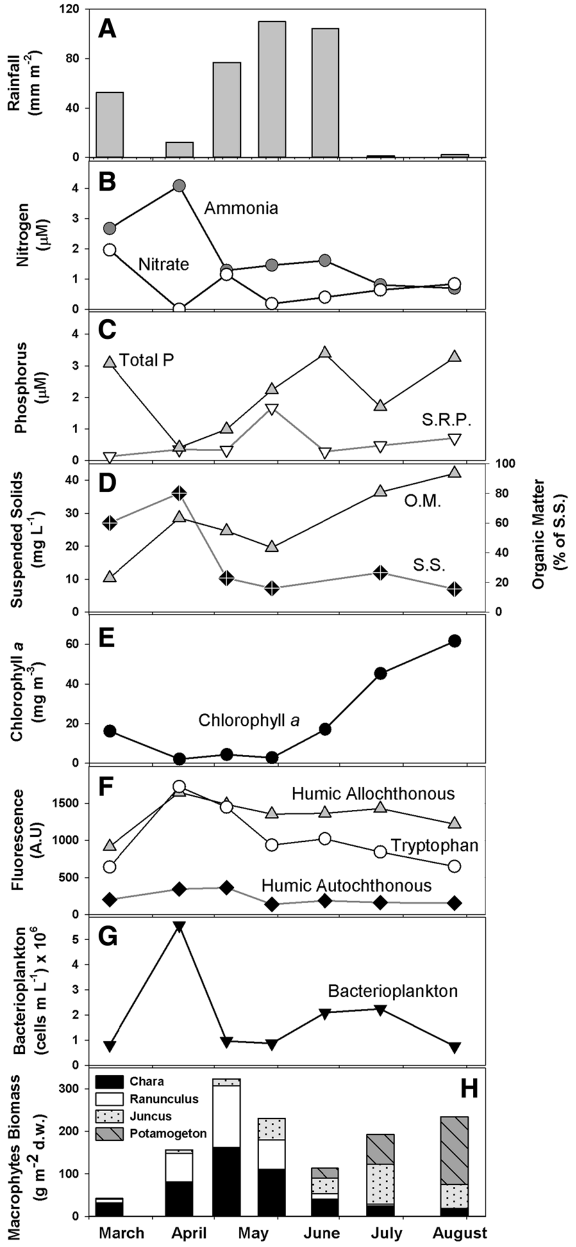

Fig. 2 **A** Accumulated rainfall between sampling events, and concentrations of **B** ammonia and nitrate, **C** total (TP) and soluble reactive phosphorus (SRP), **D** suspended solids (SS) and percent of organic matter in the SS (% OM), **E** chlorophyll-a, **F** chromogenic dissolved organic matter (CDOM); **G** bacterioplankton abundance, and **H** macrophyte biomass (with the relative contribution of each taxon), in Laguna de Talayuelas during the studied period

onwards (Fig. 2H). Later on, the floating-leaved pondweed *Potamogeton gramineus* became dominant. Through each of three hydrological (water depth) periods (early spring, late spring, and summer) the relative importance of each macrophyte's taxon varied (Fig. 2H). A two-way ANOVA test showed statistical significance for the existence of three periods with differentially marked hydrology ($P < 0.00001$) and macrophytes' taxa dominance ($P = 0.018$), as well as a strong interaction among hydrology and taxa dominance ($P < 0.00001$). Additionally to the macrophytes growing in the flooded basin, a belt of common reed (*Phragmites australis*) mostly surrounds the lake, with invasive poplars (*Populus nigra*) covering small areas of the former lake basin.

Phytoplankton was scarce during the period of maximal development of submerged macrophytes, but its abundance strongly increased from late spring through summer, as shown by chlorophyll-*a* concentrations (Fig. 2E). Also, the relative contribution of the different algal groups very much fluctuated during the studied period (Fig. 3A). Chrysophytes peaked immediately after flooding, with *Chrysococcus biporus* as *main species*. Pennated diatoms (Bacillariophyta) alternated with chlorophytes (*Pedinomonas minor* as main species), as the dominant groups from early to middle spring. Chlorophytes maintained a relatively high importance also during the rest of the studied period, but shifting the dominance to colonial forms such as *Volvox aureus*. Remarkably, cyanobacteria (*Microcystis* sp., *Nostoc* spp.) became a dominant group during late spring and summer, linked to the decay of submerged macrophytes and nutrient enrichment. In general, species richness was higher during the second part of the studied period (Fig. 4A). This was mainly due to the higher taxa richness of chlorophytes and cyanobacteria, the most abundant components of the phytoplankton during this period. However, as in most of the studied period, diatoms were still the group comprising more taxa. On the other hand, bacterioplankton abundances peaked in early spring to 5.8×10^6 cell mL^{-1}, although they oscillated mostly between 1 and 2×10^6 cell mL^{-1} (Fig. 2G). Phytobenthos was less diverse than phytoplankton, with chlorophytes commonly being dominant. Though, the relative importance of both benthic diatoms and cyanobacteria fluctuated and made these groups quantitatively important in the phytobenthic assemblages during some periods (data not shown).

The zooplankton assemblages also shifted in the relative dominance of the different groups. Absolute

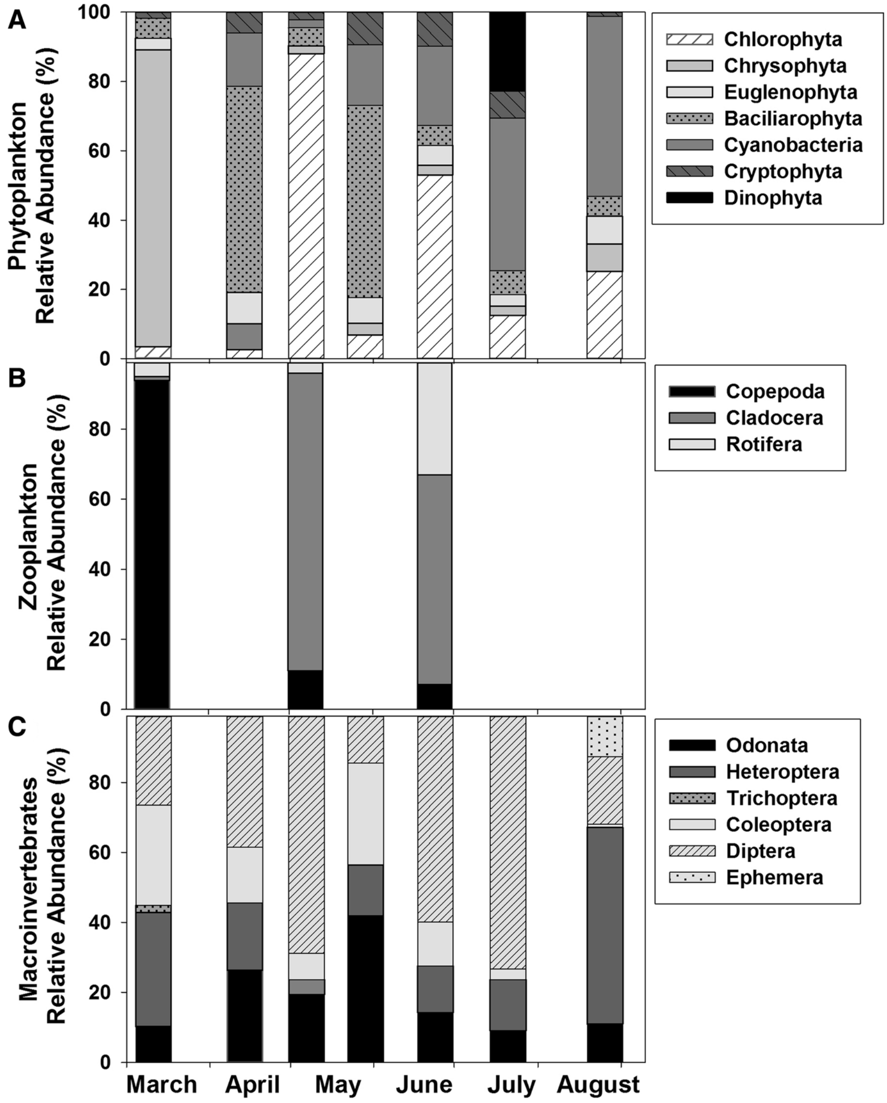

Fig. 3 Relative abundance of the different groups of **A** phytoplankton, **B** zooplankton, and **C** macroinvertebrates in Laguna de Talayuelas during the studied period

dominance of nauplii and juvenile stages of copepods (mostly *Mixodiaptomus laciniatus* subsp. *atlantis*, *Cyclops* sp., and *Acanthocyclops americanus*) was registered during the first stages of flooding, turning into a dominance of cladocerans and an increased importance of rotifers during the rest of the studied period (Fig. 3B). Daphnids (especially *Ceriodaphnia dubia* and *Daphnia curvirostris*) and the chydorid *Dunevedia crassa* dominated by middle spring. The latter maintained its relative importance during summer, but the other dominant species were replaced by *Moina* sp. In summer, when rotifers became relatively more abundant, two species of *Lecane* (*L. bulla* and *L. hamata*) were their major representatives. Overall, zooplankton species richness also dropped from the beginning of the flooding period from 11 to 7 species in summer (Fig. 4B).

Aquatic macroinvertebrates were quite diverse, with 22 different taxa of the class Insecta, mainly from the orders Odonata, Heteroptera, Coleoptera, and Diptera (Fig. 3C). Ostracods were also abundant, especially the species *Cypris bispinosa*, accompanied by *Cypridopsis* sp. and *Herpetocypris* sp. Gastropods (mainly from the family Ferrisidae), nematodes and oligochaetes were also quite abundant.

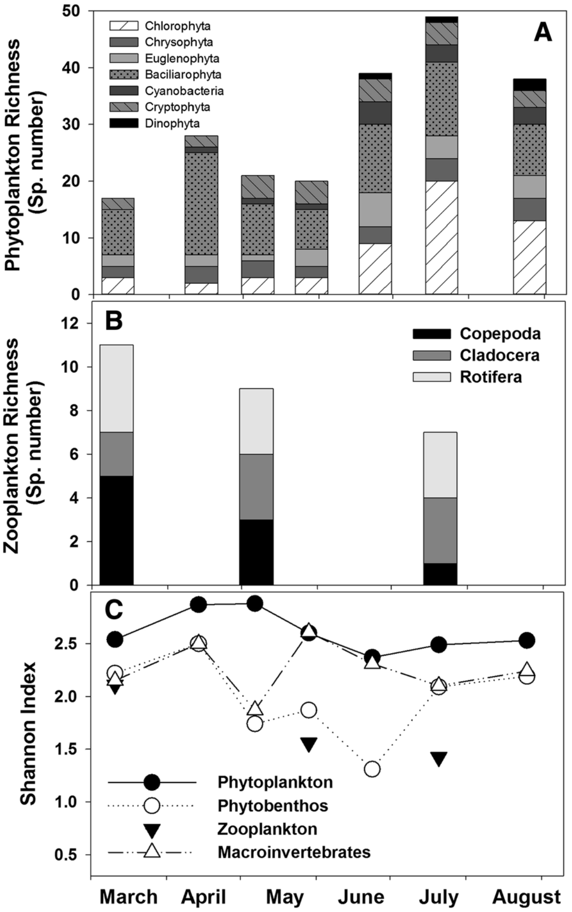

Fig. 4 Species richness of **A** phytoplankton and, **B** zooplankton; and **C** values of the Shannon diversity index calculated for the phytoplankton, phytobenthos, zooplankton, and macroinvertebrate assemblages, in Laguna de Talayuelas during the studied period

In addition to species richness, the Shannon diversity index was calculated for each group of organisms (Fig. 4C). Overall, the highest values of the index were found for the phytoplankton, ranging 2.4–2.9, being slightly higher during the spring months of maximum development of submerged macrophytes. Lower values of the Shannon index appeared for macroinvertebrates (1.9–2.6), phytobenthos (1.3–2.5), and zooplankton (1.4–2.1). Although not very clearly, for most groups the pattern showed higher values coinciding with the maximum development of submerged macrophytes in early spring, then dropping by middle spring to increase again in summer. Zooplankton was an exception, with a continuous decrease through the studied period.

Metabolic patterns: primary production and respiration

Primary production and respiration rates were clearly different in the three different functional phases (Fig. 5) associated with contrasting hydrological situations. This was also linked to the succession of submerged macrophytes and phytoplankton. During the fast development of the dense macrophyte meadow, from early to middle spring, submerged macrophytes accounted for most primary production in the lake, largely exceeding the CR (Fig. 5C). From mid May, during the macrophytes decay, CR increased and NCP rates became negative. Later on, by early summer, a new population of floating-leaved pondweed developed. The increase in respiration

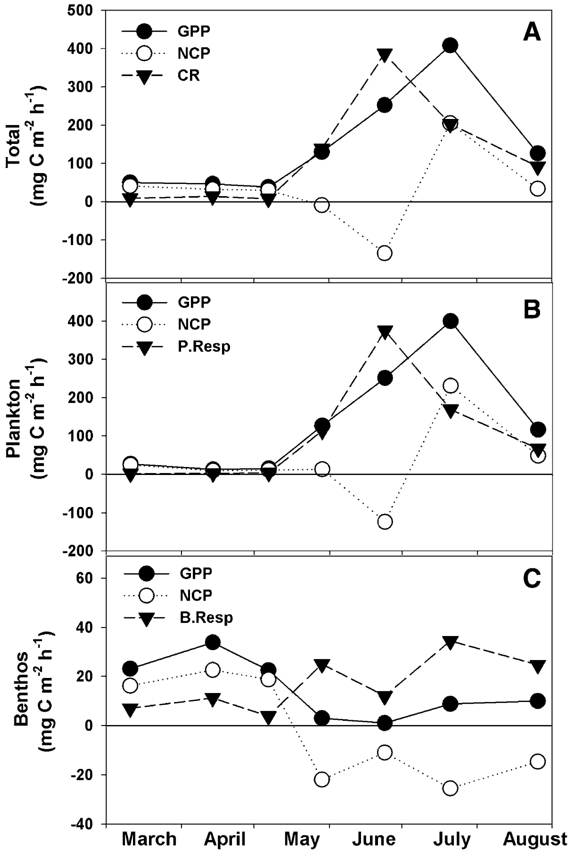

Fig. 5 Temporal patterns of photosynthesis (GPP), respiration (*CR* community respiration, *P.Resp* plankton respiration, *B.Resp* benthos respiration), and net community production (NCP) for **A** the whole system, **B** plankton and, **C** benthos, in Laguna de Talayuelas during the studied period

rates, however, maintained the macrophyte–benthos system on a net heterotrophic functioning (NCP <0) from late spring (phase 2) to summer (phase 3).

The contribution of plankton assemblages (phytoplankton, heterotrophic bacteria, and zooplankton) to the lake metabolism was comparatively low during the first period after flooding (Fig. 5B). Its relative importance, however, progressively increased through the studied period, especially after the decaying of the spring population of submerged macrophytes. Phytoplankton bloomed by summer (Fig. 5B), and its abundance and photosynthetic activity much increased (Figs. 2E, 5B). During these periods they became the dominant primary producers in the lake, which compensated plankton respiration giving a positive balance for the planktonic system in summer.

During most of the studied period the whole ecosystem behaves as an autotrophic system, with NCP >0 (Fig. 5A). This was initially supported mostly by the primary production of the submerged macrophytes until middle spring, then in summer by the primary production of phytoplankton. An exception is the end of spring, when the increases in respiration linked to the decomposition of the submerged macrophytes could not yet be enough compensated by the increase in primary production of phytoplankton, resulting in a period of net heterotrophy. Most remarkably, during summer, gross primary production increased mostly due to phytoplankton production, and the whole system turned autotrophic.

Multivariate approach

The CCA supports the existence of different functional periods in which metabolic rates and the dominance of the different biotic components varied (Fig. 6). Axis 1 clearly discriminates samples from the first phase (early–middle spring) from later periods. Samples from this first period are associated to the dominance of charophytes and *Ranunculus*, to high photosynthetic rates of the benthic component, as well as to higher water conductivity corresponding to lower water levels. Contrastingly, the positive side of axis 1, where samples from phases 2 and 3 are situated, is linked to higher depths, high photosynthetic rates by phytoplankton, high respiratory rates, and higher abundance of floating macrophytes, as the most remarkable variables. Axis 2 discriminates well the samples from the second functional period from those of the third period. The former, corresponding to late spring (late May), is located on the positive side of the axis, featured by variables such as rainfall and SRP. In contrast summer samples (June–August), situated on the negative side, are featured by the high chlorophyll-*a* concentrations and plankton photosynthetic activity resulting from the summer bloom of phytoplankton, and by the increased abundance of the floating *Potamogeton*.

Discussion

Laguna de Talayuelas is a typical Mediterranean temporary lake, whose ecological functioning is much depending on the hydrology. It is a good model to study the most determining factors for the ecological functioning of such type of ecosystems. Its normal hydrological pattern determines a variable flooding period followed by summer desiccation (Fernández-Aláez & Fernández-Aláez, 2010). However, the intrinsic variability of the Mediterranean climate makes these patterns partly unpredictable, and the moments in which flooding and desiccation occur can vary by several months. Interestingly the studied hydrological year contrasted with this normal pattern, as heavy mid-spring rainfalls supplied water enough to avoid summer desiccation. Also the scarce autumn and winter rainfalls were not enough to allow lake flooding, and the lake remained dry almost until spring. Thus, the studied hydrological year including an extreme dry period at the beginning and extraordinary rainfall events by middle spring, may represent well the increase of extreme events in the Mediterranean region predicted by the climatic models, which enhances the interest of the present study.

The length of the flooded period and the amount of water accumulated, in turn, largely influence the development of macrophytes. The species found in Laguna de Talayuelas are adapted to intermittent hydrology, and their propagules persist in the seed bank of lake sediments between flooding periods, thus allowing its seasonal development (Combroux et al., 2001; Bonis & Grillas, 2002). Macrophytes play an important role in the mobilization of nutrients from the sediments (Barko et al., 1991), especially phosphorus (Graneli & Solander, 1988). This is quite relevant, as internal load mainly sustains primary productivity in such a shallow lake with very low catchment area and

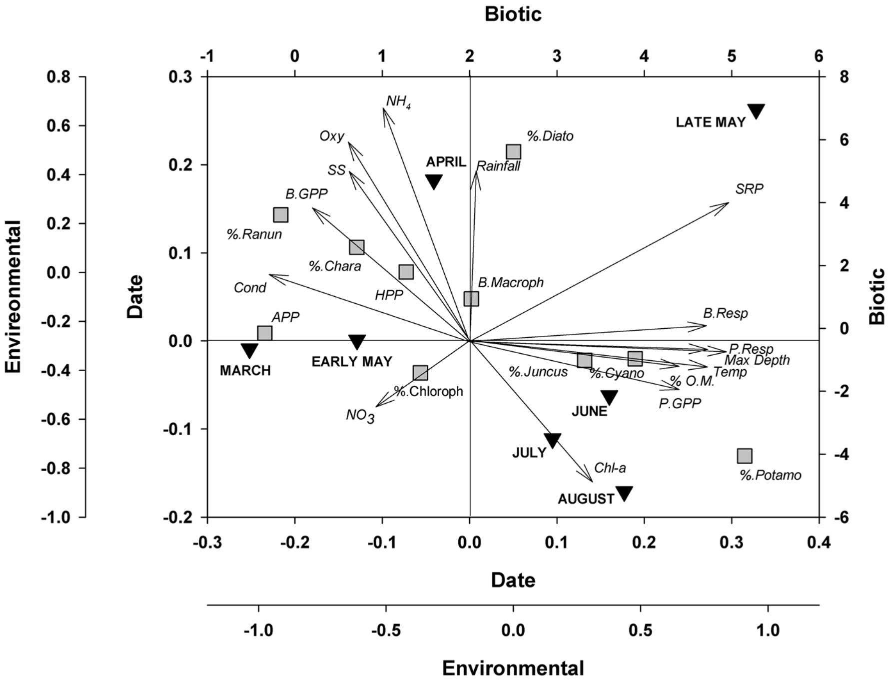

Fig. 6 Canonical correspondence analysis (CCA) with cumulative percentage of the variance explained for *two axis* of 88%. The analysis was performed with 7 cases (sampling dates), 10 variables: (biotic) referring organisms' abundance: heterotrophic bacterial abundance (HPP), abundance of autotrophic picoplankton (APP), relative abundance as % of chlorophytes (% Chloroph), relative abundance as % of cyanobacteria (% Cyano), relative abundance as % of Diatoms (% Diato), biomass of macrophytes (B.Macroph), relative abundance as % of *Chara* (% Chara), relative abundance in as of *Ranunculus* (% Ranun), relative abundance in as of *Juncus* (% Juncus), relative abundance as % of *Potamogeton* (% Potamo), and 15 environmental variables (including those of lake metabolism): water temperature (Temp), maximum depth (Max Depth), conductivity (Cond), dissolved oxygen in mg l^{-1} (Oxy), ammonium (NH_4), nitrate (NO_3), soluble reactive phosphorus (SRP), % of organic matter in water (% OM), chlorophyll-*a* (Chl-*a*), suspended solids (SSs) gross primary production by phytoplankton (P.GPP), gross primary production by benthos (B.GPP), respiration by plankton (P.Resp), respiration by benthos (B.Resp), and rainfall. Samples are coded by date from March to August 2008, previously the lake was dry. *Grey squares* represent the biotic (abundance) variables, and *black triangles* the samples

low external supply of nutrients. Nowadays the lake does not receive any point source of nutrients, and diffuse supply is quite limited since its small catchment is mostly covered by pine forest growing on poor soils, whose nutrient export capabilities are quite limited. Waterfowl, which could be an additional nutrient source (Manny et al., 1994; Sánchez-Carrillo & Álvarez-Cobelas, 2001), does not represent a significant net supply, as most of these birds are resident and its trophic contribution as nutrient importers is not as important as its role as recyclers.

In a shallow lake with small external nutrient inputs, the role of the internal nutrient load in supporting primary production is essential. The development of rooted macrophytes, that are able to use lake sediments as a main nutrient source (Bristow, 1975; Carignan & Kalff, 1982), allows nutrient mobilization. Among the species dominating the early stages of flooding in Laguna de Talayuelas, extraction of nutrients would be mainly performed by vascular plants like *Ranunculus*, since characeans mostly obtain nutrients from water (Kufel & Kufel, 2002). Decomposition of macrophytes generates dissolved and particulate OM that not only enhances the respiration of planktonic consumers, but also supplies inorganic nutrients that likely support phytoplankton growth (Flor-Arnau et al., 2013). TN/TP ratios in the lake oscillate from 25 to more than 200, which indicate that P could be the main limiting nutrient. The peaks of soluble and TP after macrophytes decay show the important role of macrophytes' senescence as a phosphorus supply process. Release of phosphorus from actively growing macrophytes (both submerged and emergent) is minimal, but decaying macrophytes may act as an internal phosphorus source for the lake and add considerable quantities of phosphorus to the water (Graneli & Solander, 1988).

The heavy rainfall occurring by middle spring had a strong influence in the ecological functioning of the lake, since it increased by six times (30–180 cm) its depth. The first consequence was that the summer desiccation process did not occur, and thus this period when heterotrophic processes usually dominate over autotrophy (Camacho et al., 2012) did not appear in the studied hydrological year. Other common consequence of the sudden increase in the water depth was the decrease in light availability for submerged macrophytes, which in turn could cause a decompensation of its metabolism (Schelske et al., 2010), and then explained the decay of their populations. Since vascular aquatic macrophytes are easily decomposed (Song et al., 2013), nutrients resulting from plant decomposition were released, and could be profited by phytoplankton. This is especially true in periods, such as middle spring and early summer, in which temperatures are milder and light availability higher, thus phytoplankton growth can be faster. The occurrence of phytoplankton blooms increased light extinction through the already deeper water column, which difficult further development of submerged macrophytes. Floating-leaved macrophytes, such as pondweeds, could, however, develop, as they were not affected by light depletion in deeper layers, and became dominant among the hydrophytic community.

The natural nutrient dynamics controlled by the rise and fall of submerged macrophytes has an effect of natural eutrophication through the hydrological cycle. Oligotrophic conditions were maintained during the initial periods of flooding when macrophytes controlled nutrient availability. Later on, more eutrophic conditions appeared, with much higher phosphorus availability (see the peak of soluble phosphorus at the end of May in Fig. 2C), as a consequence of macrophytes decomposition, which later was mostly built into phytoplankton biomass. Since TN/TP ratios in the lake waters indicate a relative deficiency in phosphorus (Guildford & Hecky, 2000), these pulses of phosphorus availability quickly promoted growth of phytoplankton, as well as that of floating macrophytes that escape light limitation. The drift towards eutrophic conditions is not only reflected by the higher phytoplankton abundance, but also by the changes in the relative abundance of phytoplankton groups. The earlier dominance of species of chrysophytes, diatoms, or unicellular flagellated chlorophytes, which are typical from oligo-mesotrophic environments, was replaced by higher abundance of taxa favoured by more eutrophic conditions, such as colonial volvocal chlorophytes and cyanobacteria (Reynolds et al., 2002).

The metabolic variables studied and the statistical (CCA and ANOVA) analyses indicated that during the studied period the lake showed three markedly differentiated functional phases, in which diverse organisms differentially exerted an important role. The first period (from flooding to middle spring), covering the development of submerged macrophytes, was featured by a high productivity of the benthic assemblages (mostly by submerged macrophytes) which in turn was low for phytoplankton. Additional variables such as the high concentrations of dissolved oxygen, which were oversaturated due to macrophyte's photosynthesis, and the low Chl-*a* concentrations and high water transparency, that denote the small phytoplankton abundance, jointly characterise this first functional period. Also community structural variables such as a high diversity and the presence of groups of algae featuring oligo-mesotrophic conditions featured this first hydrological period. In this period, the excretion of organic compounds by macrophytes also enhanced bacterial growth on this CDOM (Rooney & Kalff, 2003), which explains the peak in bacterial abundance found in early spring. A second phase, by late spring, was associated with the senescence and decomposition of submerged macrophytes after the sudden increase in the water depth. This is mainly featured by the high concentrations of soluble (bioavailable) phosphorus released from this decomposition, and by the increase in the respiration of the benthic system. The third phase, that substituted the normal desiccation phase in this kind of temporary lakes (Fernández-Aláez & Fernández-Aláez, 2010), was featured by all the variables related to a high phytoplankton photosynthetic activity (and high respiration rates), which are linked to the phytoplankton growth sustained by the nutrients resulting from the decomposition of macrophytes, and was also favoured by the high temperatures. Nevertheless, by the end of the period (August), this highly productive phase started to decline. Overall, phases 1 and 3 are autotrophic, with both total and planktonic NCP >0, although in phase 3 the benthic component had a net heterotrophic behaviour (NCP <0) and dissolved oxygen saturation did not totally recovered. The net autotrophy was initially supported by the strong photosynthetic activity of submerged macrophytes, then in summer by that of phytoplankton. Contrastingly phase 2 was a net heterotrophic period, with NCP <0 for both the planktonic and the benthic components explained by the decomposition of the submerged macrophytes.

NCP for the flooding period in Laguna de Talayuelas averaged 28.5 mg C m^{-2} h^{-1}, ranging from −134.8 to 205.1 mg C m^{-2} h^{-1}. This annual positive average supposes that the lake acted as a net autotrophic system. Since the lake is endorheic, with almost negligible export rates, sediments are the major sink for the excess production. OM contents in the sediment range 3.39–9.47%, but since the NCP rates are quite similar through the whole basin (data not shown), the differential organic contents would depend more on diagenetic processes within the sediments rather than on differential rates of accumulation of decaying macrophytes. In any case, the excess flux of OM to the sediments can, through mineralization, become a nutrient source acting as an internal load.

Though there are not many available data, our rates can be compared with other temporary wetlands from the same latitudes, such as those from Doñana National Park (southwest Spain). Average rates of NCP of Laguna de Talayuelas (28.5 mg C m^{-2} h^{-1}) are quite similar to those reported for Doñana temporary wetlands (25.4 mg C m^{-2} h^{-1}; Geertz-Hansen et al., 2011). Similarly the reported rates of gross primary production (123.1 mg C m^{-2} h^{-1}) and CR (133.1 mg C m^{-2} h^{-1}) for Laguna de Santa Olalla (López-Archilla et al., 2004), also within the Doñana National Park, are similar to our average rates (150.3 for GPP and 121.8 mg C m^{-2} h^{-1} for CR, respectively), although in that lake phytoplankton accounted for most primary production.

The three functional phases are also reflected in the composition and properties of the biological community. Maximal values of the Shannon diversity index were found during phase 1 for all the different groups (phytoplankton, phytobenthos, zooplankton, and macroinvertebrates). Then, the development of submerged macrophytes offers better life conditions, such as more diversified food sources for consumers (Benetti et al., 2014), moderate nutrient supply for primary producers, highly oxygenated waters, and shelter for invertebrates to decrease the predation risk (Jeppesen et al., 1997). Phase 2, that gives less favourable conditions, resulted in a drop in the Shannon diversity index and species richness for these groups. Later, on phase 3, there was a recovery of the Shannon index for most groups, except for zooplankton, when rotifers became relatively more abundant.

In conclusion, the hydrological pattern of Laguna de Talayuelas is encompassed with the development of aquatic vegetation during the growing period, whose metabolism, mainly through primary production, respiration and nutrient acquisition/release, largely influences the ecological functioning of the lake. Small Mediterranean shallow lakes, such as that studied here as a model ecosystem, are extremely sensitive to hydrological alterations that change their natural ecological patterns. These alterations modify their functional features and affect the biological community degrading the ecosystem health (Camacho et al., 2012; Correa-Araneda et al., 2014). Climate change, likely modifying the rainfall and temperature patterns, with more extreme events in the Mediterranean region (IPCC, 2013), can change the ecological functioning of these Mediterranean temporary lakes (Dimitriou et al., 2009; Coletti et al., 2013). This is especially important in lakes and ponds that, as Laguna de Talayuelas, hold an epigenetic mode of water supply and small catchments, thus a quick hydrological response to both extreme rainfall events as well as to dry periods. As demonstrated here, the alteration of the flooding patterns and the stronger activation of respiration compared to photosynthesis by temperature increases could also differentially alter the balance between autotrophic versus heterotrophic processes. This would likely modify the carbon cycle of these ecosystems, changing its balance for carbon sequestration versus emission.

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