

Trade-offs in plankton species richness arising from drought: insights from long-term data of a National Park wetland (central Spain)

Carmen Rojo · Miguel Álvarez-Cobelas · José Benavent-Corai ·
María Mercedes Barón-Rodríguez · María A. Rodrigo

Received: 6 October 2011 / Accepted: 21 May 2012
© Springer Science+Business Media B.V. 2012

Abstract Wetlands are considered vulnerable ecosystems of both high species richness and socio-economic value. In semi-arid regions, these ecosystems often experience long drought periods that are usually aggravated by local water overexploitation. Drought leads to: (i) reduced flooding area, (ii) isolation of water bodies, (iii) increased areas of dry sediments and shoreline length, and (iv) increased ionic concentration. These processes affect aquatic populations in a species-specific way and can have antagonistic effects on taxon richness. Here, we highlight long-term (1997–2008) trade-off effects on plankton species richness linked to drought in a semi-arid wetland (Las Tablas de Daimiel National Park, central Spain). Annual average phytoplankton species richness increased from wet- (1997–1998) to dry years (2001–2002) and taxon richness diminished again when drought was more severe (2007–2008). Zooplankton changes were more complex depending on taxonomic groups and the body size of the organisms, total species loss being related to hydrological conditions. Half of the algal species recorded in 2007–2008 and one-tenth of total zooplankton taxa were new comers in the wetland, because salinization, eutrophication and submerged macrophytes occurring in different sites enhanced species turnover and mitigated homogenization of beta diversity. Maintenance of one water body with a constant water level and macrophytes was the key to preventing the collapse of plankton richness. Our study has demonstrated that plankton can be very useful for tracking environmental changes of wetlands, thus giving the environmental manager another tool to enhance the conservation of wetlands and their biota.

Electronic supplementary material The online version of this article (doi:[10.1007/s10531-012-0307-1](https://doi.org/10.1007/s10531-012-0307-1)) contains supplementary material, which is available to authorized users.

C. Rojo (✉) · J. Benavent-Corai · M. M. Barón-Rodríguez · M. A. Rodrigo
Institute Cavanilles of Biodiversity and Evolutionary Biology, University of Valencia, C/Catedrático
José Beltrán n° 2, 46980 Paterna, Spain
e-mail: carmen.rojo@uv.es

M. Álvarez-Cobelas
National Museum of Natural History (CSIC), Madrid, Spain

Keywords Beta diversity · Connectivity · Microbial diversity · Salinisation · Species turnover · Trait selection

Introduction

Wetlands are systems characterized by a broad spectrum of environments and/or remarkable heterogeneity within each environment, caused by complex interactions between surface water, groundwater and riparian systems, which result in high values of species richness (Ward and Tockner 2001; Pithart et al. 2007). Moreover, they provide a number of local ecosystem services, including water supply, raw material, food and recreation (Zedler 2000, 2003), and regional or global benefits such as pollutant retention (Engelhardt and Ritchie 2001), increased biodiversity of the whole region (Keddy 2000) and sink of greenhouse gases (Bondavalli et al. 2000; Rojo et al. 2010). Unfortunately, they are also seriously threatened due to water overexploitation for irrigation practices, contamination by agricultural and urban catchments (Hanson et al. 2005; Stralberg et al. 2011) and drying due to climatic change (Millett et al. 2009). The physical results of drought are numerous and complex due to their interaction; for example, loss of flooding area (Sánchez-Carrillo and Angeler 2010), isolation of water bodies (Angeler and Álvarez-Cobelas 2005), changes in the role of sediment and shoreline length due to water-level fluctuations (Sánchez-Carrillo and Álvarez-Cobelas 2001; Valdovinos et al. 2007) and increase in ionic concentrations (Jolly et al. 2008; Millett et al. 2009; Álvarez-Cobelas et al. 2010). These processes are particularly pronounced in wetlands of semiarid regions due to long drought periods associated with dry climates (Iglesias et al. 2005). Competing demands from socioeconomic sectors in form of overexploitation of water resources, as occurs, for example, in Southern Europe and Southern USA further aggravate the environmental stress on wetlands (Cirujano et al. 2010; Stralberg et al. 2011). These impacts are expected to increase with global warming (Álvarez-Cobelas et al. 2005; de Castro et al. 2005), thereby challenging water resource management in the long term.

Plankton species richness and composition, their changes and variability, are related to flooding area because habitat reduction leads to species losses (Pithart et al. 2007) and increased habitat heterogeneity affects the nature of the metacommunity (Rodrigo et al. 2003a, b; Rojo and Rodrigo 2010); moreover, plankton species richness and diversity depend on abiotic disturbances (Hutchinson 1959; Connell 1978), such as hydrological changes (Reyes et al. 2008; Rojo et al. 2000; Angeler et al. 2010). Therefore, the plankton community can be expected to reflect the effects of drought on wetland species richness. Water connectivity enables dispersal of organisms, thus counteracting the decrease in species numbers arising from the effect of isolation (Scheffer et al. 2006) and preventing strong competition between populations (DeClerck et al. 2011; Mazaris et al. 2010). From this perspective, a long period of isolation of water bodies due to persistent drought must enhance the occurrence of very different communities among sites; and thus, at a beta diversity level this local community divergence could mitigate species loss due to the reduction of flood area (Pithart et al. 2007). However, when isolation and areal reduction are severe, other stress factors, such as eutrophication and salinisation, may be triggered (Mitsch and Gosselink 2000; Álvarez-Cobelas et al. 2010), resulting in regional biotic homogenisation because populations enable to live in those environments should be most adapted to stress, thus giving rise to a more similar species composition among sites and therefore resulting in a regional biodiversity loss (Dodson et al. 2000; Thackeray 2007; Fox 2008).

Here we consider a wetland studied long-term, Las Tablas de Daimiel National Park (TDNP hereafter; central Spain; Sánchez-Carrillo and Angeler 2010), to show how some of the above-mentioned drought-related processes (habitat reduction, water body isolation, stressful ionic concentration, etc.) can produce antagonistic effects on plankton species richness and composition. Moreover, we analyse long-term changes in plankton richness since 1997, covering wet and dry periods, to elucidate the trade-offs between the described processes in semiarid wetlands, subject to increasingly persistent water shortage, which is expected according to global change predictions for the area.

Study site

This study was carried out at TDNP, a floodplain wetland situated in the Guadiana River watershed in semiarid central Spain (39°08'N, 3°43'W; Fig. 1). TDNP is located in a semiarid landscape with average yearly rainfall slightly exceeding 400 mm year⁻¹ (Álvarez-Cobelas and Cirujano 1996). This wetland was coupled with an upwelling aquifer until 1986 when over-exploitation due to excess irrigation discontinued groundwater discharge (Sánchez-Carrillo and Angeler 2010). During the second half of the last century, the wetland received scarce water inputs almost exclusively from surface runoff, precipitations and some artificial pumps (Sánchez-Carrillo and Angeler 2010) that changed natural hydroperiod regimes and flood frequencies. TDNP suffered several episodes of drought in the last 30 years (Fig. 2), but never experienced water shortages such as those occurring in 2007 and 2008 when the area of water masses only covered 1 % of the maximal inundation area (16 km²). During the study period the wetland only received water inputs from its catchment in 2007 (May and June), annual rainfall being closer to the long-term average (~415 mm l⁻¹).

Two further environmental processes, salinisation and eutrophication, which have already been recorded in the past (Álvarez-Cobelas et al. 2010), are also reported here. TDNP has historically experienced strong flooding periods leading to the connection between most floodplains in the wetland, but these periods are followed by dry phases during which most water bodies remain isolated, reducing overall wetland size (Angeler et al. 2010). The wetland hydrology, typical of semiarid areas, leads to local ecological differentiation (spatial heterogeneity) causing higher plankton species richness in the floodplain wetland than in any of its isolated water bodies (Rojo and Rodrigo 2010). Additionally, these sites are close enough together in the wetland to connect easily when water supply is sufficient (Angeler et al. 2010; Sánchez-Carrillo and Angeler 2010), hence permitting hydrology-mediated dispersal of organisms.

Further information on the TDNP wetland can be found in Álvarez-Cobelas and Cirujano (1996) and Sánchez-Carrillo and Angeler (2010).

Materials and methods

Field work in the driest years and the synoptic survey in earlier years

This study deals with the richness and composition of the plankton community inhabiting three wetland sites, which remained flooded throughout the study period (2007–2008). These years corresponded to the lowest water surface area in decades, being the end of the longer drought period ever known for TDNP. These study sites differed in their trophic

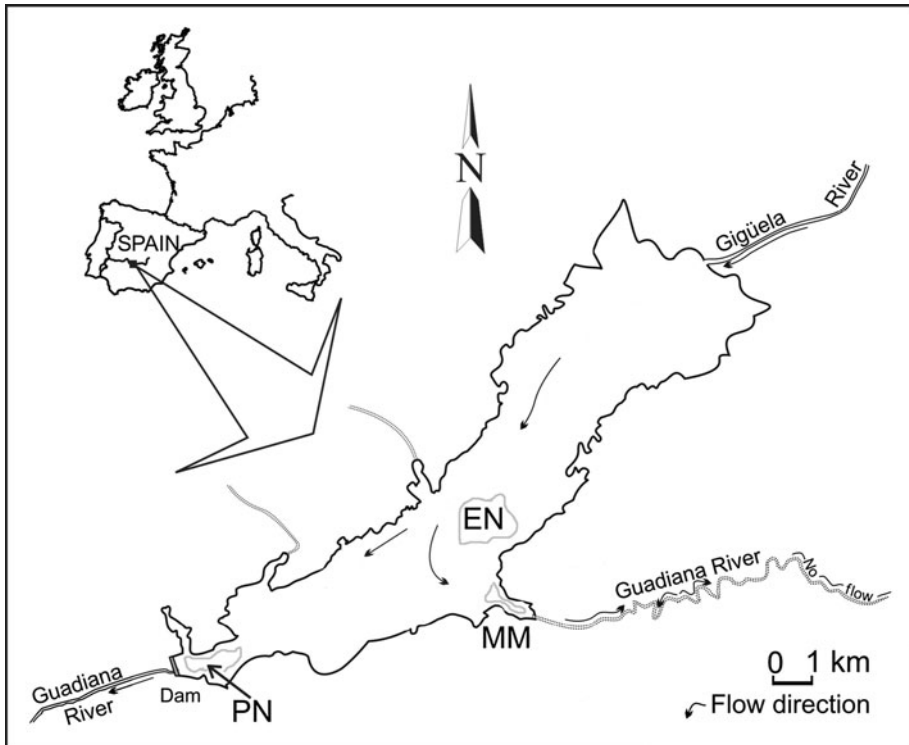


Fig. 1 Las Tablas de Daimiel National Park (TDNP), showing sampling sites (EN, MM and PN); the grey line delimits the flooded areas during the years of extreme drought (2007–2008)

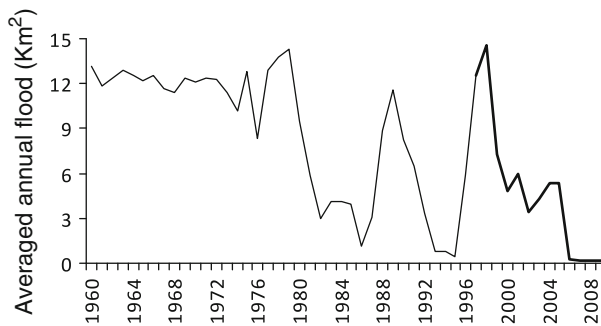


Fig. 2 Dynamics of flooded area in TDNP since 1960. Stationary until the 70s, this flood allowed connection between sites; after that the last three hydroperiods reaching drought. The bold line indicates years included in this study

status, submerged vegetation occurrence and changing hydro-periods, and showed distinct forms of decreasing flooded area during this severe hydrological disturbance. Because spatial heterogeneity varies substantially as a function of the hydrological disturbance regime, different sites, with remaining water and then lentic conditions, have been included in the long-term monitoring program (1996–2008), allowing comparison of plankton

dynamics under different hydrological situations of connectivity (Angeler et al. 2010; Rojo and Rodrigo 2010). The sampling sites (EN, MM and PN; Figs. 1, 2) represented distinct limnological situations (Sánchez-Carrillo and Angeler 2010). EN, located at the centre of the wetland, was 0.3–0.7 m deep and characterised by extensive *Chara hispida* meadows; it was artificially maintained by pumping water from a well, which led to its salinisation. MM was a shallow area, 0.5 m deep, located in the middle of the wetland. This site had dried up intermittently since 1986 because of severe aquifer overexploitation due to agricultural irrigation in the catchment area. Dark grey peat served as a source of dissolved organic matter that increased water colour and frequent winds contributed to sediment re-suspension and high turbidity. Consequently, submerged macrophytes are poorly developed at this site. PN, in the terminal south-western outlet site, was a 0.4 m deep place without vegetation when drought was more severe; it harboured saline waters with a great content of organic material.

Samples were collected with a horizontal Niskin bottle 10 cm below the water surface, avoiding sediment disturbance. Sampling frequency was monthly from April 2007 to December 2008. Phytoplankton samples were collected in 250-ml PVC bottles and fixed immediately with iodine-Lugol's solution; the same samples were also used to count ciliates. Metazooplankton (rotifers, cladocerans and copepods) was collected by filtering up to 30 l of water through a 45- μ m mesh that retained rotifers and crustaceans. Each sample was fixed immediately with sucrose-formalin (Haney and Hall 1973). Autotrophic picoplankton (APP) and bacterial samples were manipulated as described by Rodrigo et al. (2003a).

To compare the results of the field study reported herein (2007–2008) with previous studies conducted in TDNP, we have used our own monthly database of plankton studies from 1997 to 2002 in different sites within the flooding area of the wetland, in an attempt to capture both the spatial and temporal heterogeneities. Data from the inlet site in the wetland (PG; Angeler et al. 2010; Rojo and Rodrigo 2010) were used for some comparison. Most information on plankton in TDNP has been published in the last decade (Ortega-Mayagoitia et al. 2000, 2003; Rojo et al. 2000; Rojo and Rodrigo 2010). No plankton samples were gathered from 2003 to 2006 in the wetland, which remained flooded; thus, we consider information about these sites in similar time intervals and of similar duration: the last wet years recorded (1997–1998) and years (2001–2002) affected by drought.

Plankton observation and classification

APP and bacterial biomass were determined as described in Rodrigo et al. (2003a). To study phytoplankton, aliquots of the fixed material were counted using an inverted microscope (Olympus CK2) from 200 to 1,500 magnifications. Utermöhl counting chambers were used following Rott (1981), the same method being used since 1997. All species observed in the volume of water containing at least 500 individuals of the most abundant population were recorded, implying less than 9 % error in the total phytoplankton density considered (Lund et al. 1958). Autotrophic organisms were classified following size classes for pelagic plankton as defined by Sieburth et al. (1978): nanoplankton (2–20 μ m) and picoplankton (0.2–2 μ m). The same samples and observational method were used for identification of ciliates. Furthermore, metazooplankton counts were continued until species accumulation curves levelled off. Plankton biomass was calculated following Hillebrand et al. (1999) and Dumont et al. (1975).

Specific book collections and reviews were used for phytoplankton identification, such as *Archiv für Hydrobiologie (Algologische Studien)*, monographic series of *Süßwasserflora*

von Mitteleuropa (Gustav Fischer Verlag, Stuttgart) and *Das Phytoplankton des Süßwassers* (Ed. Schweizerbart'sche Verlagsbuchhandlung); manuals were used for the identification of ciliates and metazooplankton taxa (Dussart 1967, 1969; Koste 1978; Segers 1995; Einsle 1996; Foissner and Berger 1996; Foissner et al. 1999; Orlova-Bienkowskaja 2001; Nogrady and Segers 2002).

Environmental variables

Water temperature and dissolved oxygen were measured in situ using an YSI-550A meter. Electrical conductivity was used as a surrogate of salinity. The measurements of electrical conductivity and pH were also conducted in situ using a multimeter MM40—CRISON. Two-liter samples for nutrient analysis were collected in acid-washed PVC bottles, stored in ice boxes, and analysed on the next day in the laboratory (CSIC-National Museum of Natural Science, Spain). Water for soluble nutrients was filtered through 0.45 µm Millipore filters in the field. Chemical analyses included the measurement of total nitrogen (TN), total phosphorus (TP), soluble reactive phosphorus (SRP), nitrite, nitrate and ammonia. TN and nitrate were analysed following the method of Bachmann and Canfield (1996), while the remaining nutrients and dissolved solids were analysed following standard methods (APHA 1992). Chlorophyll *a* was measured following Marker et al. (1980). TP was used as a surrogate of eutrophication following OECD (1982) suggestions.

Calculations and statistical analyses

Although there are criteria for excluding non-planktonic populations in planktonic studies (Dodson 1992), each species whose known distribution is littoral, benthic or that inhabit vegetation and could be found in plankton, has been included in our analysis, thus highlighting their relevance for species richness in studies carried out during drought. We then obtained a presence/absence matrix of micro-algal species inhabiting the water column; this matrix was derived from the species lists of each sample (three sites sampled monthly for 2 years). Species were recorded in columns at each sampling event (rows).

We undertook our study at two spatial scales, i.e. landscape and local. Following Thackeray (2007) for a landscape approach, we distinguished the “mean richness” as the averaged value of richness found in each different pond within the wetland area during the study period, and the “temporal richness” as the cumulative species richness from all sampling sites during the study period. Moreover, for the local study, the mean species richness for each water body (EN, MM and PN) was calculated from the monthly sampling occasions that made up the 2007–2008 survey.

Beta diversity was considered to be the difference in species composition between two or more ecosystems, expressed as the total number of species unique to each of the compared ecosystems (Vellend 2001). To estimate this degree of dissimilarity in the species composition of water bodies, complementarity between pairs of sites (Colwell and Coddington 1994) was also calculated during the studied periods, as the sum of the species unique to each of the two sites compared, divided by the total species richness of both sites combined. This species turnover rate was expressed as a percentage. Moreover, beta diversity (dissimilarity), referred to the change of species between two stations-samples (Pielou 1975; Magurran 1988), was calculated as one minus the Jaccard similarity index (Jaccard 1912) which expresses the degree of similarity between two samples depending upon the shared species. Dissimilarity ranged between 0, when two stations have the same composition of species, and 1, when there were no species shared between both stations.

We studied this beta diversity at each spatial scale as the mean beta diversity index among pairs of water bodies over time.

Differences in beta diversity among samples from different sites (EN–MM, EN–PN and MM–PN) and temporal beta diversity (instability) within samples from each water body (EN–EN, MM–MM and PN–PN) were tested with a one-way ANOVA with repeated measures of the dissimilarity matrix. We only considered data when the three water bodies (EN, MM and PN) were flooded. We performed orthogonal contrasts a priori to test pairwise comparisons (Gotelli and Ellison 2004). The p value was obtained permuting (10,000 times) the presence–absence values of the data matrix, re-calculating the dissimilarity matrices from simulated data and obtaining the F ratio distribution from simulated data (Gotelli and Ellison 2004). Restricted permutation and permuting exchangeable units (Anderson and ter Braak 2003; Gotelli and Ellison 2004) were employed to preserve temporal autocorrelation and species factor.

To obtain a hierarchical classification of samples, cluster analysis (Podani 2000) of sampling stations was performed with the statistical software package “pvclust” (<http://cran.r-project.org/>) using the UPGMA clusterisation method and the binary index which corresponds to beta diversity. “pvclust” automatically computes p values for all clusters contained in the clustering of original data and this p value indicates how strongly the cluster is supported by data (Shimodaira 2004; Suzuki and Shimodaira 2005).

The Pearson correlation coefficient on log-transformed variables was used to determine the possible covariation of biotic and abiotic variables. When analysis included correlations between multiple variables, the significance of the correlation coefficient was adjusted according to Bonferroni procedures (Bland and Altman 1995).

Results

Environmental variables and dominant plankton during years of severe drought (2007–2008)

Table 1 shows average values of main environmental variables measured over the study period in each of the three sites (EN, MM and PN). Higher average electric conductivity occurred in EN and PN than in MM, often reaching salinities higher than 10 g l^{-1} . However, peaks in suspended material, dissolved solids, organic carbon and total nutrient concentrations occurred at the wetland outlet (PN). TP, used as an index of eutrophication, was very variable in all three sites throughout the study period, but the wetland outlet (PN) showed the highest values, often suggesting hypertrophic conditions. In the other sites high TP contents were also recorded, albeit less frequently. All these variables, however, did not display seasonal dynamics. In fact, only a few of them co-varied and these correlations (after Bonferroni’s correction) were particular for each site. In EN, water level and dissolved solids were correlated ($r = -0.69$; $p < 0.0001$), TP correlated with SRP ($r = 0.87$; $p < 0.0001$) and the latter was significantly correlated with the inorganic N:P ratio ($r = -0.72$; $p < 0.0001$). In MM, a decrease in water level was correlated with a decrease in TP ($r = 0.95$; $p < 0.0001$), which, in turn, was related to SRP concentration ($r = 0.87$; $p < 0.0001$).

Some data about plankton biomass during that period complement the limnological view of these three sites. In EN the average biomass (biovolume) of phytoplankton over time was $15 \text{ mm}^3 \text{ l}^{-1}$ (SD $22 \text{ mm}^3 \text{ l}^{-1}$), being the dominant species, i.e. highest mean of percentage of biomass reached in each sample, the benthic alga *Amphora lineolata*

Table 1 Average (X), standard deviation (SD), coefficient of variation (CV%), minimum value (Min) and maximum (Max) of physical and chemical variables and chlorophyll in three different sites of flooding wetland TDNP during 2007–2008: EN, MM and PN (see Fig. 1 for location)

	Units	EN			MM			PN								
		X	SD	CV	Min	Max	X	SD	CV	Min	Max					
Water level	m	0.43	0.11	26	0.20	0.60	0.25	0.08	31	0.12	0.35	0.17	0.07	41	0.10	0.38
Temperature	°C	17.3	6.8	39	4.6	30.9	20.6	7.6	37	9.7	32.6	22.2	9.1	41	5.9	36.2
Conductivity	mS cm ⁻¹	8.9	2.1	24	3.1	13.3	2.6	0.9	36	2.0	5.7	11.8	4.3	37	2.5	19.3
pH		7.59	0.28	4	7.08	8.30	7.77	0.26	3	7.27	8.37	8.20	0.57	7	7.30	9.15
DO	mg l ⁻¹	11.0	4.5	41	4.4	21.6	9.5	3.1	33	5.2	16.5	8.7	3.6	42	0	13.7
SS	mg l ⁻¹	101	210	208	2	897	51	29	58	4	104	331	258	78	42	884
DS	mg l ⁻¹	9,850	1,161	12	6,782	12,345	2,304	586	25	412	2,863	16,522	7,650	46	6,292	36,556
TN	mg N l ⁻¹	1.7	0.9	52	0.2	3.7	2.3	1.3	56	1.0	6.3	7.2	3.0	41	2.9	11.9
Nitrite	mg NO ₂ ⁻ l ⁻¹	0.06	0.04	74	0.01	0.16	0.12	0.09	74	0.02	0.39	0.11	0.08	71	0.00	0.25
Nitrate	mg NO ₃ ⁻ l ⁻¹	1.6	1.8	113	0.01	6.9	4.3	2.6	60	0.7	8.5	2.3	1.4	63	0.8	4.5
Ammonia	mg NH ₄ ⁺ l ⁻¹	0.31	0.28	91	0.09	1.12	0.19	0.14	72	0.09	0.59	2.63	2.63	100	0.18	8.30
TP	mg P l ⁻¹	0.06	0.05	89	0.01	0.19	0.08	0.06	81	0.03	0.27	0.50	0.23	47	0.18	1.07
SRP	mg P l ⁻¹	0.01	0.01	105	0	0.04	0.01	0.02	200	0	0.09	0.08	0.05	68	0	0.22
N:P (tot)		124	108	87	6	327	83	35	43	15	137	39	27	68	9	91
N:P (inorganic)		233	238	102	8	954	532	358	67	14	1126	105	132	126	1	493
DOC	mg C l ⁻¹	5.4	1.8	34	4.3	13.2	4.2	0.8	18	3.5	6.0	33	15.4	47	7.6	58.3
Chlorophyll <i>a</i>	µg l ⁻¹	9	12	130	2	57	10	9	82	3	28	131	142	109	10	477

DO dissolved oxygen, SS suspended solids, DS dissolved solids, SRP soluble reactive phosphorus, TN total nitrogen, TP total phosphorus, N:P (tot) ratio of molar TN and TP concentrations, N:P (inorganic) ratio of molar dissolved nitrogen and phosphorus concentrations, DOC dissolved organic carbon

(Appendix 1 in Supplementary material). Averaged biovolume in MM was $65 \text{ mm}^3 \text{ l}^{-1}$ (SD $174 \text{ mm}^3 \text{ l}^{-1}$) and a mean of 34 % of total biovolume indicated that the dominant taxon was *Euglena* sp. (Appendix 1 in Supplementary material). Finally, PN showed an average of phytoplankton biovolume through the study period of $166 \text{ mm}^3 \text{ l}^{-1}$ (SD $144 \text{ mm}^3 \text{ l}^{-1}$) with *Microcystis flos-aquae* reaching numerical dominance (Appendix 1 in Supplementary material). In EN total zooplankton reached $117 \mu\text{g DW l}^{-1}$ (SD $298 \mu\text{g DW l}^{-1}$), ciliates were on average one-third of that biomass and the copepod *Acanthocyclops robustus* was the dominant population (Appendix 1 in Supplementary material). Total zooplankton biomass average was $2,700 \mu\text{g DW l}^{-1}$ (SD $3,300 \mu\text{g DW l}^{-1}$) in PN, where ciliates were the main relevant group with a biomass average of $2,202 \mu\text{g DW l}^{-1}$ (SD $3,321 \mu\text{g DW l}^{-1}$). In MM, the average of total zooplankton biomass was $405 \mu\text{g DW l}^{-1}$ (SD $543 \mu\text{g DW l}^{-1}$), ciliates were on average 30 % of that biomass and also *A. robustus* was dominant (Appendix 1 in Supplementary material).

Phytoplankton richness during years of severe drought (2007–2008)

The ratio of benthic microalgae to the total algal species found in plankton varied between sites (EN $15 \pm 7 \%$, MM $7 \pm 9 \%$, PN $6 \pm 5 \%$), reaching more than 25 % on some occasions (May 2008 in EN; December 2007 in MM). Thus, we decided to include them in all subsequent analyses, where microalgae captured in the water column are referred to as phytoplankton, for simplification (Appendix 1 in Supplementary material).

Phytoplankton richness ranged between 6 and 28 species in individual samples and its dynamics followed its own pattern in each site (Appendix 1 in Supplementary material; Fig. 3a). EN and PN had higher richness (more than 20 species) than MM, whose richness only peaked in summer. Trajectories of the phytoplankton species richness in EN and PN presented significant correlation ($r = 0.56$, $p = 0.035$), whereas MM richness was not correlated with any of the other sampling sites. Considering all phytoplankton richness values, they were only correlated with electrical conductivity ($r = 0.49$, $p = 0.001$), the N:P ratio ($r = -0.36$, $p = 0.02$) and nitrate ($r = -0.35$, $p = 0.02$). No relationship was found between richness and an indicator of wetland productivity (the TP, $p > 0.05$).

The temporal average of richness was the highest in EN (Fig. 3b), with a value of 21 ± 5 , followed by 19 ± 4 species in PN and 12 ± 6 species in MM, richness exhibiting the highest temporal variability in this site (Coefficient of Variation, CV = 51 %). Average richness of the three sites over time (Fig. 3c) was highest in summer 2007 (24 ± 4 species, CV = 15 %). The greatest variation (CV = 64 %) occurred in winter months of 2008 and the lowest took place in the spring of 2007 (CV = 7 %). The CV among the three sampling sites showed an increasing trend from autumn 2007 until spring 2008 (MM and PN sites were dry later on). However, a one-way ANOVA test on mean species richness among months (averaging richness from the three sampling sites) showed that there were no statistically significant differences ($p > 0.05$).

The total number of species found throughout the study in the wetland was 118 (including 14 benthic algae), but only 16 of them were shared by the three sampling sites. Sixteen species were found only in EN which accounts for 30 % of both dinoflagellate and chrysophyte species recorded in temporal algal list, 40 % of total cryptophyte richness, and 20 % of both chlorophytes and diatoms. The 13 species that inhabited only MM, accounted for 40 % of total euglenoids and 20 % of diatoms, of which some were benthic populations (Appendix 1 in Supplementary material). 11 species were exclusive for PN and they represented 20 % of cyanobacterial species and 30 % of chrysophyte taxa. Therefore,

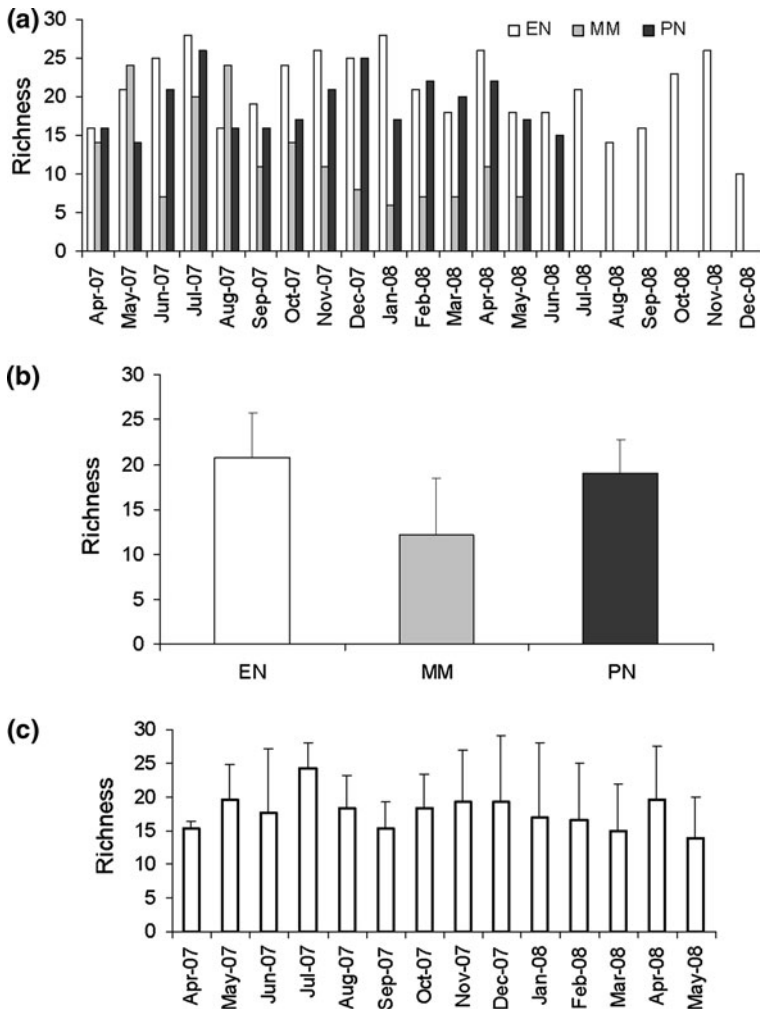


Fig. 3 **a** Phytoplankton species richness (including benthic microalgae occurring in the water column) during the study period at different sampling areas (EN, MM and PN, see Fig. 1); **b** their temporal mean and standard deviation (*bars*) and **c** mean and standard deviation (*bars*) of phytoplankton species richness for the whole period of study and sampling sites. Note that sampling sites PN and MM were dry since June and July 2008, respectively

turnover rate or complementarity was 40 % of total species, which means that 40 % of phytoplankton species were exclusive to a single location.

Beta diversity among sites, calculated on algal species occurrence in all samples (Fig. 4), suggested that phytoplankton composition was more similar within each site than temporally (lack of seasonal pattern). For temporal phytoplankton composition inhabiting each place, p values ranged between 63 and 99 %. And samples from EN and PN were clustered ($p = 73$ %) separately from MM samples ($p = 85$ %).

The lowest dissimilarity was found between EN and PN, with its average between paired samples being 0.87 ± 0.05 . Composition in the MM site seemed to differ most, as

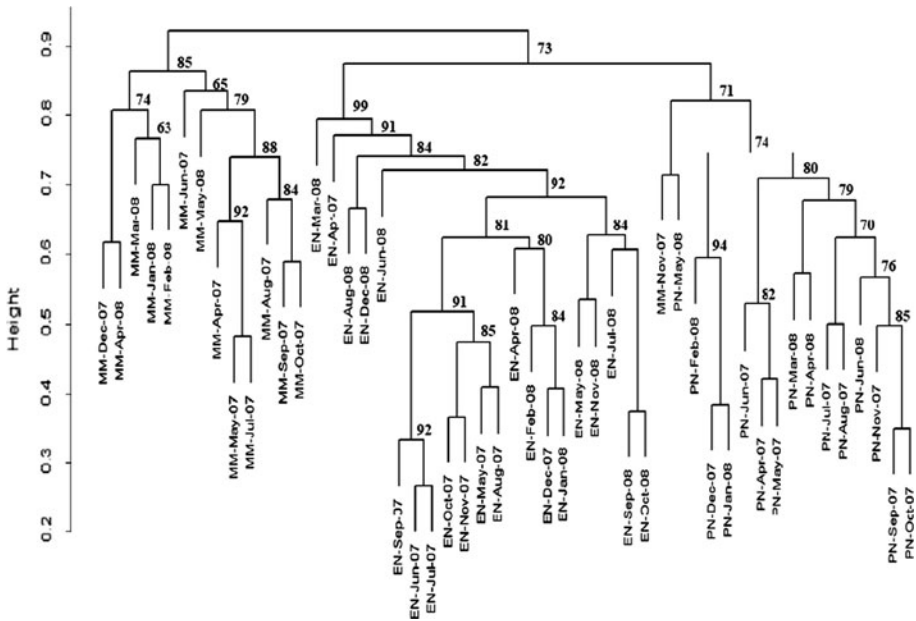


Fig. 4 Dendrogram based on dissimilarity index, obtained from the matrix of presence/absence of phytoplankton species (Appendix 1 in Supplementary material) in all sampling sites (EN, MM and PN, see Fig. 1) and months (since April 2007 to December 2008)

mean dissimilarity between MM and EN phytoplankton samples was 0.91 ± 0.05 , and between MM and PN it was 0.93 ± 0.06 , although an ANOVA of repeated measures did not show significant differences ($F = 45.04$, $p = 0.356$). Looking for an estimation of temporal stability of microalgal composition within each site, we calculated a dissimilarity average within the samples of each site, resulting in 0.63 ± 0.14 for EN which would be the most stable, 0.81 ± 0.09 and 0.69 ± 0.11 for MM and PN, respectively. An ANOVA test performed on this dissimilarity matrix with repeated measures confirmed that means were statistically different ($F = 54.37$, $p = 0.007$). Post hoc analyses highlighted phytoplankton assemblage in MM as the most unstable ($F = 97.56$, $p = 0.003$).

Zooplankton richness during years of severe drought (2007–2008)

Twenty-eight species of *Ciliophora* occurred in TDNP during the driest years (Appendix 1 in Supplementary material). Variation of ciliate richness amounted to 3 ± 2 in EN, whereas it was 2 ± 2 in PN and 2 ± 1 in MM. These temporal richness averages did not differ statistically among sampling sites (one-way ANOVA, $p > 0.05$). Richness of ciliates did not co-vary between sites. Only four ciliate species coincided in the three sampling sites (being dominant *Uronema nigricans*), eight species were only found in EN and six of them account for 78 % of *Gymnostomatea* species, three and two were exclusive to MM and PN, respectively. Thus, species turnover rate in the wetland was 48 %, which represents the percentage of exclusive species found in a single site.

The range of rotifer plus crustacean richness in TDNP (metazooplankton; Appendix 1 in Supplementary material) varied over time between 0 and 16, with no apparent seasonal patterns (Fig. 5a). There was no statistically significant correlation among the sampling

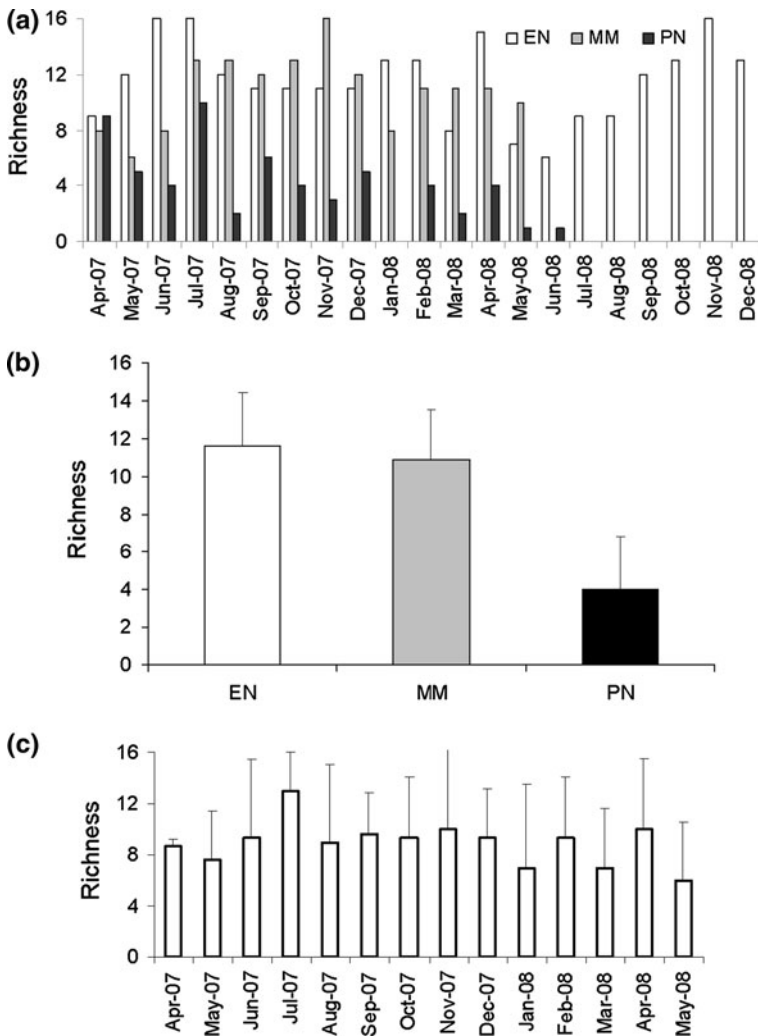


Fig. 5 **a** Metazooplankton (Rotifers, Cladocerans and Copepods) species richness (including benthic populations in the water column) during the study period in different sampling sites (EN, MM and PN, see Fig. 1); **b** their temporal mean and standard deviation (*bars*) and **c** mean and standard deviation (*bars*) of zooplankton species richness for the whole period of study and sampling sites. Note that sampling sites PN and MM were dry since June and July 2008, respectively

sites ($p > 0.05$). EN and MM showed similar average species richness over time (Fig. 5b; 12 ± 3 and 11 ± 3 species, respectively), and higher than in PN (4 ± 3 species) where temporal richness was the most variable (CV = 68 %). On the other hand, no significant difference in the average of metazooplankton richness was found temporally when richness from three sites was averaged ($p > 0.05$; Fig. 5c).

The metazooplankton richness showed statistically significant negative relationships with salinisation (measured as electrical conductivity, $r = -0.44$, $p = 0.001$), TP (an index of eutrophication, $r = -0.69$, $p < 0.001$), TN ($r = -0.67$, $p < 0.001$), chlorophyll *a* ($r = -0.44$, $p = 0.001$) and total phytoplankton biovolume ($r = -0.56$, $p < 0.001$).

Hence, richness decreased with stressing environmental conditions (eutrophication and salinisation). Locally, richness presented a significant negative correlation with conductivity in EN ($r = -0.46$, $p = 0.04$), with ammonium in MM ($r = -0.68$, $p = 0.01$) and also with conductivity ($r = -0.81$, $p = 0.015$) and total dissolved solids ($r = -0.79$, $p = 0.02$) in PN. The relationship between consumer metazooplankton richness and phytoplankton richness was neither locally (EN: $r = 0.53$, $p = 0.05$; MM: $r = 0.36$, $p = 0.50$; PN: $r = 0.40$, $p = 0.50$) nor globally significant including all data ($r = 0.22$, $p = 0.11$).

The relationship between consumer metazooplankton richness and availability of its resources (biomass of different edible groups) was not significant ($p > 0.05$) for any location: either bacteria (EN: $r = -0.23$; MM: $r = -0.16$; PN: $r = -0.49$), APP (EN: $r = -0.11$; MM: $r = 0.06$; PN: $r = 0.09$) or nanoplankton (EN: $r = 0.30$; MM: $r = 0.18$; PN: $r = -0.02$). However, when all data from the wetland were considered, the relationships between either metazooplankton richness and bacteria ($r = 0.62$), APP ($r = 0.56$) or nanoplankton ($r = 0.50$) were statistically significant ($p < 0.001$).

Beta diversity in the wetland, expressed as dissimilarity between each pair of sites, was 0.81 ± 0.08 (EN–MM), 0.85 ± 0.10 (PN–MM) and 0.83 ± 0.11 (EN–PN); these averages were not statistically different ($F = 6.35$; $p = 0.79$). The cluster dendrogram (Fig. 6) highlighted that metazooplankton composition over time was more similar in EN and MM ($p = 94\%$) in comparison to PN, whose samples supported the cluster at $p = 92\%$. Instability of zooplankton composition throughout the study periods in each site was, on average, 0.56 ± 0.14 for EN, 0.71 ± 0.12 for MM and 0.81 ± 0.16 for PN. The one-way ANOVA test for repeated measures indicated that these means were statistically different

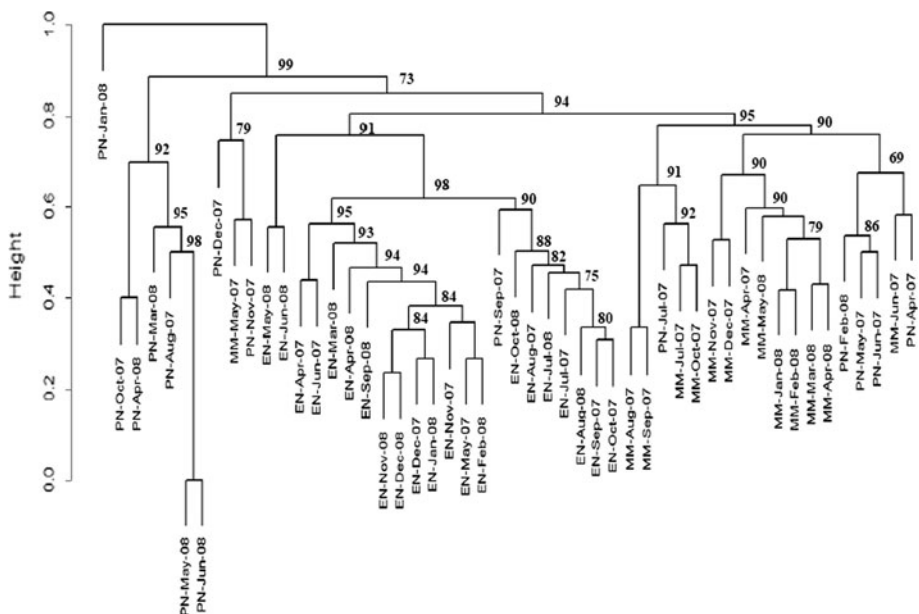


Fig. 6 Dendrogram based on dissimilarity index, obtained from the matrix of presence/absence of metazooplankton species (Appendix 1 in Supplementary material) in all sampling sites (EN, MM and PN) and months (since April 2007 to December 2008)

($F = 82.49$; $p = 0.028$), being EN metazooplankton composition the most stable one ($F = 137.45$, $p = 0.02$).

Sixteen out of the 44 species of metazooplankton found in the study were present in the three sampling sites, eight species only in EN, 12 in MM and all species that inhabited in PN were also found in either EN or MM. Thus, complementarity was 45 %.

Long-term plankton richness and composition trends (1997–2008)

By comparing the results of the latest field-study reported here (2007–2008) with previous studies conducted in TDNP during similar time intervals (1997–1998, 2001–2002; Appendix 2 in Supplementary material), it can be observed that phytoplankton richness was different between dates but similar between sites in each period (Table 2); the highest CV between sites was 16 % (2001–2002). Phytoplankton average richness varied from 43 species in the wet- (1997–1998) to 102 in the dry years (2001–2002). From then on, and after 5 years of continuous drought, species richness dropped to 60 species and this unimodal pattern was also observed in the temporal richness of the wetland (Table 2). When analysing the specific algal composition, it is observed that richness variations between studied periods were due to a particular loss or gain of species (Table 2): an incorporation of new species between wet and former dry years (1997–2002) occurred and this gain was very similar in the different sites of the wetland (mean and deviation was 68 ± 1). This increase represented 19 % more new species in the overall area (81 new species) than in sites taken separately. The wetland lost 40 % more species (16 species) than the mean local species loss (10 ± 4 species); therefore TDNP was losing species that were exclusive to each site. However, analysing the loss of species in the wetland in the second part of the drought period (2001–2008), we found a very different pattern: (i) less colonisations than extinctions, (ii) great inter-site variation in new species because the net income in TDNP was 40 % higher than the average inter-site annual income (31 ± 1 species). Moreover, the global loss of species in the wetland was only 4 % higher than the averaged losses of the sites (78 ± 4). Therefore, the remarkable richness decrease observed during the last drought period was counteracted by the site-specific colonisation of new species. Comparing zooplankton species composition in the more severe years of drought (2007–2008)

Table 2 Phytoplankton species richness in different sites of TDNP (EN, MM and PN)

	EN (PG)	MM	PN	Mean	SD	TDNP
1997–1998	41 (34)	51	45	43	7	71–86
2001–2002	(99)	102	104	102	3	120–136
2007–2008	68	51	62	60	9	88–102
1997–1998/ 2001–2002	+70, –5 (65)	+67, –16 (51)	+67, –8 (59)			+81, –16 (65)
2001–2002/ 2007–2008		+23, –74 (–51)	+39, –81 (–42)			+49, –81 (–32)
1997–1998/ 2007–2008	+54, –27 (27)	+37, –37 (0)	+48, –31 (16)			+70, –48 (22)

Average richness and its standard deviation (SD) and also the range of annual richness in TDNP are shown when taking into account all sites. Number of new species (+) and lost species (–) over the years are compared and net change in phytoplankton richness (in parentheses) as occurred in EN, MM and PN and in the entire wetland is also shown. In cursive and parenthesis data from another site closed to EN (PG) with a similar trend to other sites from 1997 to 2002

Table 3 Zooplankton species richness in different sites of TDNP (EN, MM and PN)

	EN	MM	PN	Mean	SD	TDNP
1997–1998	32	40	35	36	4	56
2001–2002		47				
2007–2008	30	32	21	28	6	42
1997–1998/ 2001–2002		+18, –11 (+7)				
2001–2002/ 2007–2008		+8, –23 (–15)				
1997–1998/ 2007–2008	+13, –15 (–2)	+9, –17 (–8)	+7, –21 (–14)			+13, –27 (–14)

Average richness and its standard deviation (SD) and also the range of annual richness in TDNP are shown when taking into account all sites. Number of new species (+) and lost species (–) over the years are compared and net change in zooplankton richness (in parentheses) as occurred in EN, MM and PN and in the entire wetland is also shown

with former years, only six species were new to the wetland and the long drying process (1998–2008; Table 3) resulted in species losses both locally and at the whole wetland scale. This loss of species, ranging from 43 to 60 % of existing species, was partially offset by the incorporation of littoral species; in this sense, nine of the 13 new species in EN were benthic and linked to submerged vegetation (Appendix 1 in Supplementary material).

Discussion

Ecology of dominant plankton species as related to long-term changes

Changes in plankton species richness over this long period of drought result from colonisation and selection of populations with adapted traits to environmental stress (salinisation and eutrophication), and the substitution of planktonic species by local benthic or littoral species. Hence, we analyzed those species that are relevant for these changes as a result of either their biomass dominance or their functional adaptations. Phytoplankton composition changes were most related to water mineralization due to drought. For example, most new species of diatoms (Appendices 1 and 2 in Supplementary material) have been found in mineralized shallow lakes of Spain (Ubierna-León and Sánchez-Castillo 1992). These species also increased in the two TDNP sites that experienced salinity increase over time, highlighting their ability to cope with salinisation stress (Taylor et al. 2007); i.e. *A. lineolata* reached 50 % of algal biomass in the first- and *Chaetoceros muelleri* 12 % in the second site (Appendix 1 in Supplementary material). In the last area where eutrophication was severe, the most shade-adapted filamentous cyanobacteria, *Planktolyngbya limnetica*, dominated. Similar findings have been made in other systems with high turbidity (Padisák et al. 2009) and low water columns (Nöges et al. 2003) (Appendix 1 in Supplementary material). *P. limnetica* coexists with *M. flos-aquae* (20 % of biomass) as a group well adapted to light and nutrient stress (Reynolds et al. 2002). However, in the place where the main environmental feature was shallowness and ongoing drought until collapse, the more exclusive and dominant populations of phytoplankton were euglenoids (Appendix 1 in Supplementary material), which are populations found in temporary ponds, usually rich in organic matter (Padisák et al. 2009). Therefore, the

differences in the three environments throughout drought periods were highlighted by both biodiversity and population dominance, resulting in a divergence of functional groups linked to extreme conditions.

The ciliate richness in the past in TDNP is unknown, but it has been reported that their abundance showed a lack of spatial heterogeneity, seasonality and inter-annual variation related to hydrological changes (Angeler et al. 2000). In the present study, the dominant and most ubiquitous species (*U. nigricans*) is a bacterivorous filter-feeder (Ayo et al. 2009), usually considered as euryhaline, and which is able to live as either a benthic- or a plankton population (Foissner et al. 1999; Mironova et al. 2009); this is a great advantage in these systems when desiccation proceeds. However, metazooplankton biodiversity, composition and dominant species followed the extreme changes in water level; then the presence of populations of planktonic genera, such as *Brachionus*, *Lecane*, *Cephalodella*, *Ceriodaphnia* and *Daphnia* (Pejler 1983; Alonso 1996), declined, and other species (*Bosmina longirostris* and *Anuraeopsis fissa*, and most species of copepods) were lost (Appendices 1 and 2). At the same time, most new species occurring in the three studied sites are considered as either benthic- or littoral populations, such as the rotifers *Cephalodella* sp., *Collotheca* sp., *Colurella uncinata*, *Dicranophorus grandis*, *Lecane punctata*, *L. nana*, *L. scutata*, *L. lamellate*, *Eosphora* sp., *Notholca squamula*, *Pompholyx sulcata* and the cladocerans *Alona rectangula*, *Leydigia acanthocercoides*, *Macrothrix hirsuticornis*, *Simocephalus exspinosus* (Usai and Margaritora 1987; Alonso 1996; Smirnov 1996; Segers 2007; Pociecha 2008; Kuczyńska-Kippen and Joniak 2010).

Changes in composition attributable to local mineralization stress (salinization or eutrophication) implied species loss rather than substitution. Cladoceran disappearance (Appendices 1 and 2) may be due to increasing salinity (Waterkeyn et al. 2010), and only few euryhaline cladocerans and rotifers were tolerant to the new conditions, such as *Daphnia magna* and *S. exspinosus* (Alonso 1996; Orlova-Bienkowskaja 2001) and *Brachionus plicatilis* (De Manuel 2000), albeit reaching conspicuous biomasses (Appendix 1 in Supplementary material). Moreover, other permanent crustaceans such as *Chydorus sphaericus*, *A. rectangula* (cladocerans) and the *A. robustus* (copepod) have been observed in eutrophic ecosystems (Pejler 1983; Alonso 1996).

Summarizing, severe drought resulted in species loss of the whole plankton community, but the replacement of some species enables to mitigate net losses of species richness. For phytoplankton species, taxa that are better adapted to new chemical conditions are the new colonizers. In the case of zooplankton, plankton species are partly substituted by local populations of benthic species.

Long-term changes in phytoplankton richness and its relationship with environmental changes

It is difficult to compare species richness of communities from different ecosystems, because they have been gathered using different sampling efforts with distinct periodicities and variable time lengths of study (Thackeray 2007). However, to test the idea that plankton richness in wetlands is high (Ward and Tockner 2001; Rodrigo et al. 2003b) and that it could be related with flooding-area (Pithart et al. 2007), we have undertaken a search that represents a variety of flooded environments (Table 4). If wetlands from disparate areas, having similar trophic status, are studied using similar sampling effort (depicted in bold letters in Table 4), then flooding area covaried with plankton richness (richness = $49 + 0.6$ flooding area (ha); $r = 0.87$; $p < 0.001$). However, as already shown, when TDNP showed a smaller flooding area and hence lower connectivity among local

Table 4 Phytoplankton richness in TDNP and other aquatic ecosystems

Ecosystem	TS	Ecosystem area (ha)	Study duration (months)	Species richness	References
Bhopal wetlands (India)	O	1,500		71–76	Neelam et al. (2009)
	E	1,500	24	33–58	
Cap de Terme wetland (Spain)	M	4	6 (11)	38	Villena and Romo (2001)
Chatla floodplain (India)		1,750	12 (4)	34	Laskar and Gupta (2009)
Colgada lake (Spain)	M	103	18 (18)	62	Rojo et al. (2007)
Doñana wetland (Spain)	E–H	2,500	24 (11)	224	Reyes et al. (2007)
Iraqi wetlands (Iraq)			24 (5)	317	Al-Obaidi et al. (2009)
La Cruz lake (Spain)	M	1.4	18 (11)	133	Dasí and Miracle (1991)
La Safor wetland (Spain)	E–H	1,300	12 (2)	128	Rodrigo et al. (2003a, b)
Menorca lagoon (Spain)	E	50	18 (18)	50	Pretus (1989)
TDNP wetland (Spain)	E–H	428–1,355	24 (24)	94	Rojo et al. (2000)
		20–400	21 (21)	102	This study
				102	This study
Valencia lagoon (Spain)	E	2,300	96	131	Romo and Miracle (1994)
Xeresa wetland (Spain)	M	0.5	6 (11)	49	Villena and Romo (2001)

TS trophic status, O oligotrophic, M mesotrophic, E eutrophic, H hypertrophic

Ecosystem area is flooding area. Study period and number of sampling events in brackets. In bold lettering are data used for some calculations described in the main text

areas, higher plankton richness occurred (Rojo and Rodrigo 2010). Similar results were found by Kruk et al. (2009) when studying a landscape of small water bodies that were located very close to each other. Thus, the topic arising here is that of the importance of spatial scale to study patterns of species richness (Leibold et al. 2004).

Our study shows that hydrology is not an important factor shaping phytoplankton richness at the scale of a few hectares in the short term (two annual cycles). For instance, during the driest years in decades, both phytoplankton species richness and its dynamics were similar in two very different sites: an artificially constantly flooded area and one of the two sites undergoing severe desiccation. Moreover, this species richness was substantially different between two water bodies experiencing a severe desiccation process. This lack of pattern can be explained by antagonistic effects. For example, species loss can be a result of decreasing flooding area at different spatial and temporal scales (Pithart et al. 2007); at the same time and in accordance to the intermediate disturbance hypothesis (Connell 1978), hydrological perturbation can result in highest species richness in this wetland (Rojo and Álvarez-Cobelas 2003).

Another effect related to decreasing flooding area is the ionic concentration increase (eutrophication, salinisation). In TDNP, nutrients do not appear to be the determinants of either local or landscape phytoplankton richness, as demonstrated in other groups of water bodies (Kruk et al. 2009). Therefore, the expectation that “more resources imply more richness” (Barnett and Beisner 2007) could be observed in sites across oligo-mesotrophic gradient, but did not occur when the range of nutrient concentrations corresponded to eutrophic-to-hypertrophic conditions as is the case in TDNP (Álvarez-Cobelas et al. 2010).

However, it seems that increased salinity is linked to richness in TDNP, and the two water bodies with increased water conductivity exhibited greater richness independently of water level stability, and also they have higher similarity in planktonic flora. This is in accordance to spatial insurance hypothesis (Shurin 2001; Loreau et al. 2003): species that are maladapted, for example, to salinisation are replaced by stress-tolerant species from the regional species pool.

Furthermore, the process of isolation and disconnection between sites, occurring since 1998, has promoted heterogeneity and thus an increase in species richness (Rojo 2004; Angeler et al. 2010). If disconnection proceeds for a long time, flooding areas are diminished, a greater isolation between them occurs and hence a net loss of species takes place, as evidenced in our study. Furthermore, the ongoing process of this extreme situation makes such a loss be made up of common species to all sites, and the newly occurring species are more adapted to local conditions and hence differ among sites. This seems to be due to the action of two different stressful environmental processes, which explain the replacement of flora: salinisation, mostly enhancing diatom richness, and eutrophication increasing cyanobacterial taxa. Therefore, in 2007–2008, community trajectories in each site appeared to be unique and different from communities located in other sites of the wetland. Data analysed here may better correspond with the idea of a net loss of species due to extreme conditions, such as reduced habitat (Pithart et al. 2007), although, at times, severe drought provides a beneficial effect for beta diversity when different types of environmental stressors act as filters for species selection (Loreau et al. 2003; Fox 2008).

Long-term changes in zooplankton richness and its relationship with environmental changes

When spatial scale was changed, we proved the importance of flooding area as related with zooplankton species richness in other flooding periods of TDNP (Table 5) and other places as well. The information of Table 5 enables us to search for correlations between either the whole zooplankton plankton richness or rotifer richness and flooding area ($r = 0.94$, $p = 0.014$ and $r = 0.94$, $p = 0.016$, respectively) for places smaller than 1,000 ha. When crustacean data of Table 5 were compared with those of Thackeray (2007) and Dodson (1992) for 10–1,000 ha European lakes, whose species richness is lower than 10 species, it can be shown that crustacean richness is higher in wetlands. These data are not enough for a meta-analysis, but they are suggestive of a relationship between flooding area and zooplankton metacommunity richness, albeit in a different way for different zooplankton groups. Again, spatial scale is important to consider when comparing richness of metacommunities (Declerck et al. 2011). Therefore, when studying spatio-temporal changes of secondary producers' richness, we must consider two hypotheses. On the one hand, one involving a covariance of the richness of secondary and primary producers (Hutchinson 1959; Barnett and Beisner 2007) and, on the other, one which singles out the richness behaviour of different groups because of their very different responses to environment complexity (Declerck et al. 2007; Kruk et al. 2009). We have found evidence of the second hypothesis because: (i) there was no relationship between zooplankton and phytoplankton richness at either the single site or the entire TDNP wetland and then an explanation based on a competitive local mechanism relating consumer richness with productivity (a surrogate of resource availability) was discarded, and (ii) the response of larger zooplankton (rotifers, cladocerans and copepods) is hampered by indirect effects of desiccation, such as the decreasing depth of the water column, the increase in dissolved solids and salinity and the occurrence of macrophytes. Salinity increases dissolved solids occurring in the

Table 5 Zooplankton richness in TDNP and other aquatic ecosystems

Ecosystem	TS	Ecosystem area (ha)	Study duration (months)	Species richness				References
				ROT	CLA	COP	TOT	
Bhopal wetlands (India)	O E	3,229	24				23–26 32–40	Neelam et al. (2009)
Doñana wetland (Spain)	E–H	2,500	4 (2)	37	17	12	66	Fahd et al. (2000)
Empordá wetland (Spain)			54	19	2	6	27	Brucet (2004)
La Concepción reservoir (Spain)	E	292	12	25	10	2	37	Fernández-Rosado and Lucena (2001)
Menorca lagoon (Spain)	E	50	18 (18)				22	Pretus (1989)
TDNP wetland (Spain)	E–H	45–800	12 (5)	33	6	5	44	García Sánchez-Colomer (1996), Velasco (1996), Ortega-Mayagoitia et al. (2000), this study
		428–1,355	24 (24)	66	15	10	91	
		20–400	21 (21)	34	7	3	44	
Valencia lagoon (Spain)	E	2,300	96	62	9	5	76	Alfonso and Miracle (1990)
Villa wetland (Peru)		5	10 (3)	17	7	3	27	Iannacone and Alvaríño (2007)

TS trophic status, O oligotrophic, M mesotrophic, E eutrophic, H hypertrophic, ROT rotifer species richness, CLA cladoceran species richness, COP copepod species richness, TOT overall zooplankton richness

Ecosystem area is flooding area. Study period and number of sampling events in brackets. Vacant cells lack data in the original studies

shallower site, resulting in diminished zooplankton richness, which can be due to both a decrease in hatching (Brock et al. 2005; Nielsen et al. 2007) and a lower compensation by regional salinity-tolerant taxa (Thompson and Shurin 2012). Moreover, the grouping of zooplankton inventories shows similar communities, at different times, in sites having submerged vegetation, and this composition differed greatly from the site without vegetation, corroborating the importance of these plants for zooplankton richness, an effect shown in other floodplains (van den Brink et al. 1994; Serrano and Toja 1998).

The zooplankton beta diversity of the wetland is higher than phytoplankton beta diversity and this could arise from the maintenance of a flooded area with vegetation (Declerck et al. 2005, 2007) and the greater difficulty of inter-site dispersal, as compared with that of phytoplankton, due to more limited dispersal abilities of zooplankton because of larger body size (Beisner et al. 2006). Therefore, our information supports the above mentioned second hypothesis, i.e. a mismatch between the richness of primary producers and consumers: the abiotic selection of traits would be more meaningful than the competitive relationship and niche distribution (Fox 2008).

Wetland conservation as suggested by plankton indicators

Plankton is able to respond to severe changes in wetlands, like those inflicted by droughts as a result of both its extremely high sensitivity of environmental changes and its dispersal

abilities (Brock et al. 2005; Kruk et al. 2009). These facts promote the substitution of planktonic populations by those better suited to environmental conditions prevailing in any site. Thus, plankton species are good environmental indicators of the changes that a wetland is experiencing (Rojo and Rodrigo 2010). This study shows how three isolated sites of a semiarid wetland harbor different planktonic populations among sites and how biodiversity is enhanced temporally by ongoing environmental change. On the one hand, dispersal may increase the resistance of local sites to environmental stress by providing regional species with traits adapted to novel conditions, but compensation by regional taxa depended on both the source of stress (Thompson and Shurin 2012) and the dispersal abilities of all aquatic microorganisms (Kruk et al. 2009; Beisner et al. 2006). On the other hand, when the stress factor promotes a strong species reduction, a beta-diversity loss can be also expected because the pool of species able to be adapted to the new extreme conditions is small and hence there will be more species shared among the sites that experience the same stress factor (Fox 2008; Tomašových and Kidwell 2010). Therefore, only the fact that in TDNP the incorporation of new species responds to different stress conditions (salinisation and eutrophication) hinders the homogenisation of phytoplankton occurring between sites, and zooplankton loss is only mitigated by the incorporation of species from the shore and the maintenance of macrophyte beds as niches.

Therefore, it seems clear that several factors prevent the collapse of TDNP planktonic biodiversity: the maintenance of an area with constant flooding and a submerged macrophyte meadow and, moreover, the fact that stressful desiccation intensifies the different processes of degradation, such as salinisation and eutrophication. Accordingly, from the viewpoint of TDNP conservation and management, we recommend the maintenance of a water body, albeit with an artificially constant water level, with submerged vegetation that can also promote the heterogeneity of isolated areas. We believe this is the key to preventing the planktonic richness from collapsing. Plankton is usually a neglected component of wetland studies, as compared with higher plants and vertebrates. Our study has demonstrated that plankton can be very useful to track environmental changes of wetlands, thus giving the environmental manager a tool to enhance the conservation of wetlands and their biota.

Acknowledgments The authors would like to thank the Spanish Ministry of the Environment and Ministry of Science and Innovation for projects 001/2008 and CGL2009-10292, respectively. The study has been possible thanks to a fellowship awarded to María Mercedes Barón-Rodríguez by the University of Valencia. We are indebted to colleagues from the Aquatic Ecology Group (National Museum of Natural History, CSIC) for their help in the field and their laboratory work on nutrients. Suggestions by two anonymous referees are also acknowledged. The English language has been corrected by Fabiola Barraclough, a native English reviewer of scientific texts www.interglobe.es.

References

- Alfonso MT, Miracle MR (1990) Distribución espacial de las comunidades zooplanctónicas de la Albufera de Valencia. *Scientia Gerundensis* 2:11–25
- Al-Obaidi GS, Salman SK, Rubec CDA (2009) Key biodiversity areas: rapid assessment of phytoplankton in the Mesopotamian Marshlands of southern Iraq. *BioRisk* 3:111–126
- Alonso M (1996) Crustácea, Branchiopoda. In: Ramos MA, Alba J, Bellés X et al (eds) *Fauna Ibérica*, vol 7. Museo Nacional de Ciencias Naturales, CSIC, Madrid
- Álvarez-Cobelas M, Cirujano S (eds) (1996) *Las Tablas de Daimiel: Ecología acuática y Sociedad*. Ministerio de Medio Ambiente, Madrid

- Álvarez-Cobelas M, Catalan J, García-Jalón D (2005) Impacts on inland water ecosystems. In: Moreno JM (ed) A preliminary general assessment of the impacts in Spain due to the effects of climate change. Spanish Ministry of Environment, Madrid
- Álvarez-Cobelas M, Sánchez-Carrillo S, Cirujano S (2010) A story of the wetland water quality deterioration: salinisation, pollution, eutrophication and siltation. In: Sánchez-Carrillo S, Angeler DG (eds) Ecology of threatened semi-arid wetland long-term research in Las Tablas de Daimiel. Wetland: ecology, conservation and management, vol 2. Springer, Berlin, pp 109–133
- Anderson MJ, ter Braak CJF (2003) Permutation tests for multi-factorial analysis of variance. *J Stat Comput Simul* 73:85–113
- Angeler DG, Álvarez-Cobelas M (2005) Island biogeography and landscape structure: integrating ecological concepts in a landscape perspective of anthropogenic impacts in temporary wetlands. *Environ Pollut* 138:420–424
- Angeler DG, Álvarez-Cobelas M, Rojo C et al (2000) The significance of water inputs to plankton biomass and trophic relationships in a semi-arid freshwater wetland (central Spain). *J Plankton Res* 22:2075–2093
- Angeler DG, Álvarez-Cobelas M, Rojo C et al (2010) Phytoplankton community similarity in a semiarid floodplain under contrasting hydrological connectivity regimes. *Ecol Res* 25:513–520
- APHA (1992) Standard methods for the examination of water and wastewater, 18th edn. American Public Health Association, Washington, DC
- Ayo BA, Latatu A, Artolozaga I et al (2009) Factors affecting preference responses of the freshwater ciliate *Uronema nigricans* to bacterial prey. *J Eukaryot Microbiol* 56:188–193
- Bachmann RW, Canfield DE (1996) Use of an alternative method for monitoring total nitrogen concentrations in Florida lakes. *Hydrobiologia* 323:1–8
- Barnett A, Beisner BE (2007) Zooplankton biodiversity and lake trophic state: explanations invoking resource abundance and distribution. *Ecology* 88:1675–1686
- Beisner BE, Peres PR, Lindstrom ES et al (2006) The role of environmental and spatial processes in structuring lake communities from bacteria to fish. *Ecology* 87:2985–2991
- Bland JM, Altman DG (1995) Multiple significance tests—the Bonferroni method-10. *Br Med J* 310:170
- Bondavalli C, Ulanowicz RE, Bodini A (2000) Insights into the processing of carbon in the South Florida Cypress Wetlands: a whole-ecosystem approach using network analysis. *J Biogeogr* 27:697–710
- Brock MA, Nielsen DL, Crossle K (2005) Changes in biotic communities developing from freshwater wetland sediments under experimental salinity and water regimes. *Freshw Biol* 50:1376–1390
- Bruet S (2004) Zooplankton structure and dynamics in Mediterranean marshes (l'Empordà wetlands): a size-based approach. PhD Thesis, University of Girona, Spain
- Cirujano S, Álvarez-Cobelas M, Sánchez-Andrés R (2010) Macrophyte ecology and macrophytes long term dynamics. In: Sánchez-Carrillo S, Angeler DG (eds) Ecology of threatened semi-arid wetland long-term research in Las Tablas de Daimiel. Wetland: ecology, conservation and management, vol 2. Springer, Berlin, pp 175–195
- Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. *Philos Trans R Soc Lond B* 345:101–118
- Connell J (1978) The intermediate disturbance hypothesis. *Science* 199:1302–1310
- Dasí MJ, Miracle MR (1991) Distribución vertical y variación estacional del fitoplancton de una laguna cársica meromítica, la Laguna de la Cruz (Cuenca, España). *Limnetica* 7:37–59
- de Castro M, Martín-Vide J, Alonso S (2005) The climate of Spain: past, present and scenarios for the 21st century. In: Moreno JM (ed) A preliminary general assessment of the impacts in Spain due to the effects of climate change. Spanish Ministry of Environment, Madrid
- De Manuel J (2000) The rotifers of Spanish reservoirs: ecological, systematical and zoogeographical remarks. *Limnetica* 19:91–167
- DeClerck SAJ, Vandekerckhove J, Johansson L et al (2005) Multi-group biodiversity in shallow lakes along gradients of phosphorus and water plant cover. *Ecology* 86:1905–1915
- DeClerck SAJ, Vanderstukken M, Pals A et al (2007) Plankton biodiversity along a gradient of productivity and its mediation by macrophytes. *Ecology* 88:2199–2210
- DeClerck SAJ, Coronel JS, Legendre P et al (2011) Scale dependency of processes structuring metacommunities of Cladocerans in temporary pools of High-Andes wetlands. *Ecography* 34:296–305
- Dodson S (1992) Predicting crustacean zooplankton species richness. *Limnol Oceanogr* 37:848–856
- Dodson SI, Arnott SE, Cottingham KL (2000) The relationship in lake communities between primary productivity and species richness. *Ecology* 81:2662–2679
- Dumont HJ, van de Velde I, Dumont S (1975) The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia* 19:75–97

- Dussart BH (1967) Contribution à l'étude des Copépodes d'Espagne. Publicaciones del Instituto de Biología Aplicada de Barcelona 42:87–105
- Dussart BH (1969) Les Copépodes des Eaux continentales. II. Cyclopoides et Biologie. N. Borbée and Cie, Paris
- Einsle U (1996) Copepoda: Cyclopoida. Genera *Cyclops*, *Megacyclops*, *Acanthocyclops*. In: Dumont HJF (ed) Guides to the identification of the microinvertebrates of the continental waters of the world, vol 10. SPB Academic Publishing BV, Amsterdam
- Engelhardt KAM, Ritchie ME (2001) Effects of macrophyte species richness on wetland ecosystem functioning and services. *Nature* 411:687–689
- Fahd K, Serrano L, Toja J (2000) Crustacean and rotifer composition of temporary ponds in the Doñana National Park (SW Spain) during floods. *Hydrobiologia* 436:41–49
- Fernández-Rosado MJ, Lucena J (2001) Space-time heterogeneities of the zooplankton distribution in La Concepción reservoir (Istán, Málaga; Spain). *Hydrobiologia* 455:157–170
- Foissner W, Berger H (1996) A user-friendly guide to the ciliates (Protozoa, Ciliophora) commonly used by hydrobiologists as bioindicators in rivers, lakes, and waste waters, with notes on their ecology. *Freshw Biol* 35:375–482
- Foissner W, Berger H, Schaumburg J (1999) Identification and ecology of limnetic plankton ciliates. Wasserwirtschaftsamt Deggendorf, Munich
- Fox JW (2008) Testing whether productivity mediates the occurrence of alternate stable states and assembly cycles in a model microcosm system. *Oikos* 117:1153–1164
- García Sánchez-Colomer MR (1996) Crustáceos. En: Álvarez-Cobelas M, Cirujano S (eds) Las Tablas de Daimiel. Ecología acuática y sociedad. Organismo Autónomo Parques Nacionales, Madrid, pp 153–158
- Gotelli NJ, Ellison AM (2004) A primer of ecological statistics. Sinauer Associates, Inc., Sunderland
- Haney JF, Hall DJ (1973) Sugar-coated *Daphnia*-preservation technique for Cladocera. *Limnol Oceanogr* 18:331–333
- Hanson MA, Zimmer KD, Butler MG et al (2005) Biotic interactions as determinants of ecosystem structure in prairie wetlands: an example using fish. *Wetlands* 25:764–775
- Hillebrand H, Dürselen C, Kirschel D et al (1999) Biovolume calculation for pelagic and benthic microalgae. *J Phycol* 35:403–424
- Hutchinson GE (1959) Homage to Santa-Rosalía or why are there so many kinds of animals. *Am Nat* 93:145–159
- Iannacone J, Alvarino L (2007) Diversidad y abundancia de comunidades zooplanctónicas litorales del humedal pantanos de Villa (Lima, Perú). *Gayana* 71:49–65
- Iglesias A, Estrela T, Gallart F (2005) Impacts on water resources. In: Moreno JM (ed) A preliminary general assessment of the impacts in Spain due to the effects of climate change. Spanish Ministry of Environment, Madrid
- Jaccard P (1912) The distribution of the flora of the alpine zone. *New Phytol* 11:37–50
- Jolly ID, McEwan KL, Holland KL (2008) A review of groundwater-surface water interactions in arid/semi-arid wetlands and the consequences of salinity for wetland ecology. *Ecohydrology* 1:43–58
- Keddy PA (2000) Wetland ecology. Principles and conservation. Cambridge University Press, Cambridge
- Koste W (1978) Rotatoria. Die Rädertiere Mitteleuropas (Überordnung Monogononta). Bestimmungswerk begründet von Max Voigt, vol 2. Borntraeger, Stuttgart
- Kruk C, Rodríguez-Gallego L, Meerhoff M et al (2009) Determinants of biodiversity in subtropical shallow lakes (Atlantic coast, Uruguay). *Freshw Biol* 54:2628–2641
- Kuczyńska-Kippen N, Joniak T (2010) The impact of water chemistry on zooplankton occurrence in two types (field versus forest) of small water bodies. *Int Rev Hydrobiol* 95:130–141
- Laskar HS, Gupta S (2009) Phytoplankton diversity and dynamics of Chatla floodplain lake, Barak Valley, Assam, North East India—a seasonal study. *J Environ Biol* 30:1007–1012
- Leibold MA, Holyoak M, Mouquet N et al (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* 7:601–613
- Loreau M, Mouquet N, Gonzalez A (2003) Biodiversity as spatial insurance in heterogeneous landscapes. *Proc Natl Acad Sci USA* 100:12765–12770
- Lund JWG, Kipling C, Le Cren ED (1958) The inverted method of estimating algal numbers and the statistical basis of estimation by counting. *Hydrobiologia* 11:143–170
- Magurran AE (1988) Ecological diversity and its measurement. Princeton University Press, Princeton
- Marker AFH, Nusch EA, Rai H et al (1980) The measurement of photosynthetic pigments in freshwaters and standardization of methods: conclusions and recommendations. *Archiv für Hydrobiologie, Ergebnisse der Limnologie* 14:91–106

- Mazaris AD, Moustaka-Gouni M, Michaloudi E et al (2010) Biogeographical patterns of freshwater micro- and macroorganisms: a comparison between phytoplankton, zooplankton and fish in the eastern Mediterranean. *J Biogeogr* 37:1341–1351
- Millett B, Johnson WC, Guntenspergen G (2009) Climate trends of the North American prairie pothole region 1906–2000. *Clim Change* 93:243–267
- Mironova EI, Telesh IV, Skarlato SO (2009) Planktonic ciliates of the Baltic Sea (a review). *Inland Water Biol* 2:13–24
- Mitsch WJ, Gosselink JG (2000) Wetlands, 3rd edn. Van Nostrand Reinhold, New York
- Neelam V, Avinash B, Dwivedi SN (2009) Planktonic biodiversity of Bhoj Wetland, Bhopal, India. *J Appl Sci Environ Manag* 13:103–111
- Nielsen DL, Brock MA, Petrie R et al (2007) The impact of salinity pulses on the emergence of plant and zooplankton from wetland seed and egg banks. *Freshw Biol* 52:784–795
- Nöges T, Nöges P, Laugaste R (2003) Water level as the mediator between climate change and phytoplankton composition in a large shallow temperate lake. *Hydrobiologia* 506:257–263
- Nogrady T, Segers H (2002) Rotifera 6: Asplanchnidae, Gastropodiidae, Lindiidae, Microcodidae, Synchaetidae, Trochosphaeridae and Filinia. In: Dumont HJ (ed) Guides for the identification of the microinvertebrates of continental waters of the world, vol 18. SBP Academic Publishers, Amsterdam
- OECD (1982) Eutrophisation des eaux. Méthodes de surveillance, d'évaluation et de lutte. Paris
- Orlova-Bienkowskaja MY (2001) Cladocera: Anomopoda. Daphniidae: Genus *Simocephalus*. In: Dumont HJ (ed) Guides for the identification of the microinvertebrates of continental waters of the world, vol 17. Backhuys, The Hague
- Ortega-Mayagoitia E, Armengol X, Rojo C (2000) Structure and dynamics of zooplankton in a semi-arid wetland, the National Park Las Tablas de Daimiel (Spain). *Wetlands* 20:629–638
- Ortega-Mayagoitia E, Rojo C, Rodrigo MA (2003) Controlling factors of phytoplankton assemblages in wetlands: an experimental approach. *Hydrobiologia* 502:177–186
- Padisák J, Crossetti LO, Naselli-Flores L (2009) Use and misuse in the application of the phytoplankton functional classification: a critical review with updates. *Hydrobiologia* 621:1–19
- Pejler B (1983) Zooplanktic indicators of trophic and their food. *Hydrobiologia* 101:111–114
- Pielou EC (1975) Ecological diversity. Wiley, New York
- Pithart D, Pichlová R, Bílý M et al (2007) Spatial and temporal diversity of small shallow waters in river Lužnice floodplain. *Hydrobiologia* 584:265–275
- Pociecha A (2008) Density dynamics of *Notholca squamula salina* Focke (Rotifera) in Lake Wujka, a freshwater Antarctic lake. *Polar Biol* 31:275–279
- Podani J (2000) Introduction to the exploration of multivariate biological data. Backhuys Publishers, Leiden
- Pretus JL (1989) Limnología de la Albufera de Menorca (Menorca, España). Universitat de Barcelona
- Reyes I, Martín G, Reina M et al (2007) Phytoplankton from NE Doñana marshland (“El Cangrejo Grande”, Doñana Natural Park, Spain). *Limnetica* 26:307–318
- Reyes I, Casco MA, Toja J et al (2008) Hydrological complexity supports high phytoplankton richness in the Doñana marshland (SW Spain). *Hydrobiologia* 614:47–54
- Reynolds CS, Huszar V, Kruk C et al (2002) Towards a functional classification of the freshwater phytoplankton. *J Plankton Res* 24:417–428
- Rodrigo MA, Rojo C, Álvarez-Cobelas M (2003a) Autotrophic and heterotrophic picoplankton in wetlands: differences with lake patterns. *Int Rev Hydrobiol* 88:464–481
- Rodrigo MA, Rojo C, Armengol X (2003b) Plankton biodiversity in a landscape of shallow water bodies (Mediterranean coast, Spain). *Hydrobiologia* 506:317–326
- Rojo C (2004) Self-organization of plankton communities: a test of freshwater restoration. In: Hobbs R, Temperton V, Fattorini M (eds) Assembly rules and restoration ecology. Island Press, Washington, DC, p 134
- Rojo C, Álvarez-Cobelas M (2003) Are there steady-state phytoplankton assemblages in the field? *Hydrobiologia* 502:3–12
- Rojo C, Rodrigo MA (2010) Plankton ecology and diversity. In: Sánchez-Carrillo S, Angeler DG (eds) Ecology of threatened semi-arid wetland long-term research in Las Tablas de Daimiel. Wetland: ecology, conservation and management, vol 2. Springer, Berlin, pp 137–173
- Rojo C, Ortega-Mayagoitia E, Rodrigo MA et al (2000) Phytoplankton structure and dynamics in the semiarid wetland National Park Las Tablas de Daimiel (Spain). *Archiv für Hydrobiologie* 148:397–419
- Rojo C, Barón-Rodríguez MM, Rodrigo MA (2007) Dynamics of the planktonic food web in Colgada Lake (Lagunas de Ruidera Natural Park). *Limnetica* 26:251–264
- Rojo C, Barón-Rodríguez MM, Álvarez-Cobelas M (2010) Sustained primary production with changing phytoplankton assemblages in a semiarid wetland. *Hydrobiologia* 639:55–62

- Romo S, Miracle MR (1994) Population dynamics and ecology of subdominant phytoplankton species in a shallow hypertrophic lake (Albufera of Valencia, Spain). *Hydrobiologia* 273:37–56
- Rott E (1981) Some results from phytoplankton counting intercalibrations. *Schweiz Z Hydrol* 43:34–62
- Sánchez-Carrillo S, Álvarez-Cobelas M (2001) Nutrient dynamics and eutrophication patterns in a semi-arid wetland: the effects of fluctuating hydrology. *Water Air Soil Pollut* 131:97–118
- Sánchez-Carrillo S, Angeler DG (eds) (2010) Ecology of threatened semi-arid wetlands long-term research in Las Tablas de Daimiel. Springer, Berlin
- Scheffer M, van Geest JG, Zimmer K et al (2006) Small habitat size and isolation can promote species richness: second-order effects on biodiversity in shallow lakes and ponds. *Oikos* 112:227–231
- Segers H (1995) Rotifera 2. The Lecanidae (Monogononta). Guides to the identification of the microinvertebrates of the continental waters of the world, part 6. SPB Academic Publishing BV, New York
- Segers H (2007) Annotated checklist of the rotifers (Phylum Rotifera), with notes on nomenclature, taxonomy and distribution. *Zootaxa* 1564:1–104
- Serrano L, Toja J (1998) Interannual variability in the zooplankton community of a shallow temporary pond. *Int Assoc Theor Appl Limnol* 26:1575–1581
- Shimodaira H (2004) Approximately unbiased tests of regions using multistep-multiscale bootstrap resampling. *Ann Stat* 32:2616–2641
- Shurin JB (2001) Interactive effects of predation and dispersal on zooplankton communities. *Ecology* 82:3404–3416
- Sieburth J, Smetacek V, Lenz J (1978) Pelagic ecosystem structure: heterotrophic compartments of the plankton and their relationship to plankton size fractions. *Limnol Oceanogr* 23:1256–1263
- Smirnov NN (1996) Cladocera: the Chydorinae and Sayciinae (Chydoridae) of the world. In: Dumont HJ (ed) Guides for the identification of the microinvertebrates of continental waters of the world, vol 11. SPB Academic Publishing, The Hague
- Stralberg D, Cameron DR, Reynolds MD et al (2011) Identifying habitat conservation priorities and gaps for migratory shorebirds and waterfowl in California. *Biodivers Conserv* 20:19–40
- Suzuki R, Shimodaira H (2005) Pvcust: hierarchical clustering with P-values. R package version 1.0-3. <http://www.is.titech.ac.jp/wshimo/prog/pvcust/>
- Taylor JC, Harding WC, Archibald GM (2007) An illustrated guide to some common diatom species from South Africa. Water Research Commission report
- Thackeray SJ (2007) Crustacean zooplankton species richness and productivity: to what extent do the conclusions depend upon the choice of metrics? *Oikos* 116:614–628
- Thompson PL, Shurin JB (2012) Regional zooplankton biodiversity provides limited buffering of pond ecosystems against climate change. *J Anim Ecol* 81:251–259
- Tomašových A, Kidwell SM (2010) Predicting the effects of increasing temporal scale on species composition, diversity, and rank-abundance distributions. *Paleobiology* 36:672–695
- Ubierna-León MA, Sánchez-Castillo PM (1992) Diatom flora of several lagoons with mineralized waters in the provinces of Málaga and Granada. *Anales del Jardín Botánico de Madrid* 49:171–185
- Usai MC, Margaritora FG (1987) Further systematic and ecological data on Italian populations of *Macrothrix hirsuticornis* Norman and Brady (Crustacea, Cladocera). *Bolletino Zoologico* 54:35–39
- Valdovinos C, Moya C, Olmos V et al (2007) The importance of water-level fluctuation for the conservation of shallow water benthic macroinvertebrates: an example in the Andean zone of Chile. *Biodivers Conserv* 16:3095–3109
- van den Brink FWB, Vankatwijk MM, Vandervelde G (1994) Impact of hydrology on phytoplankton and zooplankton community composition in floodplain lakes along the lower Rhine and Meuse. *J Plankton Res* 16:351–373
- Velasco JL (1996) Rotíferos. In: Álvarez-Cobelas M, Cirujano S (eds) Las Tablas de Daimiel. Ecología acuática y sociedad. Organismo Autónomo Parques Nacionales, Madrid, pp 147–152
- Vellend M (2001) Do commonly used indices of Beta diversity measure species turnover? *J Veg Sci* 12:545–552
- Villena MJ, Romo S (2001) Fitoplancton de dos lagunas de los humedales de Xeresa y Xeraco (Valencia, España). *Botánica Complutensis* 25:179–189
- Ward JV, Tockner K (2001) Biodiversity: towards a unifying theme for river ecology. *Freshw Biol* 46:807–819
- Waterkeyn A, Vanschoenwinkel B, Grillas P et al (2010) Effect of salinity on seasonal community patterns of Mediterranean temporary wetland crustaceans: a mesocosm study. *Limnol Oceanogr* 55:1712–1722
- Zedler JB (2000) Progress in wetland restoration ecology. *Trends Ecol Evol* 15:402–407
- Zedler JB (2003) Wetlands at your service: reducing impacts of agriculture at the watershed scale. *Front Ecol Environ* 1:65–72