

Ecological impacts of global warming and water abstraction on lakes and reservoirs due to changes in water level and related changes in salinity

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Abstract According to the Intergovernmental Panel on Climate Change report released in September 2014, unprecedented changes in temperature and precipitation patterns have been recorded globally in recent decades and further change is predicted to occur in the near future, mainly as the result of human activity. In particular, projections show that the Mediterranean climate zone will be markedly affected with significant implications for lake water levels and salinity. This may be exacerbated by increased demands for irrigation water. Based

on long-term data from seven lakes and reservoirs covering a geographical gradient of 52° of latitudes and a literature review, we discuss how changes in water level and salinity related to climate change and water abstraction affect the ecosystem structure, function, biodiversity and ecological state of lakes and reservoirs. We discuss mitigation measures to counteract the negative effects on ecological status that are likely to result from changes in climate and water abstraction practices. Finally, we highlight research required to improve knowledge of the impacts of anthropogenically induced changes on lake water level and consequent changes in salinity.

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Introduction

Globally, temperature and precipitation patterns have changed markedly in recent decades and are predicted to change even more in the future as a result of anthropogenically driven climate change (Meehl et al., 2007). Climate change models further predict increased occurrence of extreme events (flooding, extended droughts), which will magnify the seasonal and multiannual amplitude of water level fluctuations, in turn creating hydrological stresses (e.g. prolonged hydraulic retention time) in lakes (IPCC, 2014).

In particular, regions with a cold and hot semi-arid climate and the Mediterranean climate zone, one of the hotspots in future climate change projections (Giorgi & Lionello, 2008), will be markedly affected by global warming (IPCC, 2007, 2014). A 25–30% decrease in precipitation and enhanced evaporation are expected by the end of the twenty-first century in the Mediterranean region (Erol & Randyr, 2012) accompanied by an even stronger reduction in runoff, up to 30–40% in Turkey and Spain (IPCC, 2007, 2014). The IPCC 5th assessment report predicts that droughts will intensify in the twenty-first century in some seasons and in these regions due to reduced precipitation and/or increased evapotranspiration. A similar scenario of reduced precipitation and enhanced evaporation is predicted for other semi-arid regions of the world at risk of desertification such as north-east Brazil (Oyama & Nobre, 2003; Da Silva, 2004; Marengo et al., 2009). These figures do not consider compensatory increases

in water abstraction, particularly for irrigation, which is already the greatest demand on water use. Several studies have predicted an increase in irrigation depending on various climate change scenarios. For example, Yano et al. (2007) predicted a significant increase (15–22%) in the irrigation water demand for a wheat–maize cropping sequence in Turkey, while Rodriguez Diaz et al. (2007) estimated an increase of 15–20% in the seasonal irrigation demand in the Guadalquivir river basin in Spain by 2050. De Silva et al. (2007) studied the impacts of climate change on irrigation water requirements in a Sri Lankan paddy field and predicted an irrigation water demand increase between 13 and 23%. The magnitude of such changes poses a major threat to the functioning and biodiversity of freshwaters, including lakes, and can result in major contraction or even disappearance of water bodies. Dramatic examples of water bodies that have drastically declined in size due to both climatic changes and high demands for agricultural water have already been observed. The Aral Sea has shrunk by more than 50% and reached salinity levels that have resulted in almost complete loss of biodiversity (Aladin et al., 2009). Similarly, Lake Chad, West Africa, has shrunk to nearly a twentieth of its original size (UNEP, 2009). Lake Akşehir, previously one of the largest freshwater lakes in Turkey, completely disappeared due to loss of surface and ground water sources through intensive irrigation of crop farming, leading to extinction of two endemic fish species (Jeppesen et al., 2009).

Global warming reinforces the eutrophication of already eutrophic lakes (Moss et al., 2011), with significant changes in lake food web structure and community composition (Jeppesen et al., 2007; Meerhoff et al., 2007; Brucet et al., 2010; Jeppesen et al., 2010a, b; Brucet et al., 2012; Meerhoff et al., 2012), and causes higher proportions of cyanobacteria in summer (Wagner & Adrian, 2009; Kosten et al., 2012). In the Mediterranean climate zone and other areas with semi-arid desert climates, changes in water level, hydraulic retention time and salinity associated with warming may have considerable further effects on lake ecosystem structure and dynamics (reviews by Wantzen et al., 2008, and Brucet et al., 2010; Zohary & Ostrovsky, 2011; Brucet et al., 2012). Besides nutrient loading, evaporative up-concentration of nutrients in reduced water volumes becomes an additional factor enhancing eutrophication under

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warmer conditions (Özen et al., 2010), and longer water residence time may favour the growth and blooming of cyanobacteria, especially the toxin-producing ones such as *Microcystis* spp. (Romo et al., 2013). Prolonged hydraulic residence times resulting from drought also enhance salinization (Beklioglu et al., 2007; Beklioglu et al., 2011). Increased salinity not only favours cyanobacteria blooms (Sellner et al., 1988) but may also cause an ionic imbalance in salt-sensitive taxa, resulting in ion toxicity and osmotic stress accompanied by high mortality or lower reproduction and growth rates (Nielsen et al., 2003; Jeppesen et al., 2007; Bezirci et al., 2012). Such conditions can significantly reduce the resilience of lake ecosystems or even induce a state shift to turbid water (Jeppesen et al., 2007; Barker et al., 2008). Shallow lakes, which are globally the most common and widespread inland water bodies (Downing et al., 2006), are particularly vulnerable to drought and unbalanced ratios between evaporation and precipitation (Jeppesen et al., 2009; Moss et al., 2011) due to their large surface:volume ratio (Coops et al., 2003). However, there is increasing evidence that also deep (stratified) lakes respond negatively to excessive water level fluctuations (Zohary & Ostrovsky, 2011). Moreover, man-made lakes, which are common and often represent a strategic water resource in dry climates, can be significantly affected by increased water level fluctuations. Naselli-Flores (2014), and literature therein, showed an increase in the amplitude of water level fluctuations that interfered with the physical and chemical structures of these water bodies and resulted in conditions favourable for the occurrence of toxic cyanobacterial blooms.

In this paper, we use long-term data from 7 lakes and reservoirs that are located in drought-prone semi-arid climates, covering a geographical gradient of 52° of latitudes, to document how changes in hydrology and water level have affected physical, chemical and biological variables in these water bodies, and combine this with a review of literature to discuss how changes in water level and salinity related to climate change and water abstraction affect the structure and function of lake ecosystems. We further discuss possible ways to mitigate the negative effects of the global warming- and water abstraction-induced changes in water level and salinity on these ecosystems and highlight research gaps.

Materials and methods

Case studies

We present case studies for some lakes and reservoirs that have been subject to major water level changes. For the majority of the studies, the methods used are described in detail in published papers cited here. Accordingly, we provide only a brief overview of lake characteristics and methods but add more specific and detailed information when unpublished data are used. Some basic information on location and morphometry is given in Table 1.

Lake Võrtsjärv, Estonia (transition zone between a maritime and continental northern temperate climate)

Lake Võrtsjärv is a large polymictic shallow lake located in a shallow pre-glacial basin in the southern part of Estonia (Table 1) and has an average water retention time of 1 year. Large seasonal and annual fluctuations of the water level and water volume are key features of the lake (Nõges & Nõges, 2012).

Between 1924 and 2011, the average annual ice cover was 131 days (late November until early April). The annual mean air temperature in the Võrtsjärv region between 1961 and 2011 was 5.3°C (Nõges & Nõges, 2014), and mean annual precipitation from 1971 to 2011 was 641 mm. Water from the tributaries draining the surrounding moraine has an alkalinity of approximately 200 mg l⁻¹ and is dominated by hydrocarbonate and calcium ions. The lake is highly eutrophic (Nõges & Nõges, 2012).

Daily data on air temperature and precipitation at the closest meteorological station to Võrtsjärv (Tõravere) as well as data on water level and water temperature in Võrtsjärv were provided by the Estonian Meteorological and Hydrological Institute. Other data collection and analytical methods are described in Nõges & Tuvikene (2012).

Lake Doirani, Greece (warm semi-arid Mediterranean climate)

Lake Doirani is a shallow polymictic lake (Table 1) located north of Thessaloniki, at the border between Greece and the Former Yugoslav Republic of

Table 1 Information on geographical location, morphometry and catchment of the seven lake case studies (lakes arranged from north to south)

Lake	Country	Position	Altitude (m.a.s.l.)	Lake volume (km ³)	Lake area (km ²)	Mean depth (m)	Maximum depth (m)	Catchment area (km ²)
Võrtsjärv	Estonia	58°17'N, 26°03'E	34	0.756	270	2.8	6	3,374
Doirani	Greece	41°21'N, 22°47'E	142	0.098	28	3.5	5.5	276
Vegoritis	Greece	40°45'N, 21°45'E	509	1.120	40	28	40	1,853
Eymir	Turkey	39°57'N, 32°53'E	970	0.004	1.2	3.1	5	971
Biviere di Gela	Italy	37°01'N, 14°20'E	8	0.006	1.2	4.8	8.5	71
Kinneret	Israel	32°50'N, 35°35'E	−209	4.326	169	25.6	41.7	2,730
Cruzeta	Brazil	06°23'S, 36°47'W	231	0.018	6.16	3	10	1,010

Macedonia (FYROM). It is a karstic lake and a remnant of a much larger Pleistocene lake.

The lake is located in a semi-arid Mediterranean area and is typically polymictic but exhibits summer stratification in very warm and dry years (Pertsemli & Voutsas, 2007). Average annual air temperature and annual precipitation from 1961 to 2001 were $14.3 \pm 1^\circ\text{C}$ and 612 ± 18 mm, respectively. Underwater springs and surface runoff from the catchment are the main water sources. Agriculture and livestock are the major activities in the Greek part of the catchment, while the FYROM shoreline is principally used for recreational purposes. The size and depth of the lake vary from year to year. Since 1986, a drastic water level decrease of approximately 4 m has been observed.

Potential evapotranspiration was calculated from climate data based on the Thornthwaite method (Thornthwaite, 1948). Temporal data series of average monthly values of conductivity, chloride concentration, pH and oxygen saturation for 1983–2001 were obtained from the Ministry of Rural Development.

Other data collection and analytical methods are described in Stefanidis & Papastergiadou (2013).

Lake Vegoritis, Greece (warm semi-arid Mediterranean climate)

Lake Vegoritis is located in the northern part of Greece (in the Macedonia region) and is one of the largest natural lakes in Greece. It is a deep lake with an average depth of 28 m (Table 1) and a surface area of approximately 40 km².

The lake is surrounded by high mountains to the north–east and north–west, while a large plain extends from the southern bank of the lake (Skoulikidis et al., 2008). Agricultural activities and urban settlements are

mainly located in the southern part of the basin. The dominant geology in the area comprises metamorphic siliceous rocks and calcareous formations (Skoulikidis et al., 2008). The climate is semi-dry, Mediterranean, with two distinct warm–dry and cold–wet periods, while during winter, the lake remains ice-free (Gianniou & Antonopoulos, 2007). Average annual air temperature and annual precipitation from 1961 to 2004 were $12.2 \pm 0.08^\circ\text{C}$ and 654 ± 24 mm, respectively.

For the last five decades, the lake has been impacted by environmental pressures, including agricultural and industrial pollution. More importantly, the water level of the lake decreased approximately 32 m from the mid-1950s to 2002, mainly due to water abstraction for hydro-electrical power generation in the period 1956–1985 (Gianniou & Antonopoulos, 2007). Since then, the trophic state of the lake has changed from oligotrophic at the beginning of the 1980s to mesotrophic during the 1990s (Skoulikidis et al., 2008).

Data on potential evapotranspiration, mean monthly conductivity and chloride concentrations were obtained for the same years and from the same sources as for Lake Doirani. Long-term water level data were acquired from the Department of Environment, Region of Western Macedonia, for the period 1896–2001. Data on the productivity of fisheries for the period 1979–1999 were acquired from the PESCA database project (Paschos & Kagalou, 2000).

Other data collection and analytical methods are described in Stefanidis & Papastergiadou (2013).

Lake Eymir, Turkey (cold–dry steppe/cold semi-arid climate)

Lake Eymir is a shallow alluvial dam lake (Table 1), created by damming of a river valley in a basin formed

by tectonic depression. It is located 20 km south of the capital, Ankara. The climate exhibits dry steppe characteristics, i.e. cold winters and hot, dry summers with inter-annual shifts between dry and wet periods. Average air temperatures and precipitation over a 32-year period (1980–2012) were $12.1 \pm 1.0^\circ\text{C}$ and 407 ± 78 mm, respectively (Turkish State Meteorological Service). The lake is fed by two tributaries and by groundwater. The major water source is the outflow from upstream Lake Mogan, especially during spring and autumn. Groundwater is the major water source during summer; however, the water level has decreased dramatically during the last two decades due to excessive urban use as well as drought periods with less precipitation and intensified evaporation.

Methods of data collection and analysis are described in Beklioğlu et al. (2003) and Beklioğlu & Tan (2008).

Lake Biviere di Gela, Sicily, Italy (warm semi-arid Mediterranean climate)

Lake Biviere di Gela is the largest natural lake in Sicily (Table 1), situated 1.3 km from the south-eastern Mediterranean coast. The lake was already known in the Antiquity and is mentioned as “Lacus Gelonius” by Pliny the Elder in his *Naturalis Historia*.

The catchment is characterised by Neogene and Quaternary deposits. The former consists of clay, marly clay and evaporitic deposits, resulting in the brackish nature of the lake water. The lake has no surface outflow and no important inflow but is fed during the rainy season by an ephemeral surface stream. The main water losses from the lake are evaporation from the water surface and underground outflow to groundwater. The long-term (1968–2008) mean water level was 5.6 m above sea level (m.a.s.l.), fluctuating between 0.75 and 8.0 m in the period. The lowest values were recorded in summer 2001 and 2002 when the depth was less than 1 m, and the lake was separated into two basins (“Lago Grande” to the east and “Lago Piccolo” to the west), which gives rise to concerns about its conservation.

The lake is subject to a typical Mediterranean semi-arid climate: mild, relatively rainy winters and warm, dry summers, and the lake experiences seasonal water level fluctuations. In the period 1968–2008, the annual mean air temperature in this part of Sicily was 19.7°C , and mean annual

precipitation was 358 mm (Barone et al., 2010). The imbalance between precipitation and evaporation rates results in a hydrological deficit in the lake budget, mainly compensated by surface runoff. A hydrogeochemical analysis of the isotope composition of local rainwater and groundwater revealed that more than 90% of the water recharge of the lake is from autumn and winter precipitation (Manno et al., 2007).

Methods of data collection and analysis are described in Barone et al. (2010).

Lake Kinneret, Israel (warm semi-arid Mediterranean climate)

Lake Kinneret is a large deep (Table 1) warm-monomictic lake, surrounded by mountains, with a relatively simple topography and morphometry, located in the hot (range of monthly mean air temperatures: $9\text{--}36^\circ\text{C}$) and semi-arid (direct annual rainfall: ~ 400 mm) northern part of the Syrian-African Rift Valley. The lake is atypical in its region as there are no other natural freshwater lakes of substantial size in Israel or the neighbouring countries. Lake Kinneret is located at an exceptionally low elevation (Table 1) within the Dead Sea tectonic depression, the Dead Sea being the lowest freshwater lake on Earth. The Mediterranean climate brings rainfall only in the cool winters; the summers are hot and dry. Consequently, riverine inflows, nutrient loads and lake water levels also exhibit a highly variable seasonal pattern. This seasonal pattern plays a major role in the lake’s physical and biogeochemical processes. The Jordan River supplies about 70% of the total inflow, $\sim 90\%$ of the TN and $\sim 80\%$ of the TP loads from riverine sources. Other important external sources of nutrients are aeolian, through wet (rain) and dry (dust) deposition. In particular dust is a major source of phosphorus in summer (Nishri & Leibovici, 2014). The salinity of Lake Kinneret, which fluctuates between 190 and 280 mg Cl L^{-1} , is significantly higher than in the surface streams flowing into the lake. The sources of salinity are brines emerging from off-shore and on-shore springs.

Since the beginning of the last century, Lake Kinneret and its catchment were subject to major anthropogenically induced hydrological changes, including damming of the outflow in 1932, draining of

a natural shallow lake, Lake Hula, and adjacent wetlands upstream of Kinneret in the 1950s, annually abstracting $\sim 350\text{--}450 \times 10^6 \text{ m}^3$ of water for drinking and irrigation, and re-flooding of parts of the previously drained Hula Valley in 1994. The discharge of the Jordan River decreased from ca. $500 \times 10^6 \text{ m}^3 \text{ y}^{-1}$ in the 1970s to ca. $400 \times 10^6 \text{ m}^3 \text{ y}^{-1}$ in the early 2010s. This 20% decrease was attributed to a reduction of effective rain in the watershed and to increased water consumption upstream of the lake. The consequence of increased demand for freshwater and declining inflows was increased amplitude of water level fluctuations, from a natural amplitude of $\sim 1.5 \text{ m}$ annually to amplitudes of $>4 \text{ m}$ (Zohary & Ostrovsky, 2011). Other anthropogenic changes included a population increase in the catchment, fish stocking and human development around the lake shores.

Being a major source of Israel's drinking water, the lake has been well studied. A summary of current knowledge on Lake Kinneret is given by Zohary et al. (2014a) where methods of hydrological, meteorological, physical, chemical and biological data collection and analyses are also described.

Lake Cruzeta, Brazil (tropical/warm semi-arid climate)

The climate of the Lake Cruzeta catchment is tropical or warm semi-arid with an average annual precipitation of 585 mm and a potential evapotranspiration of 3,323 mm (1936–1985). This man-made lake was constructed in 1929 to serve as a drinking water supply, but since 1977 it has also been used for irrigation of 196 ha of bean and corn crops. The lake is shallow and polymictic. The ratio of catchment area to maximum lake area is 164, the largest ratio among the case study lakes (Table 1). A large catchment to surface area ratio is characteristic of semi-arid man-made lakes (Thornton & Rast, 1993), which together with their lengthy water residence time (from months to years) makes these systems highly vulnerable to eutrophication and siltation due to high retention of nutrients and sediments exported from the catchment. Over the last eight decades, the lake has lost one-third of its maximum storage capacity, resulting in an average annual siltation rate of 0.4% (Freitas et al., 2011).

Data on lake volume and area were provided by the water resources management agency (SERHID-RN)

and calculated from the original lake depth–area hypsographic curve. Therefore, the morphometric data are not corrected for the volume lost due to siltation. Water samples in the lake were collected every 2 weeks between March 2007 and May 2008 at five different points along its longitudinal axis; from the delta of the main tributary to the dam. Depth-integrated samples were collected with a Van Dorn sampler for determination of total P, chlorophyll *a* and suspended solids concentrations (APHA et al., 1998).

Literature review

For the literature survey, we used the Web of Science (<https://webofknowledge.com/>), which comprises the three Institute for Scientific Information (ISI) citation databases. For each search query, we used every combination of object/cause/effect shown in Table S1 (e.g. shallow lake “water level” macrophyte OR shallow lake “water level” phytoplankton OR ...). For water level, all effects were taken into account in the search query, whereas for salinity only biological variables (i.e. macrophytes, phytoplankton, chlorophyll *a*, zooplankton and fish) were included (Table S1). All searches together resulted in 1,101 unique papers. However, only 114 papers were selected as relevant for this review by focusing on the effects of water level/salinity decrease/increase rather than those of seasonal or small water level fluctuations. This approach means though that the single impacts cannot exclude synergic or antagonistic effects due to multiple stressors, so the table has to be interpreted with caution. Causes of water level changes were also considered, and the observed effects were classified according to drivers of water level change. To better interpret the results of our review, the climatic distribution of the lakes was divided according to the updated Köppen–Geiger classification (Peel et al., 2007; A = tropical; B = arid or desert; C = temperate; D = cold or continental and E = polar or alpine) (see Table S1). In addition, papers were categorised according to “water body” (shallow and deep lakes, shallow and deep reservoirs and experimental setups), which were subset in Table S2 according to the causes (water level reduction/increase and salinity increase) and their effects (e.g. phytoplankton and TP increase, zooplankton decrease, change in macrophyte community).

Results

Case studies

Lake Võrtsjärv: major changes due to climate-induced variation in the water level

The annual maximum surface water temperature (SWT) varied from 20.4 to 27.5°C with a long-term average of 23°C during the period 1947–2000 (Järvet, 2004). Daily data on the ice-free period 1961–2004 revealed a highly significant ($P < 0.001$) temperature increase of 0.42°C per decade in August (Nõges, 2009). The annual mean air temperature close to Võrtsjärv (in Tartu) has increased by 0.09°C per decade since 1866 and by 0.44°C per decade since 1961. In 1947–2011, SWT increased by 0.25°C per decade in August, while over the last 50-year period (1961–2011) the increase accelerated, reaching 0.39°C per decade.

The water level in Võrtsjärv is unregulated and is characterised by a winter minimum usually at the end of March, a flood peak in April or May after snow melt and an autumn minimum usually in September or October (Järvet, 2004). The annual water level follows the dry–wet periodicity determined by the NAO cycle (Nõges et al., 2003).

Climatic and hydrological trends were calculated for the period 1978–2012 for which we had also homogeneous water chemistry and plankton data (Fig. 1). During this 35-year period, the yearly average air temperature was 5.73°C and increased by 0.52°C per decade. There was no clear trend in yearly average precipitation (662 mm) and water level (33.7 m.a.s.l.), whereas average daily precipitation between January and March increased by 0.165 mm per decade.

Salinity during the ice-free period (May–Oct) was positively correlated with May–Oct water temperature ($r = 0.37$, $P < 0.05$) and yearly average air temperature ($r = 0.47$, $P = 0.005$), which could indicate that the concentration of major ions is sensitive to evaporation. However, the positive correlations of salinity with air temperature and precipitation in January–March, before snow melt and spring flood ($r = 0.46$, $P = 0.005$ for both), and with the annual mean water level in Võrtsjärv ($r = 0.38$, $P < 0.05$), reflect the strong effect of higher substance loading in warmer and wetter years. Substance concentration due to

evaporation does not seem to play a major role for salinity in temperate climates even in such a shallow lake as Võrtsjärv.

Due to slow water exchange, the annual average, minimum and maximum water levels depend strongly on antecedent conditions, specifically those in the preceding year, showing autocorrelation from 0.41 to 0.54. The second most important descriptor of the annual mean water level (after the water level of the preceding year) was the amount of precipitation during the ice-free period (Pearson, $r = 0.40$, $P < 0.001$), determining also the annual minimum water level ($r = 0.48$, $P < 0.001$). Mainly, the annual maximum water level occurred during the flood period in spring and was significantly related to precipitation between January and March ($r = 0.25$, $P = 0.017$). The annual mean water level depended almost equally on the annual minimum and maximum ($r = 0.90$, $P < 0.001$ and $r = 0.92$, $P < 0.001$, respectively).

By controlling the frequency and intensity of sediment resuspension, water level changes remain the most powerful factor in Võrtsjärv, affecting all common water quality parameters and masking the effects of management measures on the status of the lake (Tuvikene et al., 2010). Correlations for the ice-free periods since 1978 demonstrated that periods of low water level, when surface sediments become disturbed by wave action, were characterised by low Secchi depth ($r = 0.63$, $P < 0.001$) and high total phosphorus (TP; $r = -0.52$, $P < 0.01$), high orthophosphate ($r = -0.47$, $P < 0.05$), high total suspended solids (TSS; $r = -0.60$, $P < 0.01$) and high chlorophyll *a* (Chl *a*; $r = -0.37$, $P < 0.05$) levels. Both TSS and Chl *a*, influenced by sediment resuspension, were non-linearly related to water level, whereas Chl *a* additionally showed strong temperature dependence, especially at low water levels (Fig. 2). The biomass of both main groups of phytoplankton—diatoms ($r = -0.50$, $P < 0.01$) and cyanobacteria ($r = -0.46$, $P < 0.05$)—as well as total phytoplankton biomass ($r = -0.52$, $P < 0.01$) increased significantly with decreasing water level. Despite extensive management efforts to reduce nutrient loading, Secchi depth decreased and Chl *a*, total phytoplankton biomass as well as the biomasses of cyanobacteria and diatoms increased (Fig. 1b, f), which is indicative of an ongoing deterioration of the ecological state of the lake.

Lake Võrtsjärv, Estonia

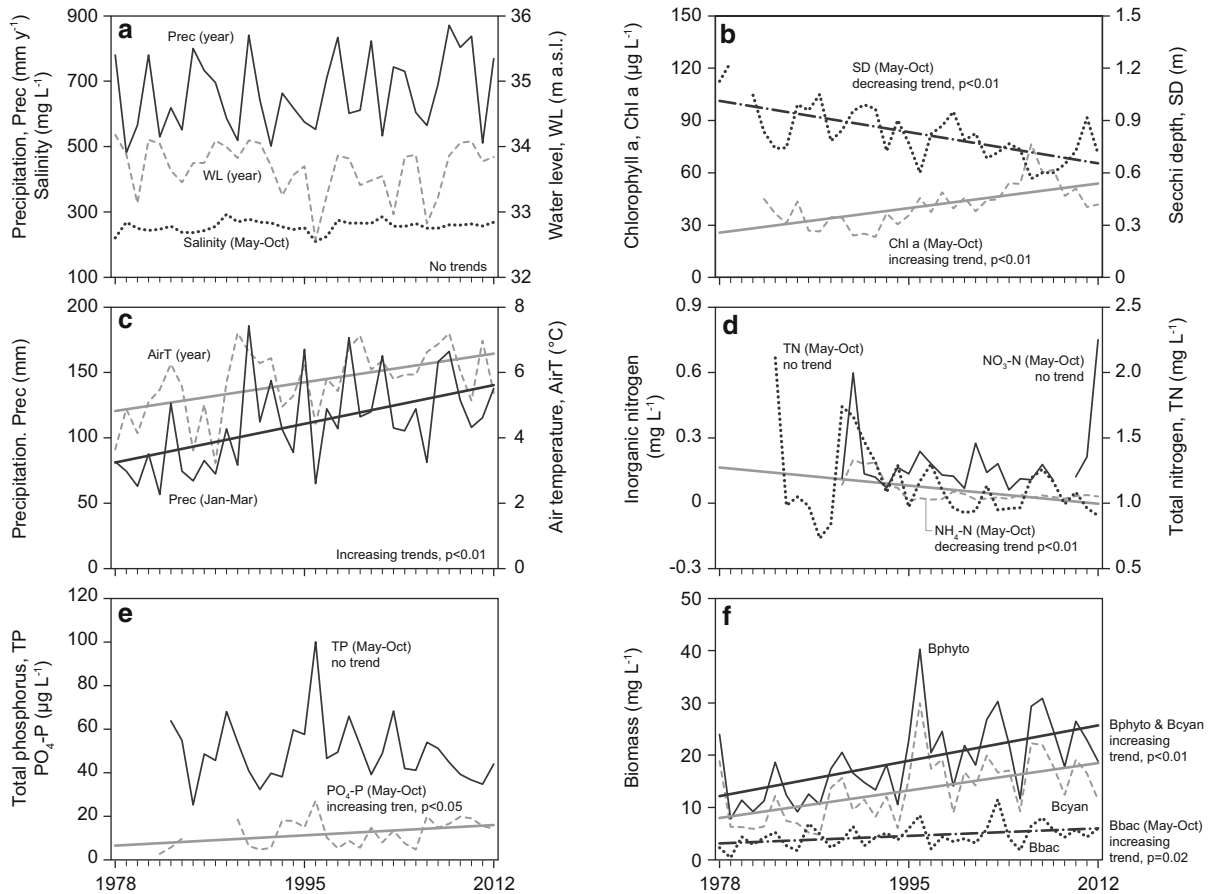


Fig. 1 Temporal changes and trends in 1978–2012 of **a** annual precipitation, annual mean water level and mean salinity in the ice-free period May–Oct, **b** mean Secchi depth and chlorophyll *a* in May–Oct, **c** annual mean air temperature and precipitation in Jan–March, **d** mean nitrate (NO_3) and ammonium (NH_4) and

total N concentrations in May–Oct, **e** mean phosphate (PO_4) and total P concentrations in May–Oct, **f** mean total phytoplankton (Bphyto), blue-green (Bcyan) and diatom (Bbac) biomasses in May–Oct in Lake Võrtsjärv

Lake Doirani: drought and water abstraction responsible for a major increase in conductivity

Air temperature and precipitation did not show any significant trends for the period 1961–2001. Annual precipitation fluctuated from 392 to 817 mm (mean 612 mm). From 1987 to 2001, the water level decreased by almost 4.3 m (Fig. 3a, b). Myronidis et al. (2012) demonstrated that the water level of the lake was strongly affected by the major drought events during the period 1985–2002. However, they also noted that drought could not be the only driver responsible for the reduced water level. It is likely that water abstraction for irrigation contributed to the

decline. The annual water abstraction for irrigation and water supply has been estimated to 4.8×10^6 and $0.2 \times 10^6 \text{ m}^3$, respectively (Nikolaidis et al., 2002).

Conductivity and chloride concentrations increased drastically from 0.49 mS cm^{-1} and 0.6 meq l^{-1} to 1.24 mS cm^{-1} and 2.4 meq l^{-1} , respectively, and showed a significant correlation with the water level reduction ($r^2 = 0.9$ and 0.91 , respectively, $P < 0.001$) (Fig. 3c). At the same time, the lake showed strong signs of eutrophication. Temponeras et al. (2000) recorded high concentrations of orthophosphate during the summer of 1996–1997 (max. $90 \mu\text{g l}^{-1}$), while TP ranged from 60 to $140 \mu\text{g l}^{-1}$ with a summer average of $103 \mu\text{g l}^{-1}$ (Fig. 3e). Petaloti et al. (2004)

Lake Võrtsjärv, Estonia

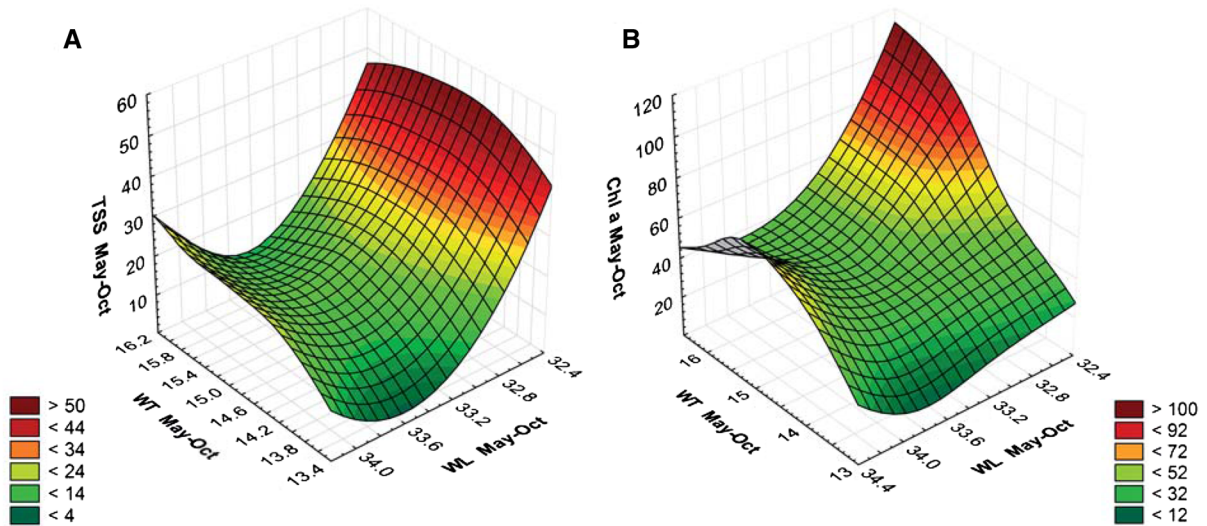


Fig. 2 3D surface plots of the May–October mean values of **A** suspended solids (TSS, mg l⁻¹) and **B** chlorophyll *a* (Chl *a*) against water temperature (WT, °C) and water level (WL, m.a.s.l.) (all May–Oct) in Lake Võrtsjärv in 1978–2012. TSS

and Chl *a* are non-linearly related to water level, whereas Chl *a* additionally shows strong temperature dependence at low water levels <33.3 m a.s.l. ($r = 0.92$, $P = 0.027$)

recorded high concentrations of TN, varying from 1.25 to 3.08 mg l⁻¹. During 1996–1997, total phytoplankton biomass reached a summer average of 20 mg l⁻¹ and was dominated by cyanobacteria (*Snowella lacustris*) (Cooke et al., 2005; Vardaka et al., 2005). More recently, Ioakimidou (2010) observed that cyanobacteria dominated the phytoplankton community of the lake, accounting for more than 86% of total abundance. Since 1996, toxic cyanobacteria blooms have commonly been recorded during summer (August). Due to cyanobacteria dominance and a low zooplankton:phytoplankton ratio, the ecological quality of the lake has been classified as poor.

Lake Vegoritis: dramatic reduction in water level due to abstraction with strong ecological implications

Analysis of precipitation and air temperature data local to Lake Vegoritis did not reveal any significant trends. For the period 1961–2003, the annual precipitation ranged from 329 to 994 mm with an average value of 654 mm (Fig. 4a). The potential evapotranspiration during the same period ranged from 687 to 797 mm with an average value of 736 (Fig. 4b), resulting in a negative hydrological balance.

The decline in water level began in 1956 due to water abstraction from a nearby power plant. However, the water level continued to decline even after the cessation of water abstraction in 1985 (Fig. 4b). From 1972 to 2011, the lake's surface area declined by approximately 32%, while the area used for agriculture in the surrounding area increased by almost 200%.

The expansion of agriculture is likely to have intensified irrigation and therefore water abstraction from the lake, causing a further reduction of the water level. From 1983 to 2001, conductivity rose from an annual average of 0.50–0.61 mS cm⁻¹, which correlated significantly with the water level decline ($r^2 = 0.73$, $P < 0.05$; Fig. 4c). Other physico-chemical parameters such as pH and dissolved oxygen did not show any clear trends (Fig. 4d). TP and nitrate concentrations also did not appear to follow any specific trend, although TP was notably higher in 2006 and 2007 with an average of 161 and 118 µg l⁻¹ (Fig. 4e). During this period, charophytes disappeared from the lake and *Potamogeton pectinatus* increased in abundance (Stefanidis & Papastergiadou, 2010). Between 1987 and 1988, charophytes occurred in 33% of the sampling plots, while *Potamogeton pectinatus* and *Myriophyllum spicatum* were found in 38 and 52% of the total sampling plots, respectively

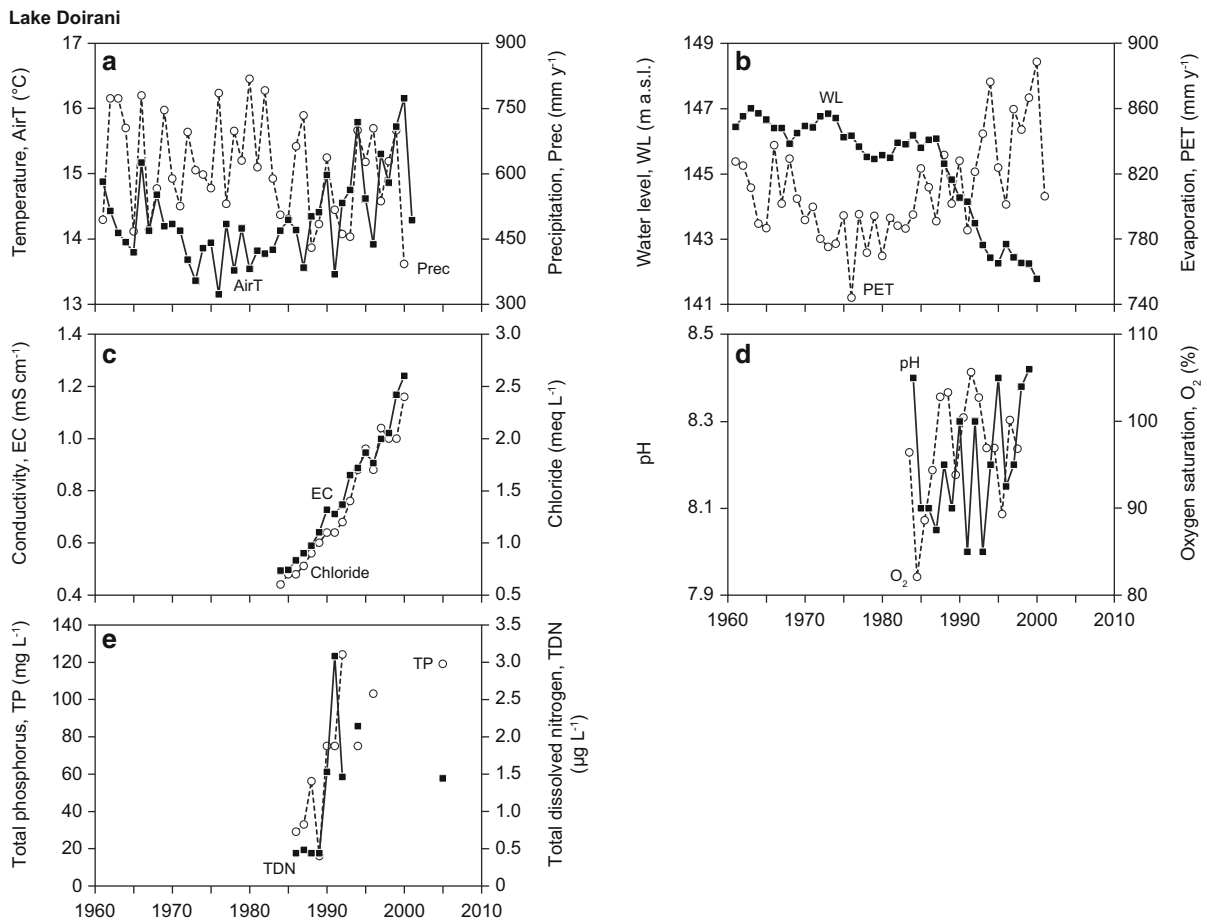


Fig. 3 Temporal changes in **a** annual mean air temperature and precipitation, **b** annual mean water level and potential evapotranspiration, **c** annual mean conductivity and chloride

concentration, **d** annual mean pH and oxygen saturation and **e** annual mean total dissolved nitrate and summer mean total phosphorus concentrations in Lake Doirani

(Papastergiadou & Babalonas, 1993). Almost 20 years later, charophytes were absent from all macrophyte samples between 2006 and 2008, while the relative frequency of *P. pectinatus* and *M. spicatum* increased to 59 and 67%, respectively (Stefanidis & Papastergiadou, 2013). Long-term fisheries data have shown an increasing abundance of cyprinids (roach, *Rutilus rutilus*, and carp, *Cyprinus carpio*) (Fig. 4f), while at the same time European whitefish (*Coregonus lavaretus*) declined and eventually disappeared from the lake between the late 1990s and early 2000s (Stefanidis & Papastergiadou, 2013).

Overall, it appears that the long-term water level reduction has significantly influenced the biotic and several abiotic variables. The lake has become shallower, and reed beds have expanded across the littoral

zone. Nutrient-tolerant angiosperms have replaced the charophytes, and cyprinids appear to be the dominant fish species.

Lake Eymir: large variations in ecological state due to alterations in water level and biomanipulation

The water level has fluctuated with an amplitude of 1.5 m in response to changes in precipitation and evaporation regimes following drought and wet periods (Fig. 5a). Salinity and conductivity changed as a result of the altered water levels and increased from 1.04‰ and 1.93 mS cm⁻¹ to 1.94‰ and 3.33 mS cm⁻¹, respectively, as the water level declined from 5.1 to 3.8 m (Fig. 5b). Furthermore, over the study period (1993–2010), the water

Lake Vegoritis

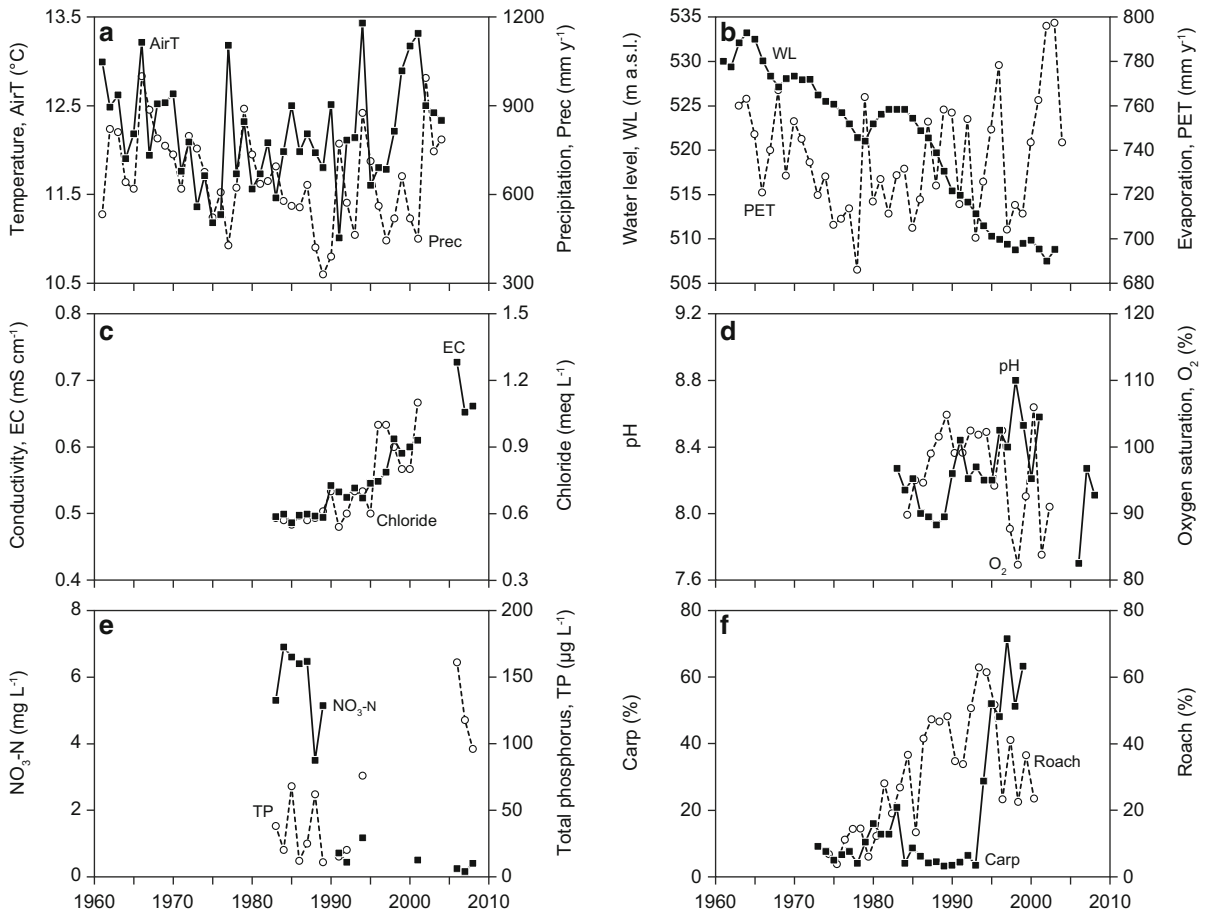


Fig. 4 Temporal changes in **a** annual mean air temperature and total precipitation, **b** annual mean water level and total potential evapotranspiration, **c** annual mean conductivity and chloride

concentration, **d** annual mean pH and oxygen saturation, **e** annual mean nitrate and total phosphorus concentrations and **f** proportional annual carp and roach harvests in Lake Vegoritis

temperature increased by $>1^{\circ}\text{C}$, and dissolved oxygen concentrations decreased during the warmer, drier periods and increased more recently during the cooler period (2009–2010) (Fig. 5c).

The lake received raw sewage effluents for more than 25 years (Altınbilek et al., 1995) until sewage effluent was diverted in 1995, leading to 88 and 95% reductions in the loading of TP and dissolved inorganic nitrogen (DIN), respectively (Beklioğlu et al., 2003). Following sewage effluent reduction, fish stock biomanipulation was undertaken to reinforce recovery by removing the dominant fish, tench (*Tinca tinca*) and common carp, in 1998 and 1999. This biomanipulation, undertaken in hydrologically wet years, resulted in a twofold decrease in

chlorophyll *a* concentrations and a fourfold increase in annual Secchi depth (Fig. 5d) (Beklioğlu & Tan, 2008). Submerged macrophyte coverage was low before biomanipulation (2.5%), but it subsequently increased (40–90% coverage) (Fig. 5e) and was particularly high in the dry year 2001. However, 5 years after the biomanipulation, with the onset of a series of low-rainfall years, the water level dropped significantly (>1.3 m), and the lake lost one third of its volume. The water quality deteriorated with the increases in lake TP and DIN concentrations, despite the low external loading as a result of internal mechanisms (Özen et al., 2010; Fig. 5f, g). The prolonged drought period increased the hydraulic retention time from 0.6 to 12 y^{-1} (Beklioğlu & Tan,

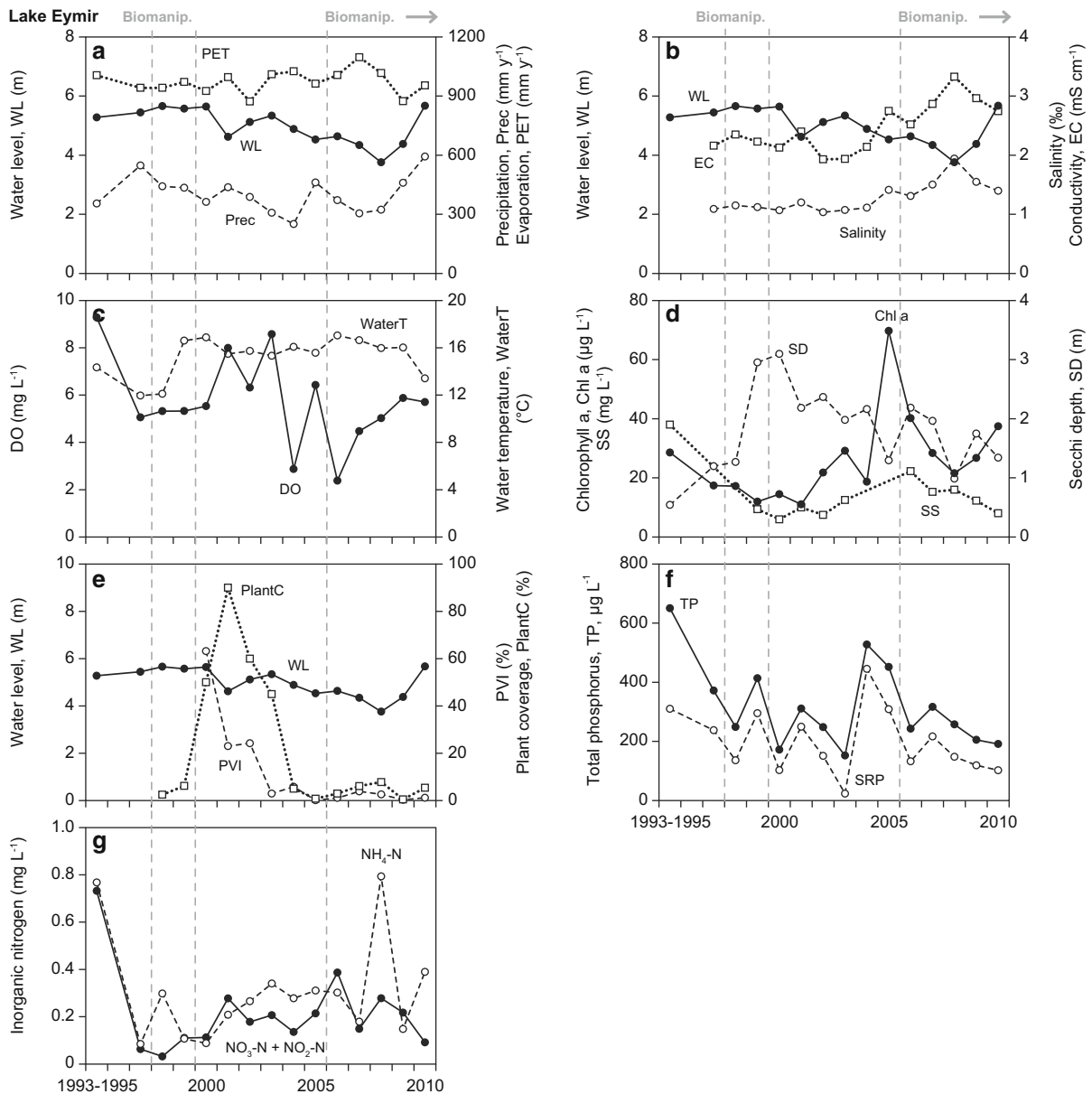


Fig. 5 Temporal changes in **a** annual precipitation, evaporation and water level, **b** annual mean water level, conductivity and salinity, **c** mean annual water temperature and dissolved oxygen concentration, **d** annual chlorophyll *a* (Chl-*a*) and suspended solid (SS) concentrations and Secchi depth, **e** annual mean water

level, plant coverage and percent plant volume inhabited, **f** annual mean concentrations of percent total phosphorus and soluble reactive phosphate (SRP), **g** mean annual values ammonium ($\text{NH}_4\text{-N}$), nitrite and nitrate ($\text{NO}_2\text{-N} + \text{NO}_3\text{-N}$) in Lake Eymir 1993 and 2010

2008). Meanwhile, the fish biomass increased again to the pre-manipulation level, and in 2004 the lake shifted back to a turbid state with scarce submerged vegetation cover (Fig. 5e) and higher biomass for both tench and carp and lower pike (*Esox lucius*) biomass (Bekliöglü & Tan, 2008). Biomaniipulation was

undertaken again in 2006 and led to improved lake water quality, with a twofold decrease in chlorophyll *a* and a 50% increase in annual Secchi depth (Fig. 5d). The water level rose again in 2009 in response to hydrologically wet years, and the water quality improved even further. Salinity and conductivity

declined to regular levels (Fig. 5b), but no recovery of macrophytes occurred as the water level was probably too high (Fig. 5e) (Beklioglu et al., 2011).

Lake Biviere di Gela: shift from clear to turbid with reduction in water level

Analysis of annual precipitation for the period 1968–2008 showed no significant trend (Fig. 6a). Conversely, a significant increasing trend in average air temperature occurred, accompanied by increased evapotranspiration in the catchment (Fig. 6b), resulting in a negative hydrological balance (Barone et al., 2010).

During the 1980s, the lake water level fluctuated around the maximum depth (Table 1), but water level fluctuations did not exceed 1 m. In the subsequent years, inflows from surface runoff and groundwater rapidly decreased due to the intensification of the agricultural water demand in the surrounding area. The lake level decreased, and by the end of the 1990s it ranged between 1.2 and 1.5 m (Fig. 6a). Conductivity increased (Fig. 6a), probably as a result of lowering of the groundwater outflow, favouring sea water intrusion, and due to higher evaporation. Secchi transparency decreased, whereas TP and Chl *a* concentrations increased (Fig. 6c), as did dissolved nutrients (Fig. 6d). Accordingly, the phytoplankton assemblage changed significantly. Higher phytoplankton biomass values were progressively recorded, and a shift occurred from dominance by cryptophytes and diatoms in winter and euglenophytes and dinoflagellates in summer during the 1980s to dominance by green algae (*Tetraselmis cordiformis*) in winter and cyanobacteria (*Microcystis* spp.) in summer from the mid-1990s to 2004 (Fig. 6e). The submerged macrophyte beds also disappeared.

As this Ramsar site was highly threatened, an artificial canal downstream of a freshwater dam reservoir (Lake Dirillo) was built in 2004 to restore the water level of the lake and to ensure lake refilling. This was followed by a lowering of conductivity, but there was no subsequent re-establishment of the macrophytes, and the lake remained turbid (Fig. 6c). In addition, the phytoplankton composition underwent further changes with winter blooms of the toxin-producing haptophyte *Prymnesium parvum*, alternating with summer blooms of *Cylindrospermopsis raciborskii* and *Chrysochloris ovalisporum*, which have persisted since. This shift in the phytoplankton

assemblage coincided with the disappearance of crustacean zooplankton (Barone et al., 2010), which were formerly dominated by the calanoid copepod *Calanipeda aquaedulcis*.

Lake Kinneret: water level fluctuations beyond natural associated with declining ecosystem stability

Over the last 3–4 decades the lake has been managed to maximise its storage capacity. In low-rainfall years, water abstraction exceeded the rate of renewal, leading to declining water levels, between 1994 and 2001 and again during the period 2005–2009. The continued abstraction was to ensure a continuous water supply, while at the same time anticipating an expansion of the capacity for water storage during the high-rainfall years. This policy, as well as a series of drought years, resulted in the water levels shown by the long-term record in Fig. 7a. This record exhibits much greater fluctuations in water levels since the early 1990s compared to those in the 1970s and 1980s, and certainly greater than the natural fluctuations of about 1.5 m. The salinity of the lake, expressed as the concentration of chloride (Fig. 7a), and the conductivity (data not shown) both have inverse relationships with water level. Low inflows caused both water level declines and increases in salinity, and vice versa for high inflows. Annual precipitation over the Lake Kinneret region, averaging 400 mm, was highly variable but did not show a significant trend over the last 40 years, whereas the water temperature of the upper 0–10 m layer has increased over the same period by about 1°C (Fig. 7b).

Annual nutrient loads were highly variable but did not exhibit a long-term trend (Fig. 7c). In particular, the exceptionally high-rainfall winters of 1991–1992 and 2002–2003 were characterised by exceptional rises in water levels (4 and 4.7 m, respectively) and in TN and TP loads. The last substantial rise in water level occurred over two winters: 2011–2012 and 2012–2013 (Fig. 7a).

In-lake nitrate and ammonium concentrations did not show a long-term trend, whereas the annual mean total dissolved phosphorus declined (Fig. 7d). In-lake nitrate concentrations closely followed the TN load, with a pattern of increased amplitude of fluctuations since 1992. Annual mean Secchi depth, total primary production and depth-integrated Chl *a* (Fig. 7e, f) showed no long-term trend, although for Chl *a* greater

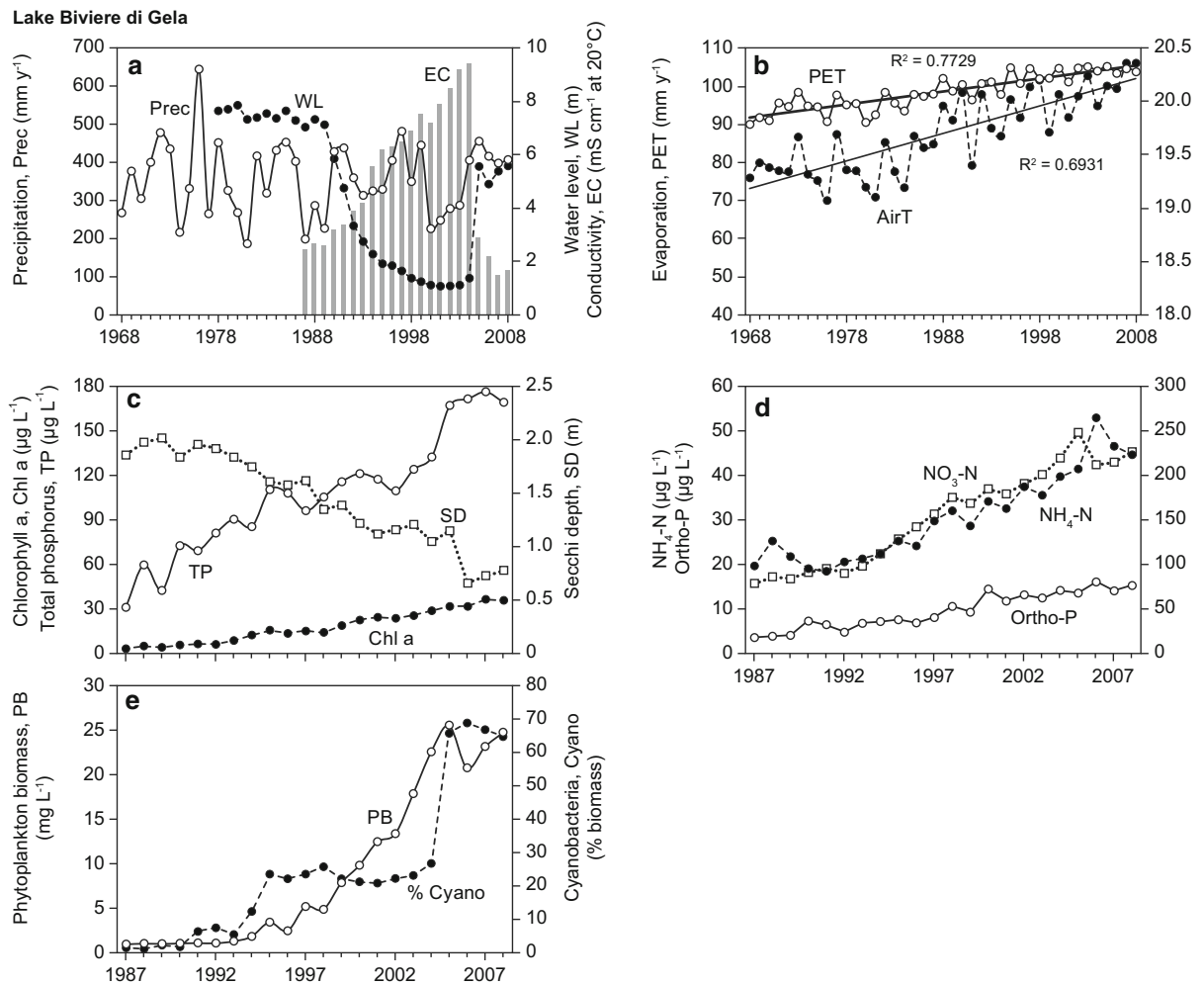


Fig. 6 Temporal trends in **a** annual precipitation, summer water levels (WL) and conductivity, **b** annual mean air temperature and evapotranspiration, annual mean water level and total potential evapotranspiration, **c** annual mean values of chlorophyll *a* (Chl-*a*), total phosphorus and Secchi depth,

d annual means of ammonium-nitrogen (NH₄-N), nitrate-nitrogen (NO₃-N) and reactive phosphorus (ortho-P), **e** annual mean phytoplankton biomass and percentage of cyanobacteria in Lake Biviere di Gela

amplitude of annual values was evident from the mid-1990s onwards.

The most striking long-term changes in the lake were observed in the temporal dynamics of the phytoplankton. From 1970 until 1993, the dinoflagellate *Peridinium gatunense* bloomed every spring and its mean depth-integrated biomass for January–June ranged between 60 and 120 g m⁻² (Fig. 7g). However, from 1994 onwards, it bloomed in only 7 out of 19 years and, when blooming, the biomass was considerably higher than in the previous period, i.e. the amplitude of fluctuations in mean biomass

increased. Similarly, cyanobacteria bloomed occasionally in the summers between 1975 and 1985 and then disappeared completely from the summer plankton. However, since the mid-1990s there has been a bloom every summer (Fig. 7g). Lastly, the annual mean abundance of zooplankton showed major fluctuations over time, but no clear long-term trend (Fig. 7h).

Berman et al. (1995) concluded that the lake showed remarkable stability from 1970 to 1993 despite considerable environmental changes, population growth and intense economic development. Later

Lake Kinneret

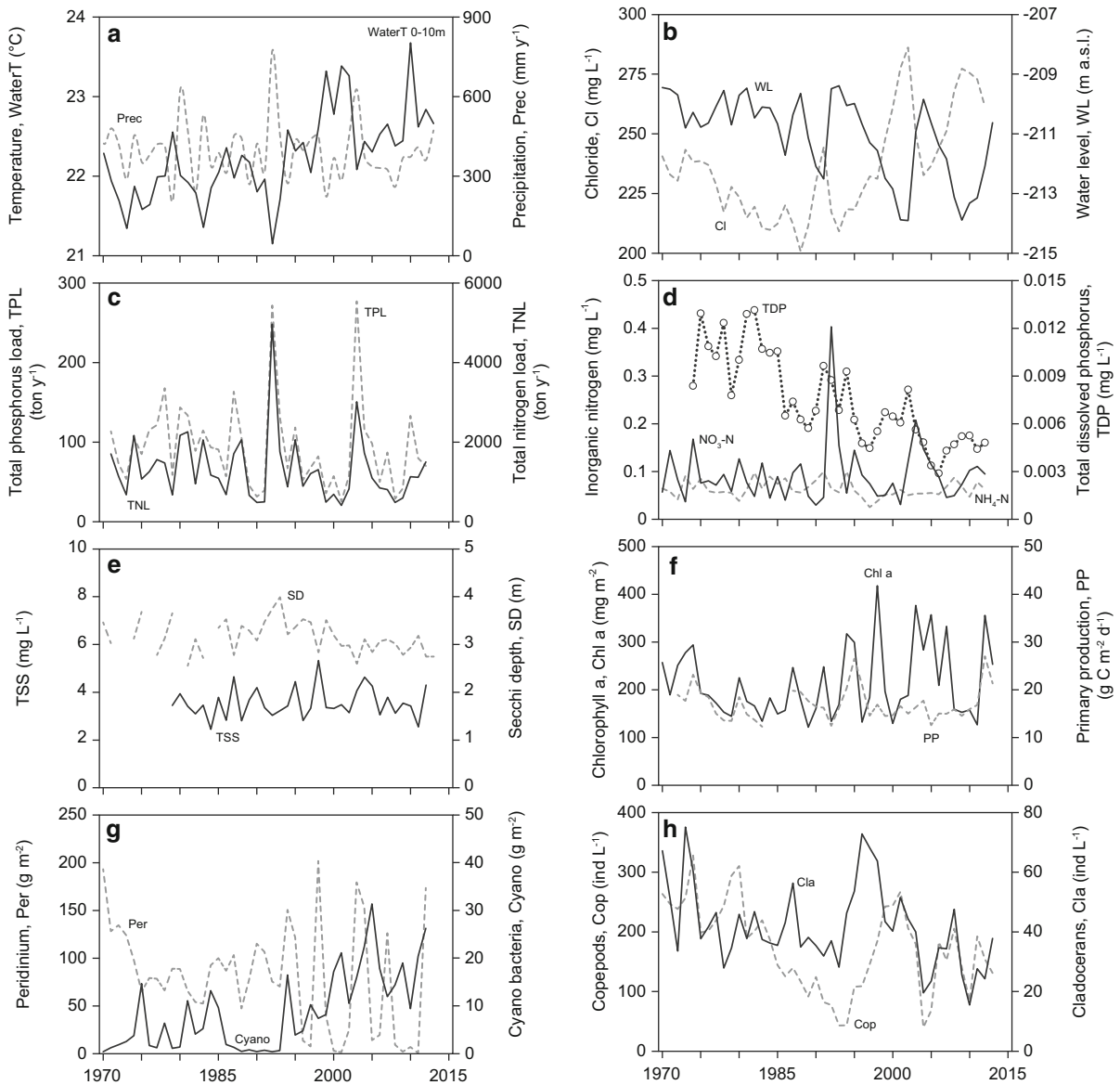


Fig. 7 Temporal changes in annual mean values of a series of limnological variables from Lake Kinneret 1970–2013, based on weekly measurements. Values of in-lake parameters are means for the upper 0–10 m layer unless stated otherwise. **a** Water temperature and annual (hydrological year) precipitation, **b** water level and chloride concentration, **c** annual riverine loads of total phosphorus and total nitrogen, **d** in-lake nutrient concentrations: nitrate, ammonium and total dissolved P, **e** in-lake total suspended solids and Secchi depth, **f** depth-integrated (0–15 m) Chl *a*, primary production, **g** phytoplankton: mean depth-integrated wet weight biomass

of the dinoflagellate *Peridinium gatunense* for Jan–Jun and of total cyanobacteria for Jul–Dec, **h** zooplankton abundance: copepods and cladocerans. *Data sources* Hydrological Service of Israel (water level); Israel Meteorological Services (precipitation); Mekorot Water Company (nutrient loads, chemical analyses); Kinneret Limnological Laboratory monitoring programme (other variables: water temperature—courtesy of A Rimmer, nutrients—courtesy of A Nishri, zooplankton—courtesy of G Gal; Chlorophyll and primary production—courtesy of YZ Yacobi, phytoplankton—T Zohary)

studies, based on longer records (Zohary, 2004; Roelke et al., 2007), have concluded that the lake has become considerably less stable since the mid-1990s, following a 4 m rise in water level over a single winter (1991–1992) recorded for the first time. Not only did *Peridinium* fail to bloom every year and cyanobacteria became dominant in summer, but the summer assemblage also changed, with filamentous morphotypes becoming dominant as opposed to the nanoplanktonic unicells and coenobia that dominated in the past. Phytoplankton species diversity also declined and several alien species invaded the lake and assumed dominance (Zohary et al., 2014b).

The zooplankton also exhibited a shift in the mid-1990s (Gal & Anderson, 2010). Copepod abundance declined to very low levels in 1993 after which it recovered but then declined again in 2004. These sudden shifts were attributed to population explosions of bleak (*Mirrogrex terraesanctae*), the major zooplanktivorous fish in the lake. This was associated with the exceptional water level rises in the winter of 1991–1992 and again in 2002–2003 (Fig. 8), resulting in exceptional reproductive success of bleak (Zohary & Ostrovsky, 2011). The two biggest blooms of cyanobacteria recorded in Lake Kinneret occurred a year after the zooplankton decline, following the bleak population explosion and water level increase. While the mechanism explaining the blooms is not evident, it is likely that these phenomena are linked, leading to the series of events described in Fig. 8.

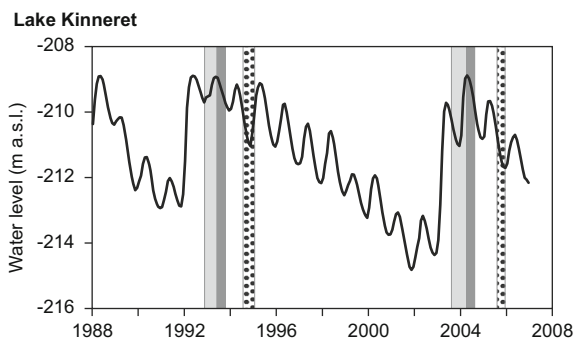


Fig. 8 Long-term changes in daily water levels in Lake Kinneret (black line data courtesy of A Givati, Hydrological Service of Israel). Bars indicate the timing of major biological response events that followed steep water level rises in winter 1991–1992 (4 m rise) and again in winter 2002–2003 (4.7 m rise). Light grey bars bleak population explosion events due to exceptional reproduction success; dark grey bars zooplankton biomass crash events; dotted bars events of highest recorded summer blooms of N-fixing cyanobacteria

Lake Cruzeta: sediment resuspension leads to lower phytoplankton biomass at low water level

Man-made lakes in warm semi-arid north-eastern Brazil show seasonal variations in water volume and increasing concentrations of nutrients and Chl *a* with decreasing water level (Attayde, personal communication). However, below a critical threshold of water volume, the high levels of abiotic turbidity, caused by sediment resuspension by wind and fish, may inhibit phytoplankton growth, leading to a reduction in both Chl *a* and TP concentrations. This is shown by data from Lake Cruzeta where the water volume dropped from $21.7 \times 10^6 \text{ m}^3$ after the rainy season of 2007 to $8.4 \times 10^6 \text{ m}^3$ before the rainy season of 2008 (Fig. 9a). During this period, mean depth remained relatively constant, but Secchi depth decreased, while suspended solids increased (Fig. 9b). Data on the organic and inorganic fractions of suspended solids indicate that in December 2007, when the lake volume reached 25% of its maximum capacity, the major source of turbidity shifted from biogenic to abiotic (Fig. 9c). This was caused by a collapse of phytoplankton biomass due to high levels of suspended sediments, leading to a decrease in both Chl *a* and TP (Fig. 9d). In tropical and sub-tropical lakes, the phytoplankton often constitutes a major component of the TP in the water column.

Literature overview

The reviewed case studies mainly focused on lakes and reservoirs situated in temperate (49 lakes and 15 reservoirs) and continental climate zones (23 lakes and 2 reservoirs). Eight studies centred on arid/semi-arid climate zones (6 lakes and 2 reservoirs), 12 on tropical climate zones (6 lakes and 6 reservoirs) and one on the polar climate zone. Furthermore, nine case studies are based on mesocosm experiments dealing with changes in water level or salinity, of which most came from the temperate climate zones (6 studies) and zones with a cold semi-dry climate (Table S2).

The literature review (Table S3), although not exhaustive, indicates that a water level reduction often results in higher TP concentrations, higher phytoplankton biomass and lower water transparency either in shallow and deep lakes or in shallow and deep reservoirs. Likewise, a water level increase often leads to a reduction of TP and phytoplankton biomass

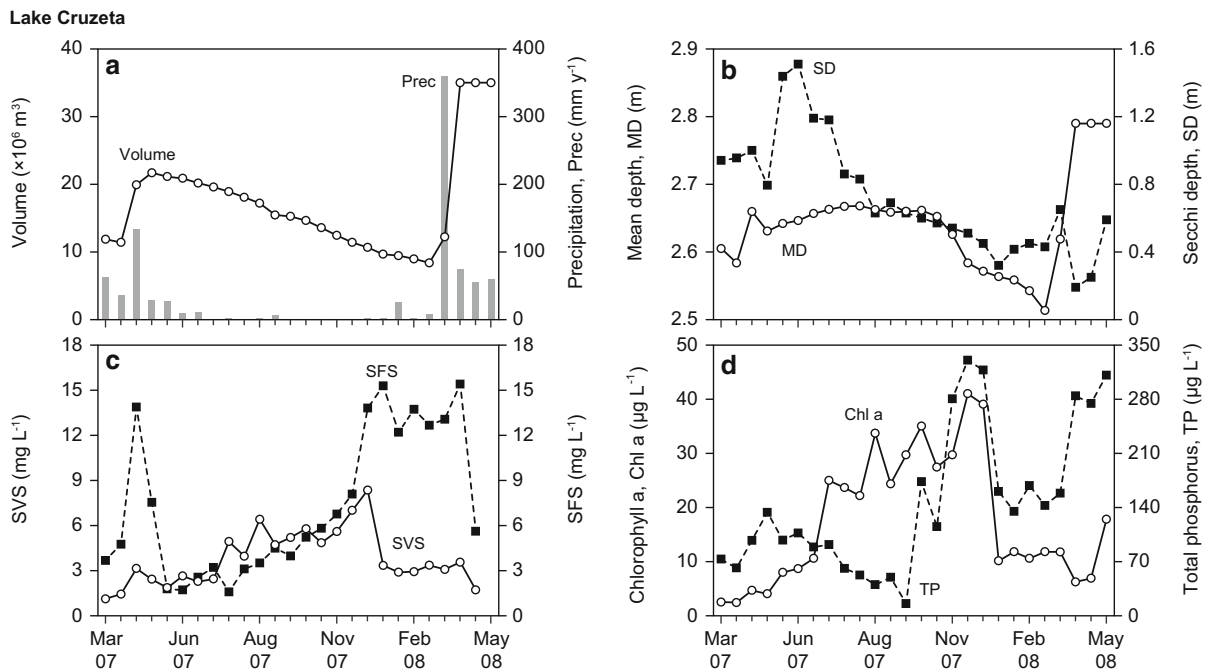


Fig. 9 Temporal changes in **a** precipitation and lake volume, **b** mean depth, Secchi depth, **c** suspended volatile (SVS) and fixed (SFS) solids, **d** Chlorophyll *a* and total phosphorus concentrations in Lake Cruzeta from March 2007 to May 2008

through dilution and improved flushing. The majority of studies on shallow lakes also revealed that a reduced water level can result in an increase in macrophyte coverage, although the reverse pattern also occurs, especially in deep lakes and deep reservoirs. The effects on zooplankton and fish are less straightforward and require further research, but effects of water level on fish reproduction and spawning have been reported in several studies.

The overview achieved from the literature review indicates that changes in salinity due to climate warming can markedly alter the community composition of phytoplankton, zooplankton, macrophytes and fish and often lead to a decrease in the biomass and diversity of each of these organism groups. Several studies have shown effects of increasing salinity on zooplankton and macroinvertebrate diversity, the effects on macrophytes and fish being less studied.

Most of the reviewed literature focused on the effects of increased salinity produced by a water level decrease and increased evapotranspiration, but some studies assessed the consequences of increased salinity caused by intrusion of sea water into freshwater coastal lakes (Schallenberg et al., 2003; Flöder &

Burns, 2004), a phenomenon that may be aggravated as a result of sea level rise.

Discussion

Effects of changes in hydrology, external loading and water level on nutrients

The case studies all demonstrate changes in hydrology and water level though the reasons behind these vary among sites. In some cases, the changes can be attributed mainly to changes in net precipitation (Lakes Vörtstjärv, Eymir, Cruzeta). In others, hydrological loading was additionally influenced by enhanced water abstraction (Lakes Doirani, Vegoritis, Eymir, Biviere di Gela) with drastic effects on water level (Figs. 3, 4, 5), not least in the Greek lakes. In Lake Kinneret, however, the key feature was a much greater variability in hydrological loading and water level in recent decades compared with the past, which is attributed to a combination of declining inflow volumes and management of abstraction to maximise the lake's storage capacity (Fig. 8).

The effects of changes in hydrological loading on external nutrient loading are likely to vary. In Lakes Eymir, Kinneret and Vörtsjärv, nutrient loading decreased substantially in dry years. In these lakes, nutrient loading was not dominated by sewage. If sewage is a dominant nutrient source, reduced hydrological loading may have less or no effect on the external nutrient loading as the sewage will be concentrated in less water (Elliott et al., 2009). Moreover, higher climate variability may lead to sporadically extreme nutrient loading, for example as a result of extensive erosion and flooding events.

Results from Lakes Eymir and Vörtsjärv, however, clearly demonstrate that even if the external loading decreased in warm years, following reduced hydraulic loading, nutrient concentrations increased due to higher evapotranspiration, higher internal loading and, perhaps, reduced nitrification under low-oxygen conditions (Jeppesen et al., 2009; Özen et al., 2010; Jeppesen et al., 2011) and increased resuspension. Thus, global climate change is predicted to reduce the nutrient retention capacity in Lake Eymir and other shallow lakes in the Mediterranean region and thereby further exacerbates eutrophication (Özen et al., 2010). In temperate shallow Lake Vörtsjärv, nitrogen and phosphorus retention was differently affected by low water level conditions, while large amounts of resuspended TP left the lake through the outflow, nitrogen retention improved as a result of enhanced denitrification (Nöges et al., 1998).

Furthermore, with declining water levels, internal nutrient cycling increases as sublittoral strata, too deep to be impacted by internal waves at high water levels, become subjected to resuspension due to boundary mixing and seiche activity. Under extreme water level declines, the thermal regime of lakes can change dramatically whereby monomictic lakes become polymictic, with nutrients being available to the biota throughout the summer, a condition that enhances cyanobacteria abundance (Zohary & Ostrovsky, 2011; Romo et al., 2013). An example is Lake Arancio in Sicily where a drawdown of 15 m in summer 2001 caused a collapse of the thermocline, full mixing and an immediate bloom of *Microcystis* (Naselli-Flores & Barone, 2005). However, there are also examples of reduced phytoplankton biomass at low water level, such as in Lake Cruzeta, where high abiotic turbidity due to wind and/or fish-induced sediment resuspension led to a major reduction in both Chl *a* and TP.

Effects of changes in water level on biota

Macrophytes are a key structuring component of shallow lakes. The effects of water level reduction on macrophytes are, however, ambiguous (Table S3) and may be driven by local conditions, such as the local pool of available plant species or the morphometry of the basin (Naselli-Flores & Barone, 2012). In Lake Biviere di Gela, the reduced inflow led to a considerable depth decrease and shifted the lake from a clear, macrophyte-dominated state to a turbid, phytoplankton-dominated state. The re-establishment of a higher water level was not sufficient to restore the former macrophyte assemblages in the lake. Conversely, it may have caused a further decrease in water quality by favouring the establishment of phytoplankton assemblages dominated by toxin-producing organisms all year round. In other case studies, macrophytes have benefitted from a reduction in water level, although this is likely to depend on the morphometry of the basin. In such cases, the vulnerability of macrophytes to turbidity may increase during high water level periods due to reduced light penetration at the lake bottom, whereas low water levels during summer may enhance macrophyte growth, as has been seen in different geographical locations (Blindow, 1992; Engel & Nichols, 1994; Gafny & Gasith, 1999; Mazzeo et al., 2003; Havens et al., 2004; Beklioğlu et al., 2006; Tan & Beklioğlu, 2006). Accordingly, long-term studies of Lakes Beyşehir, Uluabat and Marmara in Turkey (Beklioğlu et al., 2006; Jeppesen et al., 2014) have shown high abundance of submerged macrophytes in periods with low water level and low or no plant coverage during high water level periods (Beklioğlu et al., 2006). Furthermore, higher shade tolerance may benefit the plants in warm lakes, a hypothesis supported by a study of 83 lakes in South America covering a lengthy latitudinal gradient. Here, macrophyte colonisation was more extensive in warm than in intermediate and cooler regions at comparable light regimes (Kosten et al., 2011). Another example is the dominance of nymphaeids (*Nymphaea alba*, *Nymphoides peltata*) in Lake Kerkini in Greece after dam construction and the consequent large fluctuations of water level during the growing season. The anthropogenically driven water level fluctuations (over 5 m in <4 months each year) for irrigation purposes have eliminated reed bed communities as well as the sedges and grasses in the wet meadows in

this lake. There, the nymphaeids appear to have adapted to the large (several metres) annual water level fluctuations by developing a terrestrial form helping them to survive during droughts and extending their stalks to the water surface during floods (Papastergiadou & Babalonas, 1992).

Two recent mesocosm studies undertaken in warm Turkish shallow lakes located in a semi-arid dry climate with major water level fluctuations (Özkan et al., 2010; Bucak et al., 2012) have shown greater resistance by macrophytes to nutrient loading owing to major water level reduction than expected from studies of northern temperate lakes. A mesocosm experiment conducted in eutrophic Lake Eymir with two water depths, 0.8 m and 1.6 m, showed that the strongest macrophyte growth occurred in the low water level fishless mesocosms (Bucak et al., 2012). However, despite high nutrient concentrations and low water clarity, macrophytes were also abundant in the fish mesocosms and abundance increased further following a water level decrease from midsummer onwards. Macrophyte growth was poor in the high water level mesocosms, even in the fishless mesocosms with high water clarity. This was ascribed to extensive periphyton development reducing the light availability for the macrophytes. Likewise, a nutrient loading mesocosm experiment by Özkan et al. (2010) revealed no effect of nutrient loading on macrophyte biomass despite a much higher periphyton biomass characterising the high TN and TP mesocosms. A 30-cm water level decline in the 1 m deep mesocosms apparently allowed enough light for macrophytes to grow and overcome the effects of nutrient enrichment in shallow waters. Thus, the beneficial effect of declining water level for macrophytes as summer progressed compensated for the negative effect of low clarity. However, it must be emphasised that experimental mesocosms are protected from wave and wind disturbance, both of which are typically stronger in shallow areas in wind-exposed lakes and may have detrimental effects on macrophytes in shallow waters. On the other hand, a reduced water level may enhance the coverage of emergent plants, exemplified by the expansion of reed beds in the littoral zone of Lake Vegorit. Furthermore, there can be a shift in the community structure of macrophytes from short-growing charophytes and turbidity-intolerant species to tall-growing angiosperms (Havens et al., 2007). This was the

case in Lake Vegorit where turbidity-tolerant angiosperms replaced the charophytes. Expansion of reed beds and emergent vegetation at the expense of submerged hydrophytes also occurred in the Greek shallow lakes Stymfalia and Cheimaditida (Papastergiadou et al., 2007, 2008). Here, the combined effects of lower water table and increased nutrient loading appear to have led to colonisation of open water areas by dense reed beds, primarily monospecific stands of helophytes such as *Phragmites australis* and *Typha angustifolia*.

Furthermore, a low water level may enhance winter freezing of former littoral zones, leading to reduced coverage in the following season if a lake has a sloping V-shaped basin, whereas a low water level in U-shaped lakes may prompt macrophyte development (Beklioglu et al., 2006).

While macrophytes may benefit from a water level reduction, the overriding impression from the case studies and the literature review is that lakes typically become more eutrophic with a warming-induced water level reduction, involving a higher risk of cyanobacteria blooms (e.g. *Microcystis* spp., *Cylindrospermopsis raciborskii*, *Chrysochloris ovalisporum*, *Dolichospermum* spp.). This appears to be the case for Lake Doirani where cyanobacteria blooms have become common during the last few years.

Changes in water level may also have strong implications for the fish community; low water levels may not only lead to higher temperature, but may also destabilise the thermocline with risk of disappearance of cold water refugia for some fish. Moreover, eutrophication following water level reduction due to climate warming may stimulate warm-water, eutrophic species. This may have contributed to the drastic reduction in coregonids and the increase in roach and carp in Lake Vegorit following a depth reduction of 32 m (current mean depth: 28 m). Fish spawning in the littoral zone may also be affected (Table S3).

In a future, warmer climate, we can also expect higher inter-annual and intra-annual variations in water level. In lakes with no macrophytes (e.g. Kinneret), vegetation growing on the exposed shores in low water level years is inundated, particularly in wet winters with substantial water level rises. For several months or even years after inundation, until the inundated vegetation gets uprooted and decomposes, this vegetation provides a ‘window of opportunity’ for

fish and invertebrates that find shelter, food and preferred spawning grounds in a habitat that does not exist at low water levels (Gafny & Gasith, 1999; Zohary & Gasith, 2014). Under these conditions, the reproduction success and fingerling survival of cichlid fish increase. A key message from the Lake Kinneret case study is the role of littoral–pelagic coupling: the changes in water levels impacted the habitats in the littoral zone (i.e. the abundant stony habitats at high water levels become sparse at low levels). This affected both bleak reproduction, as it spawns on stones in the shallow littoral zone, and the survival of the young-of-year fish that find refuge here at high water levels when ample shoreline vegetation gets inundated and provides shelter and food. Outside the spawning season, the adult bleak is a pelagic zooplanktivore. Exceptionally successful reproduction leads to a strong year class, preying heavily on the zooplankton with strong cascading effects on zooplankton and phytoplankton assemblages and biomass. The invasion and establishment of an alien snail and the collapse of the Kinneret fishery in 2008 (Heller et al., 2014; Ostrovsky et al., 2014) provide further indications of ecosystem destabilisation. With increasing water level fluctuations beyond those occurring naturally, littoral resources will diminish completely, leaving the pelagic system devoid of littoral services such as food resources, refugia (from predation) and fish spawning sites (Zohary & Ostrovsky, 2011), and negatively affect the species richness and abundance as is evident from comparative studies of lakes and reservoirs with major water level fluctuations resulting from hydroelectric dams (Naselli-Flores, 2011).

Effects of changes in salinity/conductivity

All case study lakes in the semi-arid Mediterranean region showed an increase in salinity/conductivity associated with a decline in lake water levels, increased hydraulic residence time and evaporation, except Lake Biviere di Gela where the enhanced salinity may also have resulted from a lowering of the groundwater outflow and subsequent sea water intrusion in addition to evaporation. It is difficult to disentangle the effect of increased salinity from the effects of changed water levels on the biota and the ecosystem in the case studies. However, the observed in community composition, diversity and water quality associated with the variation in water level and

salinity in the case studies concur with the findings from the literature review.

Salinity has often been reported as the most important factor driving the community composition in Mediterranean lakes (e.g. Boix et al., 2008; Çakiroglu et al., 2014; Levi et al., 2014; Table S3). For example, in Turkey, shallow lake studies including both the contemporary community and surface sediment remains of aquatic plants and Cladocera have shown that conductivity in the range from freshwater up to 14.5‰ was the most important environmental factor determining community composition (Çakiroglu et al. 2014; Levi et al., 2014). In Greek lakes, gradual increases in conductivity and chloride concentrations correlate with hydrological regime alterations and play a significant role in determining community composition (Stefanidis & Papastergiadou, 2013). The reduced biomass of large Cladocera species in the zooplankton samples is a key feature of the case study lakes. Large-bodied zooplankton, such as *Daphnia* species, appear to be present in low abundances, which could be an indication of an enhanced fish predation pressure (Jeppesen et al., 1999; Jack & Thorp, 2002), mainly by carp (Kagalou & Leonardos, 2009). In addition, elevated salinity can reduce the zooplankton growth rate due to osmotic stress in salt-sensitive taxa (Table S3). Similarly, in Spain and France, salinity appears to be the main environmental factor structuring the zooplankton and invertebrate communities in lakes and ponds (Green et al., 2005; Boix et al., 2008; Waterkeyn et al., 2008; Brucet et al., 2009). Not only Mediterranean regions suffer from increased salinity due to climate change. Also shallow prairie lakes in the interior plain regions of North America are sensitive to slight changes in climate, and future climate-driven increases in salinity may result in reduced algal primary productivity and macrobenthos diversity (Sereda et al., 2011).

Tolerance to salinity can vary greatly among species and also depends on ionic composition (Cañedo-Argüelles et al., 2013) and temperature (Aladin & Potts, 1995; Brucet et al., 2010). However, increases in salinity cause a decrease in the densities of most organism groups due to osmotic stress, as shown by the literature review. For zooplankton, salinity may reduce the population growth rate of the keystone species *Daphnia* (Bezirci et al., 2012), which becomes replaced by copepods, rotifers and small cladocerans at higher salinities (Jeppesen et al., 2007; Brucet et al., 2009).

Typically, *Daphnia* disappears at salinity $>2\text{‰}$ (Jeppesen et al., 1994), but in Mediterranean lakes *Daphnia magna* tolerate higher salinities, up to $>10\text{‰}$ (Brucet et al., 2010). Crustaceans are the most salinity tolerant of the major invertebrate taxon groups, whereas Ephemeroptera is among the least tolerant (e.g. Boix et al., 2008; Brucet et al., 2012). Salinity also reduces the biomass of fish (Aladin et al., 2009). Most freshwater fish are capable of tolerating at least $7\text{--}13\text{ mS cm}^{-1}$, but their early life stages are much less tolerant (tolerance below 6 mS cm^{-1} ; James et al., 2003). Freshwater species may sometimes be replaced by more salt-tolerant species such as three-spined stickleback (*Gasterosteus aculeatus*), nine-spined stickleback (*Pungitius pungitius*), mosquito fish (*Gambusia holbrooki*) or sand smelt (*Atherina presbyter*) (Jeppesen et al., 1994; Brucet et al., 2010). Macrophytes may also be negatively affected by salinity, either directly through reduced germination (Brock et al., 2005) or successional replacement of sensitive species such as charophytes (Stefanidis & Papastergiadou, 2013; Levi et al., 2014); this, in turn, results in reduced plant richness (Barker et al., 2008) or creates monospecific communities (James et al., 2003). Fewer studies have looked at the effects of phytoplankton biomass and community composition (Table S3). However, Ballot et al. (2009) reported a dramatic change in phytoplankton composition in an African lake which became dominated by cyanobacteria following salinisation from freshwater (0.66 mS cm^{-1}) towards alkaline-saline conditions (5.27 mS cm^{-1}) over 25 years.

Our review shows that the biodiversity of most lake organism groups also declines with increasing salinity, and if the salinity increase is high (e.g. from freshwater to brackish levels) its effects may in some cases override all other environmental and pressure factors such as temperature or eutrophication, as shown for zooplankton (Brucet et al., 2009). This is supported by recent studies of streams in the USA where conductivity proved to be one of the most important stressors associated with biological degradation (Vander Laan et al., 2013).

Increased salinity produced by climate warming may also affect the trophic structure of shallow lakes in different ways, with important consequences for ecological quality. Some studies have reported a shift in lake status from a clear-water macrophyte-dominated to a turbid algal-dominated state with increasing salinity (Davis et al., 2003; James et al., 2003;

Jeppesen et al., 2007; Barker et al., 2008). This shift in lake ecological quality may be due to the direct adverse effects of salinity on aquatic plants (Davis et al., 2003; Barker et al., 2008) or to salinity-induced changes in trophic structure (Jeppesen et al., 2007; Barker et al., 2008) such as a shift in zooplankton size structure (Brucet et al., 2010) towards dominance of smaller and less efficient grazer species. This may ultimately lead to reduced control of phytoplankton biomass (Jeppesen et al., 2007; Barker et al., 2008), or it may induce an increase in salt-tolerant periphyton, thereby reducing the light availability for plants (Barker et al., 2008). For example, in brackish lakes, Jeppesen et al. (2007) found a strong regime shift from clear to turbid between 6 and 8‰ salinities. Additionally, with increasing salinity, the higher abundances of small planktivorous fish (e.g. three- and nine-spined stickleback), which have more cohorts per year than fish in comparable freshwater lakes, may have important adverse consequences for the ecological quality. These small fish predate intensively on zooplankton, even within the macrophyte beds (Jeppesen et al., 1994; Brucet et al., 2010; Jensen et al., 2010). Such shifts along the salinity gradient and the subsequent decrease in the top-down control on phytoplankton may reduce the resilience of shallow lakes to enhanced nutrient loading (Jeppesen et al., 2007; Brucet et al., 2010). Changes in salinity levels may also favour the colonisation of alien and exotic salt-tolerant species, which may induce dramatic changes in biodiversity and ecosystem functioning (Aladin et al., 2009; Cañedo-Argüelles et al., 2013). Today, there is, however, limited information available on the impact of salinity on trophic interactions.

Conclusions and a way forward

The case studies and the review demonstrate that changes in water level due to climate warming and compensatory enhanced water abstraction may have strong effects on the nutrient dynamics, nutrient concentrations, water quality and trophic structure of lakes and reservoirs. The effects vary with climate region and the extent of changes in hydrology. The results presented suggest that while a water level decline will typically be associated with reduced external loading, enhanced nutrient concentrations in lakes and reservoirs and consequent eutrophication

may occur due to higher internal loading, concentration of the nutrients in less water and increasing resuspension. All the factors enhancing eutrophication will increase the risk of cyanobacteria blooms, changes in the food web structure and higher temperature being additional contributory causes. Macrophytes may benefit from a water level reduction if it is not too severe.

Reduced net precipitation in the warm or cold semi-arid and Mediterranean climatic regions will enhance salinity. Our case studies and the literature review show that, in freshwater lakes, even relatively small increases in salinity levels can lead to reduced biodiversity and abundance of most aquatic organism groups, altering trophic structure and ecosystem functioning. Furthermore, increases in salinity in coastal lakes due to sea level rise are likely to lead to a major loss in phytoplankton and zooplankton species diversity (Schallenberg et al., 2003; Flöder & Burns, 2004) unless these organisms evolve mechanisms to cope with osmotic stress within the time scale of the predicted sea level rise. Thus, salinisation due to global warming and water abstraction, as well as other anthropogenic activities (mining, irrigation, salt use), has become a major stressor of freshwaters with important ecological and socioeconomic consequences (e.g. Aladin et al., 2009).

Some of the negative cascading effects on lake ecosystems resulting from water level reductions and salinity increases may be counteracted by integrated water resource management. This should encompass reshaping of planning processes, coordinating land and water use, recognising water quantity and quality linkages, conjunctive use of surface water and groundwater, protecting and restoring natural systems and enhancing inland water storage (Kundzewicz et al., 2007). Win–win measures include those promoting sustainable water use, such as water pricing and water use prioritisation, control over abstraction of surface and ground water, implementation of water safety technologies, efficient usage and conservation technologies and reduction of water loss and water friendly farming. Further win–win measures are those that improve the storage capacity of water in the drainage basin such as reforestation and controlled drainage (Nõges et al. 2010a, b) and, in some areas, use of desalinated sea water.

To compensate for enhanced eutrophication due to global warming, attention should also be directed at

reducing the external loading of nutrients and sediment to the lakes via changes in land management and agricultural practices. This may include measures to reduce soil erosion, application of fertilisers in accordance with the soil retention capacity and crop needs, leading to less intensive land use in catchments with sensitive fresh waters, (re)-establishment of riparian vegetation to buffer nutrient transfers to water bodies and improved design of sewage works to cope with the consequences of flood events and low flows in receiving waters. In-lake measures may include sediment removal, sediment capping (chemical treatment of the sediment) and/or biomanipulation (Hansson et al., 1998; Søndergaard et al., 2007; Jeppesen et al., 2012; Spears et al., 2013).

While recent research has improved our understanding of climate change and (other) anthropogenically induced effects on water level and salinity, there are important gaps in our knowledge. These include (1) the effects of extreme variations in water level and salinity due to extreme climate events on the resistance and resilience of lake ecosystems; (2) detailed understanding of the coupling of the littoral, benthic and pelagic systems in relation to water level fluctuations; (3) interactive effects of water level fluctuations, temperature and nutrients on phytoplankton, phytobenthos and macrophyte growth; (4) ecosystem responses (e.g. macrophyte growth) to water level fluctuations in lakes with different basin morphometry; (5) the ranges of salinity changes likely to induce major ecosystem changes; (6) interactive effects of salinity, nutrients and temperature on lake ecosystems and, finally, (7) the impact of water level changes and salinisation on ecosystem goods and services. To handle these challenges, multi-faceted approaches are needed, including the establishment of long-term monitoring sites (there are currently very few of these), analyses of existing time series and snapshot data, experiments, palaeo-ecological analysis and modelling.

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