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Interannual and between-site variability in the occurrence of clear water phases in two shallow Mediterranean lakes

Enrique Moreno-Ostos · Sergio L. Rodrigues da Silva · Inmaculada de Vicente · Luis Cruz-Pizarro

Abstract It is widely accepted that clear water phases constitute a regular stage in the seasonal succession of plankton in dimictic lakes and reservoirs (i.e. PEG Model). The occurrence of such a phenomenon in Mediterranean shallow lakes is characterised by a marked interannual variability, which makes it difficult to establish reliable predictions on the dynamics and functioning of plankton in these ecosystems. In the present paper we analyse the factors influencing the occurrence of the clear water phases in the two shallow lakes of the Albufera of Adra, a coastal wetland region of south-eastern Spain: Lake Honda and Lake Nueva. Despite their geographical proximity, both lakes depicted large hydrological and limnological differences. Lake Honda is an epigenic and recharge lake that is strongly influenced by the hydrological conditions in its watershed, while Lake Nueva can be classified as a hypogenic and discharge lake and, as such, is less affected by the hydrological regime. In contrast, the morphometry, exposure and fetch of Lake Nueva make this ecosystem especially sensitive to wind forcing. Clear water phases in these shallow lakes were linked with periods of low thermal stability and the dominance of small-edible algae in the phytoplankton community, both of which allowed a *Daphnia magna* population to grow up and induce the algae collapse by grazing. In Lake Honda, those conditions were met during the spring of 2002 under the influence of intense rainfall-events, while in Lake Nueva the clear water phase was induced in the spring of 2003 by the occurrence of strong and frequent wind events. In both lakes, a relatively high water column thermal stability and the abundance of cyanobacteria early in the spring prevented the development of the *Daphnia magna* population and the occurrence of the clear water phase.

Keywords Albufera of Adra · Clear water phases · Cyanobacteria · *Daphnia* · Meteorological forcing · Shallow Mediterranean lakes

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Introduction

Clear water phases (Lampert and Schober 1978) have traditionally been considered to be a common phenomenon found in several meso- and eutrophic lakes during the spring season (Lampert et al. 1986; Sommer et al. 1986). They have been described by the PEG model (Sommer et al. 1986) as a regular stage in the seasonal succession of phytoplankton in temperate eutrophic dimictic lakes (Deneke and Nixdorf 1999). In general terms, a rapid increase in small, fast-growing *r*-strategist algae (or *C* species in Grime 1979), such as small centric diatoms and chlorophytes, is followed by a short period of very low algal biomass and high water transparency (the clear water phase itself), which draws to a close at the beginning of the summer when other phytoplankton species, such as cyanobacteria, a typical *k*-strategist, or *S* species (in Grime's classification) (Elliott et al. 2001), become the dominant phytoplankton group. Phytoplankton-zooplankton coupling is central to the initiation and development of clear water phases. Although there are also some other possible factors involved, such as nutrient decay, meteorological events and parasitism over the algae (Reynolds 1984), during the clear water phase the filtration rate of large-sized zooplankton species always exceeds the production rate of phytoplankton. Therefore, grazing can be considered to be the main force responsible for the dramatic spring algal collapse (Lampert 1978; Lampert and Schober 1978; Sommer 1983; Lampert 1987a, b; Lampert et al. 1986; Sommer et al. 1986).

George and Harris (1985) and George et al. (1990) have shown the central role of meteorological forcing (wind stress over the water surface, water temperature, rainfall) and hydrodynamical forcing (water column stability, turbulent mixing) in determining the interannual variability in the spring growth of small edible algae (i.e. chlorophytes, cryptophytes and small centric diatoms) and the summer occurrence of cyanobacteria. In this context, intermediate turbulent mixing events during late winter and early spring induce the proliferation of small edible algae and the inhibition (or reduction) of cyanobacteria growth. All of these conditions together facilitate the development of massive spring cladoceran populations and the initiation of the clear water phase. This phenomenon can be especially spectacular in eutrophic ecosystems where this short clear period contrasts sharply with the turbid situation during the other periods of growing season. However, this situation is transitory, and cladocera decay at the beginning of summer. Following the collapse of the spring peak, cladoceran populations usually do not reoccur the rest of the year (Scheffer 1998).

One explanation put forward to explain the summer collapse of the cladoceran populations has been that the quality of the algal food during the summer is poor due to the increase in inedible colonies of blue-green algae (Threlkeld 1985; Lampert et al. 1986; Scheffer 1998). In fact, based on empirical observations (Infante and Abellá 1985; George et al. 1990) as well as in vitro analyses (Lampert 1987a, b; Claska and Gilbert 1998), the presence of high masses of filamentous cyanobacteria in the water during late spring and summer has frequently been related to the rapid collapse of cladoceran populations. An alternative and widely accepted interpretation is associated with increased predation pressure on cladocera by planktivorous fish due to young-of-the-year fish development (Scheffer 1998; Scheffer et al. 2001).

Despite these general assumptions, previous studies on shallow lakes (Scheffer 1998; Schmitt and Nixdorf 1999; Moreno-Ostos et al. 2002) have revealed that clear water phases in such environments show a marked interannual unpredictability and can no longer be considered to be a frequent and regular phenomenon. In this context, the aim of the present investigation was to describe the interannual as well as between-site variability in the occurrence of the spring clear water phase in two Mediterranean shallow coastal lakes in close proximity to each other, focusing on the hydrological, physical and biological factors that both influence its initiation and are responsible for its temporal and spatial variability.

Study site

The Albufera of Adra is the most important coastal wetland located in south-eastern Spain

(Fig. 1). Due to its ecological importance as a wetland in a semiarid region, the Andalusian Government declared it as a Natural Reserve in 1989. Since 1994, the site is included in the list of Protected Areas of the Ramsar Convention.

The wetland consists of two adjacent small and shallow lakes: Lake Honda (surface area: 8.0 ha; mean depth: 1.14 m; maximum depth: 3.19 m) and Lake Nueva (surface area: 26.0 ha; mean depth: 2.28 m; maximum depth: 3.80 m). The effect of a steady process of land reclamation for agriculture became critical when new intensive agricultural practices (greenhouses) rapidly developed during the1970s–1980s. This reclamation programme resulted in water bodies of reduced size and impaired water quality due to an accelerated eutrophication process (Cruz-Pizarro et al. 2002; de Vicente et al. 2003). Lake Honda is currently classified as hypertrophic and Lake Nueva as eutrophic. Table 1 shows some of the water quality characteristics of the two lakes.

On the basis of its hydrologic regime, which is dominated by runoff water inputs (Benavente and Rodríguez 2001; Benavente et al. 2003), and following the criteria of González-Bernáldez (1992), Lake Honda can be considered to be an epigenic and recharge lake, which receives water from three temporal inflows draining a 13.7 km^2 catchment. In contrast, Lake Nueva can be classified as a hypogenic and discharge system where groundwater from Lake Honda constitutes the predominant entry of water.

The limnological dynamics of Lake Nueva is strongly influenced by wind (prevailing from the south-west) as a result of its fetch (759 m) and orientation (see Fig. 1). In contrast, the impact of wind-induced mixing in Lake Honda is reduced due to its two-basin morphology, the reduced fetch of each basin (332 m in the western basin; 164 m in the eastern basin) and the littoral vegetation shelter-effect.

Despite their geographic proximity, the limnological dynamics of Lake Honda and Lake Nueva show marked differences, although they are both characterised by the absence of ecological predictability (de Vicente et al. 2006). Consequently, the first comprehensive study on the plankton of the Albufera of Adra (Cruz-Pizarro et al. 1990) did not detect the occurrence of clear water phases in either lake during the two years of the study period (1988 and 1989) and neither did a subsequent study by Cruz-Pizarro et al. (2002) for the period 1999–2000. The first clear water phase was identified by de Vicente (2004) in Lake Honda during the 2001 spring season. Moreno-Ostos et al. (2002) described a marked clear

Fig. 1 Location of the Albufera of Adra wetland lakes in the Iberian Peninsula and bathimetry (contours every 0.5 m). *Dotted arrow* depicts the prevailing wind direction. *Dotted lines* around the lakes represent the extension occupied by the rooted vegetation (*Phragmites australis*)
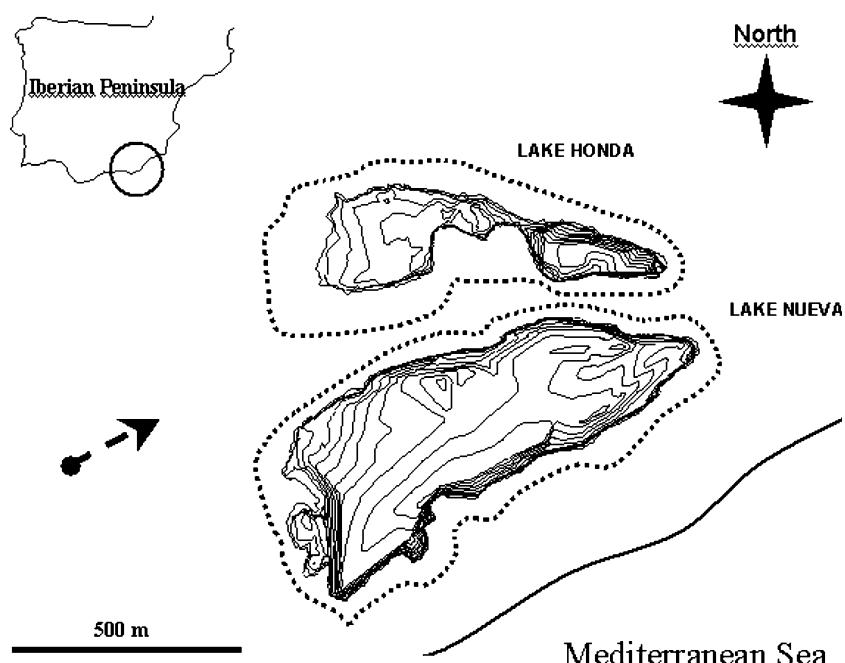
Table 1 Main limnological features of the study lakes for the period 1999–2001

[a] TP, Total phosphorus; TN, total nitrogen; Z_{SD}, water transparency; TSI, Trophic State Index as a function of the annual mean value of the TP concentration (TSI_{TP}), of the Chl-*a* concentration (TSI_{Chl-a}) and of the water transparency (TSI_{ZSD})

[b] Data correspond to mean values and the range of the variable (in parenthesis)

Parameters[a]	Lake Honda[b]	Lake Nueva[b]
Temperature (°C)	21.40 (11.63–29.60)	21.64 (11.33–30.67)
pH	8.40 (7.76–9.24)	8.62 (8.09–9.63)
Dissolved oxygen (mg l^{-1})	6.18 (1.10–12.67)	8.23 (2.57–13.29)
Conductivity (mS cm^{-1})	3.82 (1.42–7.31)	4.97 (3.94–7.39)
Alkalinity (meq l^{-1})	4.51 (3.17–6.21)	2.65 (1.46–4.14)
Z_{SD} (cm)	0.49 (0.10–2.50)	0.97 (0.30–2.10)
TP (μg P l^{-1})	275 (112–471)	89 (24–155)
PO_4^{3-} (μg P l^{-1})	59 (0–275)	6 (0–32)
TN (mg N l^{-1})	3.40 (0.99–7.14)	1.39 (0.80–2.00)
DIN (μg N l^{-1})	597 (0–1483)	46 (0–239)
TSI_{ZSD}	74	60
TSI_{Chl-a}	76	67
TSI_{TP}	83	68

water phase in the same lake during the spring of 2002. In both cases, clear water phases were associated with high densities of *Daphnia magna* and the absence (or scarceness) of cyanobacteria among the main phytoplankton groups.

Due to their shallowness and the frequent high wind speed recorded in the Albufera of Adra wetland, sediment resuspension events are frequently detected, especially in the shallower water of Lake Honda. These events promote the entrainment of particulate matter and dissolved substances from sediment and interstitial water to the water column, thereby dramatically increasing turbidity (de Vicente 2004). Runoff water input is also related to resuspension events in Lake Honda as it results in submerged macrophyte populations (*Potamogeton pectinatus* and *Najas marina*) only being able to grow in the lakes when a spring clear water phase takes place and sufficient light reaches the sediment. Once they colonise the lake bottoms, macrophytes in the Albufera of Adra water bodies show a marked sediment coverage (80% in Lake Honda and 95% in Lake Nueva; Moreno-Ostos unpublished results), and they persist until their summer collapse, at which time cyanobacteria induce more turbid phases.

The Albufera of Adra lakes constitute very well-suited ecosystems for a comparative approach to the study of the occurrence of clear water phases, as both are shallow bodies of water that are directly connected. Furthermore, the structure of the aquatic foodweb is rather simple. The composition of the phytoplankton community is, in general terms, that expected in warm waters and nutrient-rich small lakes: chlorophytes, cryptophytes and small diatoms are the dominant groups during the winter and spring period in both lakes, while large filamentous cyanobacteria occur as dense blooms during the summer and early autumn. In both lakes, the population composition of the zooplankton is very simple: it is dominated by small-sized herbivores of which the most predominant are "clusters" of congeneric species of rotifers (Fabián 2002). In contrast, a large-sized filtering cladoceran species (*Daphnia magna*) has been found during the spring in the lakes if a clear water phase develops. The only fish present is that endemic to southern Spain, the cyprionodont Andalusian toothcarp (*Aphanius baeticus*), a small-sized fish (total length usually <5 cm) that usually preys on benthic crustaceans and plant debris and detritus (Vargas and de Sostoa 1997; Clavero et al. 2005). No *Daphnia* invertebrate predators have been found in the lakes.

Materials and methods

Survey

Surveys for plankton samples and physico-chemical measures were performed every month in

Lake Honda and Lake Nueva from February 2002 to September 2003. These surveys were carried out within the framework of a wider systematic limnological research programme on the Albufera of Adra wetland. The frequency of the surveys increased during the occurrence of the spring clear water phase survey, and the lakes were monitored during this time at least once every 2 weeks.

Data and water samples for the physical and biological analyses were always taken from a fixed sampling station located at the maximum depth area of each lake. Water transparency was measured using a 20-cm-diameter Secchi disk.

Meteorological forcing and water column thermal stability

Diel meteorological information (wind speed, wind direction, rainfall, among others) was recorded by a meteorological station located close to the lake shore. Thermal profiles were recorded using a multiparametric probe (Turo Water Quality Analysis T-611), and the water column thermal stability (Idso 1973) was used as an appropriate index of the lakes mixing regime:

$$S = \frac{1}{A_0} \int_{Z_0}^{Z_m} (\rho z - \bar{\rho})(A z)(Z - Z \bar{\rho}) \mathrm{d}Z$$

where, S is the water column thermal stability (J m^{-2}); A_0 is the lake area (m^2); A_z is the area at each considered depth (m^2); ρ_z is the water density (kg m^{-3}) at depth z; $\bar{\rho}$ is the average density that results if the lake is mixed to isotherm conditions; $Z \bar{\rho}$ is the depth at which the water column has ρ density before mixing. S can be considered to be the work required to entirely mix the water column until it has reached a uniform density. As a threshold value for S, we have used the average S value for the lakes during the study period. This value was close to 2.5 J m^{-2} in both lakes.

Biological determinations

A recently developed fast-response high-resolution in vivo and in situ spectrofluorimetric probe (bbe Fluoroprobe, Moldaenke) was used to examine the composition and biomass of the phytoplankton community in the studied lakes. This probe directly measures total chlorophyll (Chl)-*a* concentration in the water and the fraction corresponding to chlorophytes, cyanobacteria, diatoms and cryptophytes. To differentiate functional groups of phytoplankton, the bbe Fluoroprobe uses five light-emitting diodes (LEDs) for fluorescence excitation. The LEDs emit pulsed light at selected wavelengths (450, 525, 570, 590 and 610 nm), while fluorimetric emission is measured at 680 nm by a photomultiplier set at an angle of 90° to the exciting light source and directly transformed to Chl-*a* concentration by the bbe FLUOROPROBE ver. 1.4 software. Additionally, the microscopic identification of phytoplankton taxa was conducted in order to check the calibration of the Fluoroprobe and determine the characteristic size of algae.

Following George et al. (1990), George (2000) and Talling (2003), phytoplankton species were grouped into two main size categories: (1) small-edible algae (length <35 μm), including chlorophytes, cryptophytes and small centric diatoms, and (2) non-edible large filamentous cyanobacteria (length >90 μm).

Phytoplankton and zooplankton samples were taken using a 16-l volume vertical tube (length: 2.0 m; diameter: 10 cm). Water samples for phytoplankton were directly taken from the tube and fixed in situ using Lugol. For zooplankton, the whole water volume contained in the tube was filtered through a 40-μm mesh that retained all cladocera. Zooplankton samples were fixed in situ using Formaldehyde.

Results

Interannual and between-site variability in the occurrence of clear water phases in the Albufera of Adra lakes

The temporal dynamics of Chl-*a* concentration, *D. magna* density and water transparency during 2002 and 2003 in the Albufera of Adra lakes were characterised by a severe interannual and between-site variability (Fig. 2). During spring

2002 a clear water phase was recorded in Lake Honda, induced by a marked proliferation of *D. magna*; the Chl-*a* concentration decreased from 228 µg l^{-1} in February to less than 5 µg l^{-1} at the beginning of April. Some discrete inconsistencies in the relationship between *D. magna*, Chl-*a* concentration and water transparency were recorded during this clear water phase (especially in May 2002) which were related to increments in non-biological turbidity derived by the frequent wind-induced resuspension of particulate matter from sediments. In contrast, in 2003 Lake Honda showed a very high Chl-*a* concentration (mean spring level: 114 µg l^{-1}), cladocera were absent and the lake was turbid.

In the case of Lake Nueva, *D. magna* was first recorded in the late winter of 2003, and the populations remained stable during the whole spring and early summer. Consequently, a very low Chl-*a* concentration was measured in the water column, with a spring mean of 4.5 µg l^{-1} and a Secchi depth reaching the lake bottom (3.80 m).

The role of physical forcing and phytoplankton composition in the initiation of the clear water phases in the Albufera of Adra lakes

Meteorological forcing in the Albufera of Adra wetland also showed a marked interannual variability along the whole study period (Fig. 3). The frequency and intensity of the rainfall events were higher during 2002 than during 2003, while wind

Fig. 2 Temporal development of Chl-*a* concentration, Secchi depth and *Daphnia magna* density in Lake Honda (**a**) and Lake Nueva (**b**). *Shadowed area* Secchi depth (m), *vertical bars D. magna* density (individuals l^{-1}), *black line* Chl-*a* concentration (µg l^{-1}). Please note the difference in the range of the *y*-scale range for chlorophyll between Lake Honda (0–450 µg l^{-1}) and Lake Nueva (0–180 µg l^{-1})
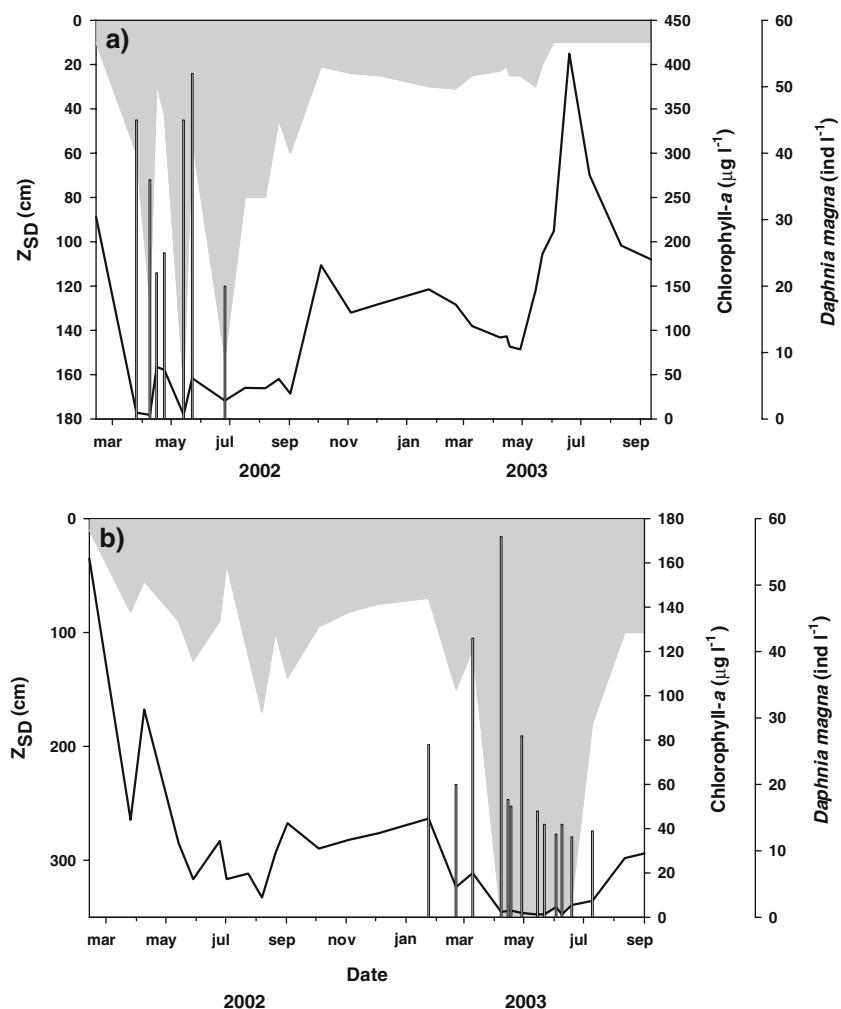
speed was higher in 2003 (Fig. 3). The thermal gradient of the water column (Fig. 4) and the thermal stability (S) in each lake (Fig. 5) reflected this meteorological variability. In the case of the epigenic Lake Honda, there were low values for S during the early spring of 2002 that were induced by the intense precipitation and runoff events. In contrast, the hypogenic Lake Nueva was not affected by the above-mentioned runoff water discharge and, consequently, thermal stability values remained relatively high during the early spring of 2002. Due to its morphology and fetch (759 m), S in Lake Nueva is especially sensitive to wind-induced turbulent mixing, and the intense winds recorded during the early spring of 2003 induced very low S in the lake. As previously mentioned, Lake Honda is far less sensitive to wind-induced mixing because of its characteristic morphology, the reduced fetch of each one of its two basins and the shelter effect induced by the rooted littoral vegetation (*Phragmites australis*). Therefore, it was characterised by high S values during the dry springer period of 2003. A correlation analysis between the thermal stability of the water column in Lake Honda and Lake Nueva, monthly-averaged wind speed and monthly-accumulated rainfall during the study period confirms the differential sensitivity of each lake to the influence of wind and rainfall (Table 2).

The composition of the phytoplankton populations in each lake during the study period was affected by the temporal variability in the meteorological and physical forcing (Fig. 6). Thus, low S values favoured a phytoplankton community dominated by small-edible algae (mainly composed of *Chlorella vulgaris*, *Coelastrum* sp., *Ankyra* sp., *Scendesmus* sp., *Cryptomonas* sp. and *Cyclotella* sp.) during the spring of 2002 in Lake Honda and the spring of 2003 in Lake Nueva. In contrast, higher water S values were related to the development of large filamentous cyanobacteria populations (*Anabena* sp., *Oscillatoria* sp., *Pseudoanabaena* sp., *Anabaenopsis* sp. and *Spirulina* sp. in Lake Nueva and *Anabaena* sp. in Lake Honda), which are non-edible phytoplankton species that can even damage the filtering structures of cladoceran populations (Rodrigues da Silva 2004). This situation corresponds to that found in the spring of 2002 in Lake Nueva and the spring of 2003 in Lake Honda, and is especially dramatic during the summer period in both lakes. Table 3 demonstrates the influence of thermal stability on the phytoplankton community composition in the two study lakes.

Fig. 3 Mean monthly wind speed (m s^{-1}) (*black line*) and monthly accumulated rainfall (*vertical bars*) in the Albufera of Adra wetland during the study period
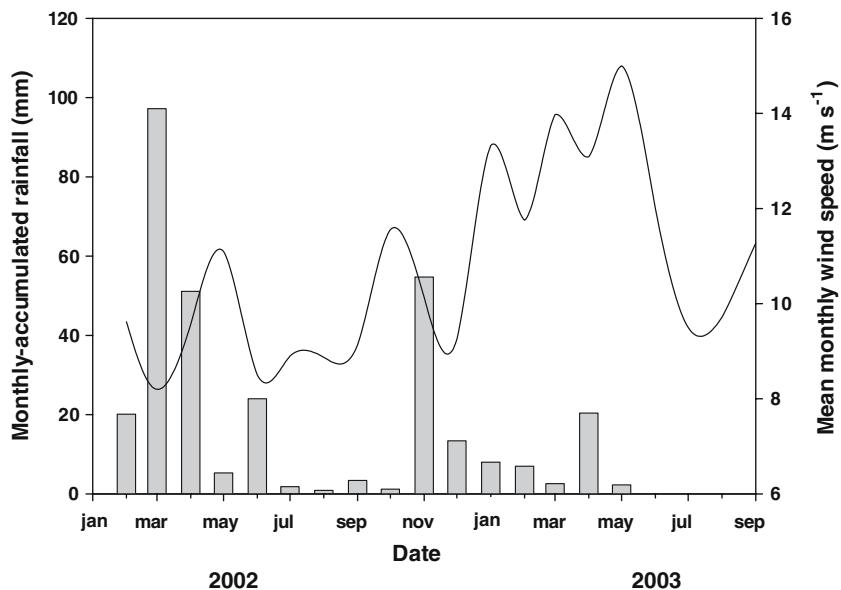
Fig. 4 Temporal development of surface (*black line*) and bottom (*dotted line*) water temperature in Lake Honda (**a**) and Lake Nueva (**b**) during the study period
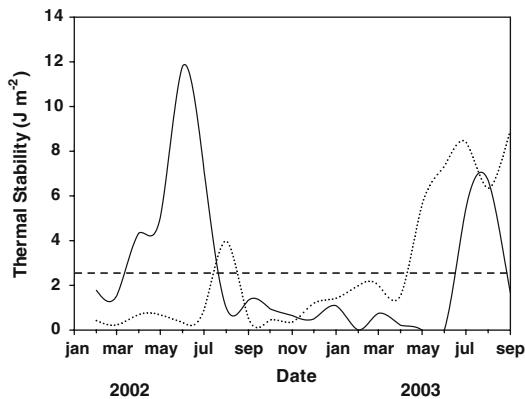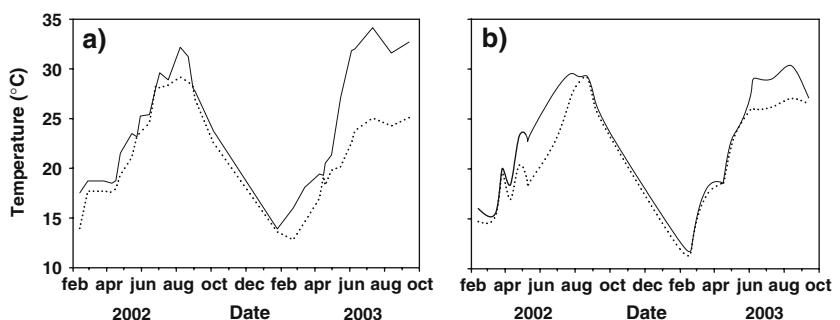
Fig. 5 Temporal development of thermal stability in Lake Honda (*dotted line*) and Lake Nueva (*black line*) during the study period. The *horizontal dotted black line* represents the S threshold value for the lakes (2.5 J m^{-2})

Fig. 6 Temporal development of the relative abundance of small-edible algae (length <35 μm) (*grey area*) and large filamentous cyanobacteria (length >90 μm)(*black area*) in Lake Honda (**a**) and Lake Nueva (**b**) during the study period. The biomass of different phytoplankton groups was measured by means of in vivo spectrofluorescence (bbe Fluoroprobe)

Table 2 Results of a Pearson correlation analysis between water column thermal stability (*S*), wind speed and rainfall in the two study lakes

	Pearson correlation parameters	Wind speed	Rainfall
S Lake Honda	*r*	0.21	−0.46[a]
	P	>0.05	<0.05[a]
S Lake Nueva	*r*	−0.50[a]	−0.01
	P	<0.05[a]	>0.05

[a] Significant correlations (*P* < 0.05)

Table 3 Results of a Pearson correlation analysis between water column thermal stability (*S*), small-edible algae biomass and large filamentous cyanobacteria biomass in the two study lakes

	Pearson correlation parameters	Small algae biomass	Large cyanobacteria biomass
S Lake Honda	*r*	−0.67	0.77
	P	<0.05	<0.05
S Lake Nueva	*r*	−0.54	0.75
	P	<0.05	<0.05

Discussion

In the Albufera of Adra lakes, clear water phases were neither periodic nor regular in terms of plankton annual succession. In contrast, they did occur occasionally, and their occurrence coincided with marked differences in the interannual

dynamics of the planktonic community between the lakes.

Our results show that clear water phases developed in the Albufera of Adra lakes during the spring if the water column remained well-mixed and small-edible algae dominated in the phytoplankton. Under these circumstances, together with the optimum mean water temperature (see Fig. 4) and the characteristic spring photoperiod, the emerging *D. magna* populations grew successfully. Lampert et al. (1986) found that small algae dominated the phytoplankton populations – prevalence of more than 80% – in a small shallow lake in the period preceding the clear water phase. This situation was also found in Lake Honda in the spring of 2002 and in Lake Nueva in the spring of 2003 when the wind speed was especially high. The impact of unpredictable rainfall events on plankton dynamics in Lake Honda is also supported by the fact that the first clear water phase identified in this lake in spring 2001 occurred after an extremely wet winter (172 mm) that represented 73% of the annual mean accumulated rainfall for the period 1997–2001 (de Vicente 2004).

In contrast, when thermal stability is relatively elevated during the spring, the presence of filamentous cyanobacteria and a lower abundance of small edible algae seem to reduce the success of the *D. magna* population, resulting in the suppression of the clear water phase (Lake Honda during spring 2003 and Lake Nueva during spring 2002).

Although some empirical evidence has been reported in the literature indicating that dense *Daphnia* populations can – under certain conditions – ingest and, to certain extent, even control subsequent densities of small single-celled or short-filamented cyanobacteria (Burns 1968, 1987), previous in situ and in vitro studies on the Albufera of Adra lakes (i.e. toxicology studies, *Daphnia* gut content analyses, enclosure experiments) have clearly proven that *D. magna* is not able to prey on the larger (mean length: 97 ± 10 µm; Rodrigues da Silva, unpublished data) filamentous cyanobacteria inhabiting the study lakes. Furthermore, some of those filamentous cyanobacteria can potentially be toxic (Cruz-Pizarro et al. 2003; Rodrigues da

Silva 2004). In addition, video-monitoring experiments have demonstrated that cyanobacteria isolated from the Albufera of Adra lakes are capable of strongly inhibiting both the hatching of *D. magna* (also captured in the Albufera of Adra lakes) ephipia and the growth of neonates as well as dramatically increasing the respiration rate of mature animals and damaging their filtering systems (Rodrigues da Silva 2004). Similar results showing the negative effect of cyanobacteria of *Daphnia* have been reported by Gliwicz (1990) and Gliwicz and Lampert (1990) in different ecosystems as a consequence of both a marked deficiency in food supply (George 1974; Harper 1992), mechanical interference of food gathering by cyanobacteria filaments (Gliwicz and Siedlar 1980; Burns 1987; Heaney 1987; DeMott et al. 2001), mechanical damage induced by cyanobacteria retained in their filtering structures (Burns 1968; Gliwicz 1969, 1977; Webster and Peters 1978; Porter and McDonough 1984; Hartman 1985; Infante and Abellá 1985; de Bernardi and Giussani 1990) and the production of cyanotoxins (Lampert 1987a, b; Claska and Gilbert 1998). Porter (1972) reported that *Anabaena affinis* and *A. flos-aquae*, two species very similar to the ones described in the studied lakes, were rarely found in the gut contents of zooplankton. Similarly, Lehman and Sandgren (1985) found that *Anabaena* sp. and *Aphanizomenon* sp. were not grazed on in any of their in situ grazing experiments.

Physical factors, such as water temperature and thermal stability, among others, conditioned both the hatching of *D. magna* resting eggs and the dynamics of the phytoplankton community. Depending on the composition of the phytoplankton, the *D. magna* population would either grow in the lake, inducing a clear water phase or, in contrast, it would not be successful as the effect of the cyanobacteria is more intense on the youngest stages of *Daphnia* (Hartman 1985). In agreement with George et al. (1990) and Talling (2003), the study populations of *Daphnia* seem to depend on a "window of opportunity" which is taken advantage of when temperature and food resources become available and predation by fish and macroinvertebrates is reduced. For *Daphnia*, the main "window of opportunity" is the spring period, which is characterised by an optimum

water temperature and governed by small-edible algae prior to dominance by large summer phytoplankton (especially large filamentous cyanobacteria such as *Anabaena* sp. and *Oscillatoria* sp.). If for some reason (i.e. early increases in the stability of the water column) cyanobacteria predominate in late winter and spring, then no ''window of opportunity'' would exist for both the *Daphnia* population and the clear water phases to develop.

Mixing-stratification patterns in the study lakes varied from year to year. During low rainfall periods, Lake Nueva is more affected by wind mixing than Lake Honda. When rainfall and surface runoff are high, the thermal stability of Lake Honda is clearly more affected than that of Lake Nueva. Therefore, in these Mediterranean shallow lakes, it is not suitable to describe their plankton succession in terms of a standard yearly pattern.

The clear water phase lasted more than 3 months in both lakes, which is extremely longer than the clear water phase described by the PEG model (Lampert et al. 1986; Sommer et al. 1986) but similar to those recorded in other eutrophic shallow lakes (Theiss et al. 1990). In this context, it is especially remarkable that *D. magna* is able to maintain a moderate density population for a number of months while phytoplankton is still at a very low level, which should substantially affect its population growth. This phenomenon is a consequence of the use of alternative food sources by *D. magna*, such as bacteria, detritus and dissolved nutrients, which enter into the water column by means of resuspension events (Alonso 1991). The lack of invertebrate predators on *Daphnia*, the low fish stock and the *A. iberus* preference to prey on benthic invertebrates rather than the large-sized cladocera (Vargas and de Sostoa 1997; Clavero et al. 2005) would also contribute to a prolongation of the clear water period (Lampert et al. 1986). Finally, the proliferation of the submerged macrophytes during the clear water phases also plays an important role in the persistence of the daphnids as the former provide, among others, refuge and valuable food resources (Jeppesen et al. 1998; Scheffer 1998). Thus, a feedback mechanism between large cladoceran and macrophytes in these shallow lakes. The daphnids provide a water

transparency that enables the growth of plants, while macrophytes enhance the persistence of the populations of *D. magna* over time.

On the other hand, Scheffer (1998) concluded that the clear water phase in the Central European shallow lakes often occurs at the end of the spring. Our results demonstrate that the higher temperature at the end of winter and early in the spring allows the earlier occurrence of this phenomenon in Mediterranean shallow lakes.

The clear water phase in large temperate lakes shows little year-to-year variability in terms of occurrence (Talling 2003), and the timing of its initiation depends primarily on water temperature (as the higher the post-winter water temperature, the higher the probability of an early clear water phase), as influenced by large-scale climatic factors such as interannual variability in the NAO index (Gerten and Adrian 2000; Straile and Adrian 2000; Straile et al. 2003). In contrast, in Mediterranean shallow lakes the spring water temperature is almost never low enough to limit *Daphnia* growth (see Fig. 4), and the clear water phase depends more on the short-term and relatively unpredictable meteorological forcing that characterizes the Mediterranean region as well as on the structure of the fish communities (Romo et al. 2005). Additionally, an increase in the (already relatively high) spring water temperature in these ecosystems would favour cyanobacteria growth, which may negatively influence the large-sized grazers (Wetzel 2001; Beklioglu et al. 2006). Claska and Gilbert (1998) demonstrated a pronounced negative effect of temperature on the population-growth-rate response of *Daphnia* to toxic cyanobacteria.

Shallow Mediterranean lakes are characterized by marked temporal unpredictability (Beklioglu et al. 2006), and they require intense monitoring programmes at adequate temporal and spatial scales (de Vicente et al. 2006).

Wind and rainfall events in the Albufera of Adra wetland can be considered to be intermediate allogenic perturbations that strongly influence the limnological succession of each lake. In agreement with the Intermediate Disturbance Hypothesis (Connell 1978), when intermediate perturbations act over non-equilibrium communities (i.e. in spring), they enhance oppor-

tunities for coloniser species (*r*-strategists, or *C* species in the terminology of Grime 1979; Reynolds 1997) against large cyanobacteria *k*-strategists species (or *S* species in Grime 1979). This makes macrozooplankton capable of establishing and producing a clear water phase that may persist as long as the perturbations persist and other factors interact (e.g. predation on daphnids). Barbiero et al. (1999) correlated the occurrence of storm events on a small shallow reservoir with the temporal reestablishment of colonising algal species.

The dramatic reduction in phytoplankton biomass, the increase in water transparency and the consequent development of macrophyte populations (Moreno-Ostos et al. 2002) during the clear water phase in the Albufera of Adra lakes can be considered to be a relevant improvement in ecosystem quality, in that the ecosystem changes from being governed by phytoplankton to being dominated by macrophytes and zooplankton. In a study on the application of biomanipulation tools to control eutrophication in the Albufera of Adra wetland, Cruz-Pizarro et al. (2003) pointed out the necessity to improve our knowledge of environmental factors involved in the initiation and development of the clear water phases in Lake Honda and Lake Nueva as they constitute important windows of opportunity for the restoration of shallow waters (Scheffer et al. 2001). The present paper focuses on a short 2-year study period. In this sense, more research covering a wider temporal spectrum is needed to obtain a more general picture on the factors involved in theoccurrence and variability of the clear water phase in shallow Mediterranean lakes.

Conclusion

The results presented in this paper suggest that the special characteristics of the Mediterranean clime (i.e. extreme temporal variability) and the high sensitivity of shallow lakes to meteorological forcing make the planktonic dynamics of shallow Mediterranean lakes especially complex and – to a certain extent – unpredictable and strongly influenced by external forcing (hydrometeorological factors). An intense bottom-up control (from the physical environment to the plankton) drives

the occurrence and the temporal variability of clear water phases in shallow Mediterranean lakes, such as those of the Albufera of Adra, where predation pressure on large cladoceran (i.e. fish, macroinvertebrates) is low. Physical factors (water column thermal structure and thermal stability, among others) determine both the hatching of *D. magna* resting eggs and the dynamics of the phytoplankton community. Depending on the composition of the early spring phytoplankton populations, the emerging *D. magna* population would grow in the lakes, thereby inducing a clear water phase or, conversely, it would not be successful. In this context, during windy and rainy years, the water column remains well mixed during the spring, andthis turbulent environment enhances the growth of small-edible algae (chlorophytes and small diatoms) and, consequently, the successful development of *D. magna* and the beginning of a clear water phase. In contrast, during years characterised by a more stable thermal structure, large filamentous cyanobacteria populations (non-edible and harmful to cladocera) predominate in the spring phytoplankton community, and no window of opportunity exists for the development of the *Daphnia* populations and, consequently, the clear water phase.

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