

Phytoplankton configuration in six deep lakes in the peri-Alpine region: are the key drivers related to eutrophication and climate?

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Abstract The aim of this study was to draw a general picture of the phytoplankton community in peri-Alpine lakes, including for the first time a broad data set of six deep peri-Alpine lakes, belonging to the same geographical region. The objective was to define the main key drivers that influence the phytoplankton community composition in this particular vulnerable region, for which the impacts of climate change have been demonstrated to be stronger than on a global average. The phytoplankton was investigated with a particular focus on cyanobacteria and using a classification approach based on morpho-functional groups. We hypothesized that phytoplankton in peri-Alpine lakes is mainly driven by nutrient loads as well as by

water temperatures, variables that are strongly influenced by climate change and eutrophication. Though different phytoplankton configurations among lakes were partly due to their geographical (altitude) position, assemblages were mostly linked to temperature and nutrients. Furthermore, the results confirmed the significant role of the spring fertilization on the seasonal phytoplankton development. Cyanobacteria were related to the increasing annual average of air and water temperature gradient and therefore might become more important under future warming scenario. Air temperatures have a significant impact on water temperature in the uppermost meters of the water column, with a stronger influence on warmer lakes.

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Introduction

Physical, hydrodynamical, and ecological changes are occurring in lake ecosystems; these changes are forecasted to become greater in the future as global temperatures are increasing partly as a result of human activities (IPCC 2007; Williamson et al. 2009; George 2010;). In the course of the twentieth century, the Alpine region has been shown to be particularly vulnerable and sensitive to climate change (Beniston

et al. 1997; Beniston 2006), with higher rate of warming, at least double of the observed global average.

The question of particular interest is to assess how global warming may affect the phytoplankton community composition, which plays an important role as it is the basis of nearly all aquatic ecosystems' food supply (Arrigo 2005). Changes in the phytoplankton community exert an effect on the higher food chain and can potentially disrupt the ecological equilibrium of lakes. Moreover, particular attention is paid to the group of cyanobacteria, the only freshwater phytoplankton group that not only forms blooms, but is also able to produce a variety of toxic compounds (Sivonen and Jones 1999). Cyanobacteria thus can potentially harm lake ecosystems through food web disturbance and anoxia due to massive bloom events, affect human health (water supply, food contamination), the economy (fishing industry), and finally, social activities, as, for example, the recreational use of lakes. As the world's oldest known organisms (Schopf 2000), cyanobacteria have always been capable of adapting to environmental change (Huisman et al. 2005; Paul 2008). They have relatively high temperature optima for growth (Reynolds 2006) and are able to migrate vertically in the water column to better compete for light and nutrients (Ibelings et al. 1991; Walsby et al. 1997; Reynolds 2006). A number of studies have predicted that cyanobacteria are likely to become more abundant in the future as climate continues warming (Paerl and Huisman 2008; Paul 2008; Gallina et al. 2011; Paerl and Paul 2012).

The common phylogenetic classification of phytoplankton is based on taxonomy. However, since a traditional taxonomy does only partially reflect the ecological function of phytoplankton (Webb et al. 2002; Litchman and Klausmeier 2008), other classifications were proposed to aggregate species/genera having similar traits, for example, functional-based classifications (Reynolds et al. 2002), the morpho-functional-based classification (Salmaso and Padisák 2007), and the morphological-based classification (Kruk et al. 2010). These aggregations have the advantages to better interpret environmental mechanisms and conditions and are easier to deduce as they enclose common affinities and considerably reduce the numbers of interpreting components.

In deep lakes under a continental climate, phytoplankton communities exhibit strong seasonality in

their behavior, which is summarized by the broadly accepted Plankton Ecology Group (PEG) model (Sommer et al. 1986). The PEG model identifies the main influencing factors of the seasonal behavior, such as climate, weather, grazing, and water chemistry. Several studies debate the duality and the interaction between nutrients (mainly phosphorus) and temperature (reflecting climatological and meteorological forcing) in affecting phytoplankton communities (Moss et al. 2003; Elliot et al. 2006; Stich and Brinker 2011). Both these factors have been shown to considerably influence the seasonal phytoplankton community (Gallina et al. 2011; Salmaso et al. 2012).

As several lakes are implicated, it is noteworthy that every lake is a mirror of its environment, and therefore, the phytoplankton community growth can be presumed to differ in between lakes, as does the water chemistry and environmental factors (Reynolds and Walsby 1975; Lung and Paerl 1988; Ryding and Rast 1989; Bleckner 2005). This phenomenon implies that the hydro-morphometrical features, the surrounding landscape, origin, and history of a lake may play an important role (Ryding and Rast 1989; Bleckner 2005). Recent studies demonstrate different response of lakes to climate change (Bleckner 2005; George 2010).

The underlying assumption is that phytoplankton compositions among peri-Alpine lakes mainly represent different responses to nutrient concentrations and temperature. These factors are strongly affected by the influence of climate change and eutrophication. In deep lakes, a further element to take into account is the spring replenishment of nutrients from the deeper to the surface layer. We hypothesize that this pool could represent an important source of nutrients for phytoplankton throughout the year.

After previous research based on a smaller number of northern peri-Alpine lakes (cf. Anneville et al. 2004, 2005), this study reports a synoptic assessment of phytoplankton assemblages and their main driving factors across six peri-Alpine lakes situated north and south of the alpine chain. The main key drivers of phytoplankton composition changes will be evaluated on yearly and seasonal timescales (summer–autumn). A matrix including eight different data sets generated from six lakes (two of the lakes were sampled at two different locations) was compiled. For reasons of comparability, the six lakes are all deep and warm monomictic lakes, situated in the same geographical

region. Additionally, these lakes have the interesting features to cover a large trophic gradient and to be located along an altitudinal gradient.

Materials and methods

Lake characteristics and data sources

Figure 1 a shows the locations of the lakes. The matrix includes six different lakes at different time periods,

namely Lake Constance, Lake Zürich, Lake Walen, Lake Geneva, Lake Maggiore, and Lake Garda. Data from Lake Geneva and Lake Zürich were collected at two sampling points, named as “Small Lake Geneva” and “Big Lake Geneva,” as well as “Upper Lake Zürich” and “Lower Lake Zürich,” respectively. Consequently, eight data sets were derived from the six lakes.

The six lakes have a number of features in common: They are all deep, warm monomictic lakes (Hutchinson 1957), belonging to the same geographical

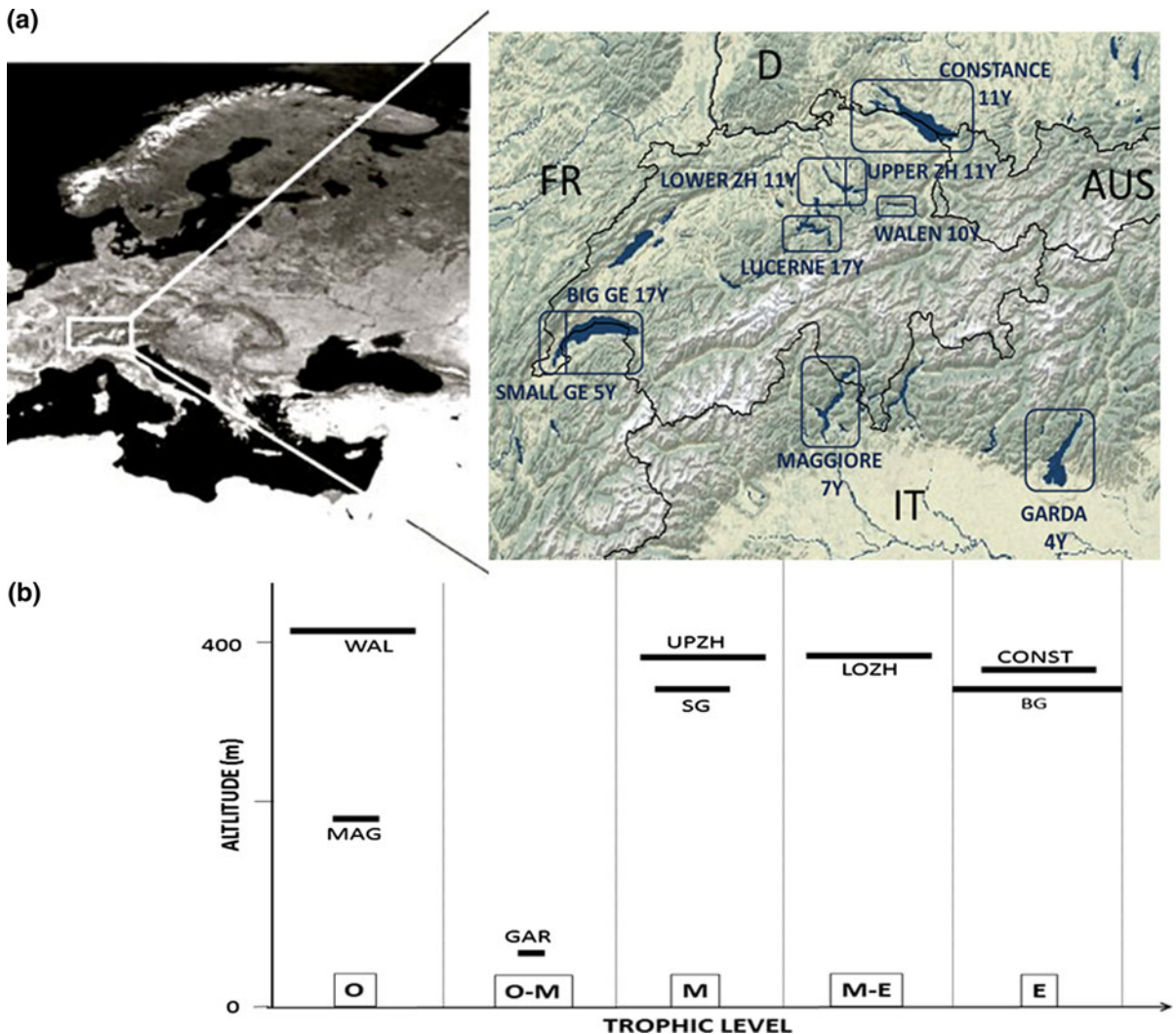


Fig. 1 a Location of the lakes in the peri-Alpine arc which were considered in this study with the length of the time series available for each lake. Lake Constance (CONST), Lower Lake Zürich (LOZH), Upper Lake Zürich (UPZH), Lake Walen (WAL), Small Lake Geneva (SGE), and Big Lake Geneva (BGE) are situated in the northern part of the alpine arc, whereas

Lakes Maggiore (MAG) and Garda (GARD) are located on the southern part. b Lake data sets represented upon their trophic level, their altitudinal position, and the length of the time series, which is indicated proportionally by the length of the black bar (O oligotroph, O-M oligo-mesotroph, M mesotroph, M-E meso-eutroph, E eutroph)

(peri-Alpine) and climatological (continental) region (see Table 1). These similarities allow for comparability and integration of the eight data sets into one data matrix, which builds the basis for the further analysis presented here.

Monthly or bimonthly environmental drivers and phytoplankton biomass recorded in the layer from 0 to 20 m were obtained from state water authorities responsible for lake monitoring as well as from limnological research institutes, namely the LUBW for Lake Constance (1980–1989), the Wasserversorgung Zürich and EAWAG for Upper (1980–1990) and Lower Lake Zürich (1980–1990) as well as for Lake Walen (1991–200), SECOE for Small Lake Geneva (2001–2005), the CIPEL for Big Lake Geneva (1977–2000), the FEM-IASMA for Lake Garda (1997–2003), and the CNR for Lake Maggiore (1997–2000). Data from discrete depths ((0, 1, 2.5, 5, 7.5, 10, 12.5, 15, 20 m) in Lake Walen, Upper and Lower Lake Zürich) have been transformed into weighted averages and integrated over the water column from 0 to 20 m depth. An exception for the sampling depth of the phytoplankton data represented “Big Lake Geneva,” for which the sampling strategy method was applied on an integrated depth from 0 to 10 m. However, a comparison strategy with the 0–20 m layer leads to the conclusion that the different biomass for both layers tends to be quite similar. Same results were found for “Small Lake Geneva” (Lavigne and Druart 2002), which allowed us for integration of those data.

Based on total phosphorus concentrations, and according to OECD (1982), the assessed lakes cover the entire trophic gradient (Fig. 1 b and cf. next paragraph).

Environmental and biological data

The choices for potential drivers to explain the phytoplankton community configuration were done upon recent findings but strongly depend on the availability of the data. In the present study, those drivers are considered, for which the same sampling strategies, standard measuring methods, and no missing values could be guaranteed, in order to ensure the homogeneity of the data.

Hydro-morphometrical descriptors include lake altitude, surface, watershed area, ratio of the watershed area and surface, maximum and mean

depth; lake volume, residence time, and outflow (cf. Table 1).

Physical–chemical descriptors (0–20 m) include conductivity (as a proxy for runoff), nitrate, total phosphorus, soluble reactive phosphorus concentrations, and water temperature. The euphotic depth was obtained by multiplying the Secchi depth by a factor of 2.5 (Vollenweider and Kerekes 1982). The trophic state of a lake was defined by the total phosphorus concentration (OECD 1982). The time series of each lake were selected to guarantee that the entire trophic gradient was presented and well balanced between the different archives: Lake Walen and Lake Maggiore are oligotrophic (O), Upper Lake Zürich and Small Lake Geneva mesotrophic (M), and Lake Constance and Big Lake Geneva eutrophic (E). Lower Lake Zürich and Lake Garda are classified, respectively, as meso-eutrophic (ME) and oligo-mesotrophic (OM) (cf. Fig. 1b). For computational reasons, the trophic states were additionally assigned in classes ranging from 1 to 5, class 1 corresponding to the oligotrophic state and class 5 to the eutrophic state (Table 1).

For the Swiss lakes, the daily average air temperature data were downloaded from the digital database of the Swiss Federal Office for Meteorology and Climatology (MeteoSwiss). Five meteorological stations were chosen, based upon their proximity to the phytoplankton sampling stations, namely Güttingen and Kreuzlingen for Lake Constance; Zürich/Fluntern for lower Lake Zürich; Glarus for Lake Walen; and Changins for Small Lake Geneva. For Big Lake Geneva, data were received from the meteorological station situated at Thonon-les-Bains belonging to the INRA Research Institute. As for Lake Garda, daily-averaged air temperature was measured at the meteorological station of Arco (ARC), at the northern border of the lake (Salmaso 2010). For Lake Maggiore, the daily-averaged air temperature was measured at the meteorological station in Verbania-Pallanza (Ambrosetti et al. 2006). The data sets derived from MeteoSwiss have been quality-checked for the homogeneity of these records (Begert et al. 2005).

The meteorological and climatological data were measured at the same days as the phytoplankton samples were taken. Zooplankton was selected as a proxy for grazing pressure on phytoplankton. Two main groups of zooplankton were distinguished: cladocerans and copepods (without nauplii) (both measured as individuals m^{-2}).

Table 1 Hydro-morphometrical characteristics of the analyzed peri-Alpine lakes are shown

Lake name	Lake abbreviation	Time period	Altitude (m a.s.l.)	Surface		Watershed area (km ²)		Ratio WSA/SURF		Max depth (m)	Mean depth (m)	Volume (km ³)	Residence time (years)	Outflow (m ³ s ⁻¹)	Trophic state	Trophic class
				SURF (km ²)	WSA (km ²)	WSA	RATIO	MaxD (m)	MeanD							
Constance	CONST	80–89	395	472	10900	23.1	252	101	48	4.3	750	E	5			
Lower Zürich	LOZH	80–90	406	65	1740	26.8	136	51	3.3	1.4	89	ME	4			
Upper Zürich	UPZH	80–90	406	20	1564	77.2	48	23	0.5	0.18	76	M	3			
Walen	WAL	91–00	420	24	1061	44.2	145	100	2.4	1.4	57	O	1			
Small Geneva	SGE	01–05	372	81	7395	91.3	76	41	3	0.4	252	M	3			
Big Geneva	BGE	77–00	372	499	7395	14.8	310	172	86	11.4	252	E	5			
Maggiore	MAG	97–03	193	213	6599	31.0	370	178	37.5	4.1	291	O	1			
Garda	GARD	97–00	65	368	2290	6.2	350	133	49	26.6	58	OM	2			

The time period in which each lake was sampled, the unities and the abbreviations of lakes and variables are also given. The trophic state are classified in *E* eutrophic, *ME* meso-eutrophic, *M* mesotrophic, *OM* olig-mesotrophic, and *O* oligotrophic state

To estimate phytoplankton abundance, standard sampling and counting methods were employed (Utermöhl 1958; Lund et al. 1958; see also Straile 2000; Morabito et al. 2002; Anneville et al. 2002, 2004; Lavigne et al. 2006; Salmaso 2011). For every single taxon, biovolumes were calculated from recorded abundances and specific biovolumes approximated to simple geometrical solids. These procedures were standardized (Rott 1981), therefore minimizing the errors associated with the estimates of single-specific biovolumes in different laboratories. Since the species nomenclature for phytoplankton changed considerably during the different periods in which the data were collected and counted, it was necessary to continuously update and quality check with the species nomenclature, before proceeding with the analysis. The update was completed following the more recent monographs of the series “Süßwasserflora von Mitteleuropa” established by A. Pasher (Gustav Fisher Verlag, and Elsevier, Spectrum Akademischer Verlag). Subsequently, the species biomass was summed to the genera biomass ($\mu\text{g L}^{-1}$). The obtained 233 genera were afterward grouped into the morpho-functional groups (MFGs) defined by Salmaso and Padisák (2007). All in all, 25 MFGs were identified. Based on this classification, phytoplankton genera were grouped following the criteria of motility, specific nutrient requirement (autotrophy, mixotrophy), size, shape, and presence of gelatinous envelopes (Weithoff 2003). This work will focus particularly on cyanobacteria, which in these lakes are mainly represented by three morpho-functional groups, namely MFG 5a (thin filaments, Oscillatoriales), MFG 5c (other large colonies, mostly non-vacuolated Chroococcales), MFG 5d (small Colonies, Chroococcales) and MFG 5e (Nostocales).

Data analysis

Annual averages were computed from the original monthly and bimonthly data set (phytoplankton MFG abundance and descriptors). The resulting matrix contained 73 averaged yearly data, which was employed to evaluate the difference in between phytoplankton configuration in peri-Alpine lakes and to define the key factors driving phytoplankton community. Moreover, seasonal averages were used to assess the role played by the spring replenishment of P on the phytoplankton assemblages during the main

growth period, from summer to autumn (June to November). Therefore, in this specific analysis, variables were averaged for the summer–autumn period, with the exception of the nutrients (N and P), which were additionally averaged for the spring period, defined as March to May.

Data were further analyzed by non-metric multidimensional scaling (NMDS) and applied to Bray and Curtis’ dissimilarity matrices (Legendre and Legendre 1998) computed on MFGs biomass values. NMDS ordination can be rotated, inverted, or centered to any desired configuration. The accuracy of fit of the projections is measured by “stress” estimates (Kruskal and Wish 1978). Environmental variables were related to the strongest gradients in species composition by fitting environmental vectors to the NMDS configurations. In the present analysis, vector fitting finds the maximum correlation of the single variables with the set of lakes in the configurations. Fitted vectors point to the direction of most rapid change in the environmental variables, whereas their length is proportional to the correlation between the environmental variable and the ordination. The significance of vectors was based on 999 random permutations of the data (Oksanen et al. 2011). Before the NMDS ordination, MFGs were double-square rooted to reduce the weight of the more abundant groups (Salmaso 2010). The descriptors were log-transformed, $Y_i = \log (+ 1)$, prior to vector fitting.

The data analyses were performed with specific packages in R (ade4 and vegan; R Development Core Team 2011). The relationship between the descriptors was analyzed through a Spearman (ρ) rank correlation matrix (stats package in R, R Development Core Team 2011).

The phytoplankton composition between lakes

To examine whether each peri-Alpine lake data set has its own phytoplankton community, a NMDS was applied upon the “Bray-Curtis” dissimilarities matrix, permuted 999 times on the yearly averaged and double root squared MFG. Following this step, the categorical variable “lake” was built to partition the rows in classes belonging to the same lake data set. The functions “ordispider” (stars) and “ordihulls” (convex hulls) from the vegan package (Oksanen et al. 2011) were applied, in which the categorical variable “lake” grouped the samples belonging to the same

lake (Legendre and Legendre 1998). The lakes are labeled at the centroid of each convex hull. To further test whether the centroids have different position, we performed the “Adonis” function with 999 permutations (Oksanen et al. 2011).

Results

Hydro-morphometrical features

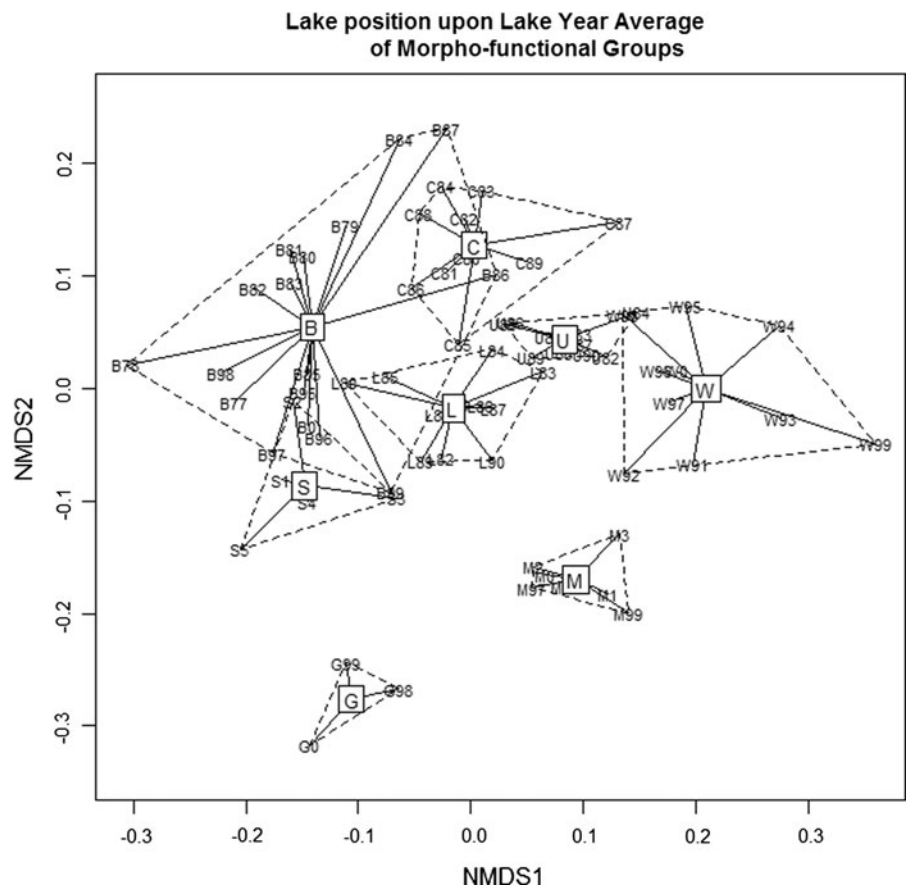
Table 1 presents the hydro-morphometrical characteristics of the eight analyzed data sets. Lake Maggiore reaches a maximum depth of 370 m, whereas the most shallow, Upper Lake Zürich, has a depth of 48 m. The lakes are located at altitudes between 420 m a.s.l. (Walen) and 65 m a.s.l. (Garda). Lake Geneva, the largest lake in central Europe, has a surface area 20 times that of Lake Walen (24 km²). The theoretical residence time ranges between 2 months (Upper Lake Zürich) and 27 years (Garda).

Upon hydro-morphometrical resemblance, namely trophic state, altitude, and size, the lakes can be differentiated into: (1) Larger lakes at lower altitudes and low trophic states (Lakes Garda and Maggiore); (2) larger lakes at intermediate altitudes and high trophic states (Lake Constance and Big Lake Geneva); (3) smaller lakes at higher altitude and low trophic states (Lake Walen); and (4) smaller lakes at higher altitude and higher trophic states (Upper and Lower Zürich). Small Lake Geneva is situated in between ranges of trophic state, altitude, and trophic levels.

Phytoplankton MFGs assemblages

Figure 2 shows the non-metric multidimensional scaling (NMDS) configuration based on the MFGs annual averages. The years belonging to the same lake are grouped together by convex hulls and labeled at their weighted centroid. The outcomes of the “adonis” function on 999 permutation indicate a significant different and non-random position of each centroid of

Fig. 2 Non-metric multidimensional scaling (NMDS) of the double-square roots transformed morpho-functional groups (MFG), which are yearly averaged. The label is situated at the centroid of each convex hull grouping the phytoplankton community for each year belonging to the same lake together (G Garda, M Maggiore, W Walen, U Upper Zürich, L Lower Zürich, C Constance, B Big Geneva, S Small Geneva)



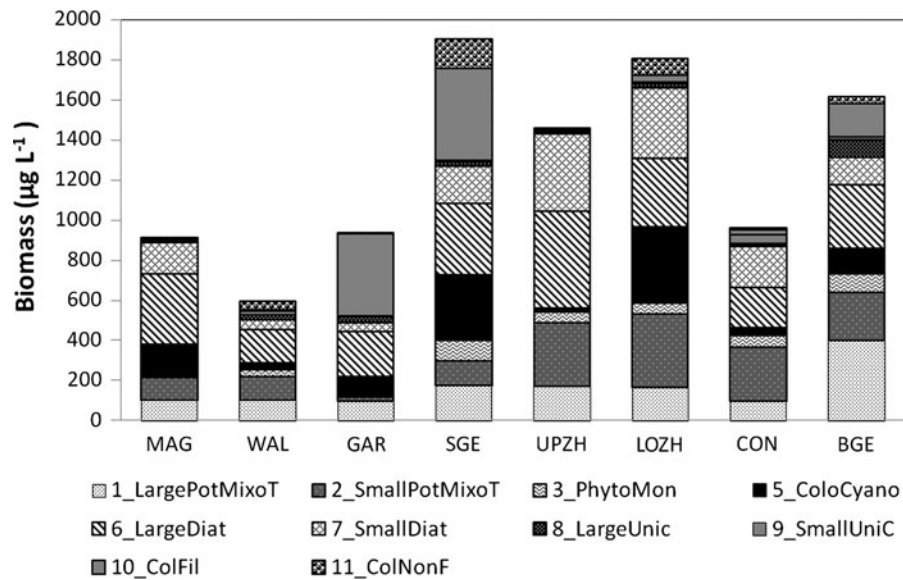


Fig. 3 Diversity of phytoplankton composition upon their morpho-functional groups (MFG) (Salmaso and Padisák 2007). The lakes are ordered following the trophic gradient from oligotrophic (Lake Maggiore, MAG) to eutrophic (Big Lake Geneva, BLG). The abbreviations of the MFG are given in the legend, and the full names are listed hereafter: 1 Large

colonial or unicellular, potential mixotrophs; 2 Small potential mixotrophs (unicellular); 3 Phytomonadina; 5 Colonial cyanobacteria; 6 Large diatoms; 7 Small diatoms; 8 Other large unicellular; 9 Other small unicellular; 10 Other filamentous colonies; 11 Other non-filamentous colonies

the lakes ($R^2 = 0.598$, $p < 0.001$). This highlights the existence of significant differences in the assemblages of the different lakes. The phytoplankton communities of Lake Constance and Small Lake Geneva overlap for some years with the one of Big Lake Geneva indicating some similarity in their composition during these years. Likewise, Lower Lake Zürich's position also suggests similarity to the phytoplankton configuration of Big Lake Geneva. In contrast, Lake Walen, Lake Maggiore, and Lake Garda display different positions, indicating a differentiated phytoplankton composition.

Figure 3 represents the biomass composition of the 11 main MFGs for each lake. For graphical reasons, the subordinated MFGs were not displayed. The lakes are ordered along the trophic gradient (see Table 1), from oligotrophy to eutrophy. Oligotrophic and oligomesotrophic states (Maggiore, Walen, and Garda) had lower phytoplankton biomass than eutrophic lakes. However, the largest quantity of biomass was recorded in the mesotrophic Small Lake Geneva, whereas Lake Constance's phytoplankton biomass was relatively low compared to its trophic state.

The MFG1 represents large flagellates including the potential mixotrophs like large chrysophytes/

haptophytes (*Dinobryon*, *Mallomonas*), dinophytes and euglenophytes (*Gymnodinium*, *Ceratium*). The MFG1 is present in all lakes, with highest biomass in Big Lake Geneva. Small potentially mixotrophic flagellates (MFG2) are present in all lakes but have higher biomass in lakes that exhibit higher trophic levels and are therefore almost absent in Lake Garda. The representative genera of MFG2 are *Rhodomonas*, *Cryptomonas*, and *Erkenia*. The MFG3, mostly autotrophic flagellates represented by Phytomonadina (especially *Chlamydomonas*, *Pandorina*, and *Phacotus*), are practically absent in Lake Maggiore and Garda, at the southern part of the Alpine chain, reaching relatively high biomass in Small Lake Geneva. Non-flagellated genera are represented by MFG5 to MFG11. The MFG5 comprises the colonial cyanobacteria, with the most representative cyanobacteria genera being *Planktothrix*, *Pseudoanabaena*, *Aphanothece*, *Aphanocapsa*, and *Aphanizomenon*. This group is present in all the lakes, however, with quite different biomass. MFG5 are most abundant in Small Lake Geneva and Lower Lake Zürich, and have important biomass in Lakes Maggiore, Garda, and Big Geneva, and low biomass in lakes Walen, Upper Zürich, and Constance. MFG5 tends to prefer lakes on

lower altitude and higher water temperature. Diatoms were subdivided into large diatoms and small diatoms represented, respectively, by MFG6 and MFG7. Large diatoms, mainly *Fragilaria*, *Asterionella*, *Diatoma*, and *Nitzschia*, are prevalent in all lakes, representing a very important contribution to biomass. Smaller diatoms (especially *Stephanodiscus*, *Aulacoseira*, *Cyclotella*, and *Navicula*) were also present in all lakes, but with lower biomass, and with a positive tendency in biomass toward higher trophic lakes. MFG8 represents the “Other Large Unicellular” Genera and MFG9 the “Other Small Unicellular” Genera. These two groups both exhibit relatively unimportant biomass. MFG8 (*Closterium*, *Staurastrum*, and *Cosmarium*) was particularly more abundant in Big Lake Geneva, whereas MFG9 (*Chlorella*, *Ankyra*) in Lake Constance. MFG10 and MFG11 represent “Others Colonials.” Filamentous colonies are grouped in MFG10 and non-filamentous colonies in MFG11. Filamentous colonies (MFG10, mostly *Mougeotia*) reach very high biomass in Lake Garda and Small Lake Geneva, but also have important biomass in Big Lake Geneva, whereas in the remaining lakes, their biomass is unimportant. MFG11, basically *Oocystis*, *Elakatothrix*, and *Scenedesmus*, showed important biomasses in Small Lake Geneva and Lower Lake Zürich.

To summarize, peri-Alpine lakes are characterized by high biomass of MFG1 and MFG6. MFG2, and MFG7 prefer lakes with higher nutrient loads, whereas the colonial cyanobacteria (MFG5) are more frequently found in lakes at lower altitude where water temperatures are higher.

Correlations between the environmental descriptors

Table 2 reports the Spearman correlation coefficients between the annual averages of the descriptors. Significant correlations ($p < 0.05$, $N = 73$) are highlighted in bold text with a larger font.

Both TP and SRP were strongly correlated with the conductivity, the duration of the stratification period, and the cladocera. Moreover, cladocera displayed a significant negative relationship with the water and air temperature and a positive relationship with the nitrate concentration. Copepods only correlated significantly with the euphotic depth.

The relationship between air temperatures and water temperature (annual averages) was adequately described by the following polynomial equation: $y = 0.06x^2 - 0.93x + 12.5$ ($r = 0.8$) (Fig. 4). Lakes Constance, Lower Zürich, Upper Zürich, and Walen are located at higher elevations with colder temperature regimes formed a distinct group from warmer lakes at lower altitudes (cf Fig. 1b). However, not only the altitudinal positions of the lakes but also their latitudinal location are responsible for the temperature gradient.

Phytoplankton configurations and relationships with the environmental variables

Analyses based on annual averages

In this section, we will interpret two NMDS configurations obtained from annual (Fig. 5a) and seasonal (Fig. 5c) averages of MFGs by vector fitting using the available environmental data. The configurations of lakes in Fig. 5a coincide with Fig. 2; however, data have been presented differently and in a similar way as in Fig. 5c. Total phosphorus was not considered because it was highly correlated with soluble reactive phosphorus (Table 2). Only SRP was used as it represents the chemical form for nutrient uptake by phytoplankton.

In Fig. 5a, the lowest stress factor (0.14) was reached after 6 runs and permuted 999 times, which guarantees a good configuration and confident interpretation (Zuur et al. 2007). The phytoplankton configuration showed a significant link with the water temperature as well as the air temperature (WT, AT), nutrients (SRP, $\text{NO}_3\text{-N}$), and conductivity (COND) ($p < 0.0001$). The grazing by cladocera and the duration of the stratification period also were linked ($0.0001 < p < 0.001$) with the lakes configuration. The euphotic depth and copepods did not show significant links with the NMDS ordination.

The direction as well the strength of SRP vectors and conductivity was similar, with lakes Constance and Big Lake Geneva, both eutrophic lakes, at the top of the arrows. In particular, MFG11a (naked colonies of Chlorococcales), MFG11c (other non-filamentous colonies), MFG10a (filaments—chlorophytes) and 8a (large unicellular conjugatophytes/chlorophytes) followed this gradient. These groups belong all to the

Table 2 Mean, standard deviation (SD), and the range (minimum and maximum values) of the yearly averaged phytoplankton descriptors are shown in the first 3 lines in *italic*, followed by the spearman rank correlation coefficient matrix

Descriptors	Conductivity at 20 °C (µS/cm)	Nitrate (µg/L)	Phosphorus tot (µg/L)	Soluble reactive phosphorus (µg/L)	Euphotic depth (m)	Water temperature (°C)	Cladocerans (Ind/m ²)	Copepods (Ind/m ²)	Air temperature (°C)	Stratification duration (month)
Abbreviation	COND	NO ₃ N	TP	SRP	EuD	WT	CLADO	COPE	AT	StratD
Mean	<i>248.8</i>	<i>544.8</i>	<i>24.4</i>	<i>13.9</i>	<i>6.9</i>	<i>10.5</i>	<i>200,369</i>	<i>370,504</i>	<i>10.5</i>	<i>6.72</i>
SD	<i>42.5</i>	<i>176.91</i>	<i>15.6</i>	<i>12.4</i>	<i>1.67</i>	<i>1.36</i>	<i>153,815</i>	<i>216,953</i>	<i>1.95</i>	<i>0.88</i>
Range	<i>137.8–292.3</i>	<i>209.7–779.3</i>	<i>5.7–51.2</i>	<i>1.39–36.9</i>	<i>3.9–10.9</i>	<i>9.1–13.9</i>	<i>13,621–495,016</i>	<i>94,764–807,471</i>	<i>8.08–13.5</i>	<i>5–8</i>
COND	1	-0.34	0.61	0.61	-0.02	0.04	0.09	-0.21	0.00	-0.25
NO ₃ N		1	0.05	-0.060	-0.23	-0.43	0.39	0.34	-0.38	-0.14
TP			1	0.98	0.05	-0.22	0.58	0.11	-0.15	-0.41
SRP				1	0.01	-0.18	0.54	0.14	-0.1	-0.38
EuD					1	0.4	-0.29	0.43	0.25	-0.33
WT						1	-0.49	0.26	0.81	0.14
CLADO							1	0.22	-0.38	0.01
COPE								1	0.12	-0.15
AT									1	0.25
StratD										1

The significant correlations ($\alpha < 0.001$) are represented in bold and larger font

green algae (including charophytes) having large life forms (colonies, filaments).

The air and water temperature vectors pointed toward Lake Garda. The main MFGs following this gradient were all filamentous forms, like the cyanobacteria MFG5a (Oscillatoriales) and the MFG10b, representing filamentous conjugatophytes. The nitrate gradient pointed toward the Upper Lake Zürich and Lake Walen. The MFGs 2a (small chrysophytes/haptophytes), 9d (small unicells from other groups than conjugatophytes and Chlorococcales) and 7b (small Pennates) followed this gradient. Even though these MFG are a heterogeneous taxonomic group, they interestingly have the same features, being small in size.

MFG5d (small colonies, Chroococcales) was nearest to Lake Maggiore, where the temperature was higher, the stratification period longer, the concentration of phosphorus and other ions low, and the concentration of nitrates high.

Cladocerans roughly had the same direction of the SRP and COND vectors (Fig. 5b). The remaining MFG's belonging to the cyanobacteria, that is, MFG 5c (large, non-vacuolated) and MFG 5e (Nostocales), were located around the middle of the environmental gradients.

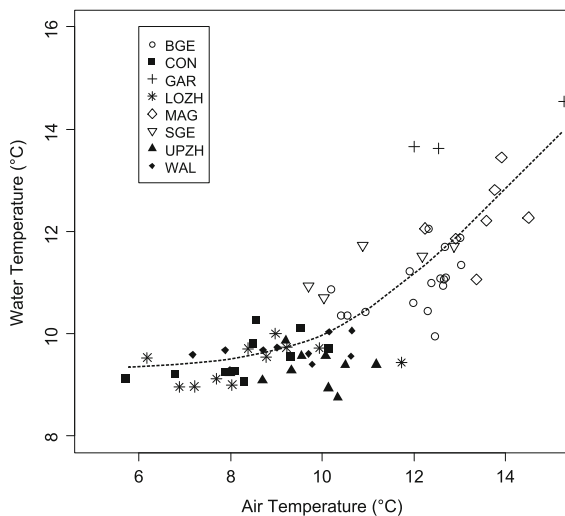


Fig. 4 Polynomial regression model in between the yearly averaged air and water temperature ($y = 0.06x^2 - 0.93x + 12.5$; $r = 0.8$; $N = 73$). Lakes situated on higher altitudes (CON Constance, LOZH Lower Zürich, UPZH Zürich Upper, WAL Walen) are represented with full symbols and differentiated from lakes on lower altitude (BGE Big Geneva, GAR Garda, MAG Maggiore, SGE Small Geneva)

Analyses carried out in the main growth period (summer–autumn)

The aim was to determine whether the spring nutrients represented an important source for phytoplankton during the main growth season (summer–autumn).

The more important variables linked with the NMDS configuration were, besides nutrient concentrations (SRP, NO_3N), the water and air temperature (WT, AT), as well as the spring pool of nutrients present during the maximum spring replenishment of euphotic layers (SRP_{sp} and NO_3sp) (Fig. 5d; $p < 0.01$). The direction and strength of the variables are practically coincident with those reported in Fig. 5b. Cladocerans and the duration of stratification did not show a link with the configuration in Fig. 5c. During the summer–autumn period, the phytoplankton composition of Lake Constance was more similar to that of Lower Lake Zürich (Fig. 5c). However, the MFG did not change the position of the Lakes Constance and Lower Zürich significantly. MFGs belonging to cyanobacteria were anew dispersed, with the difference that during the main growth season, MFG5c is more linked to the phosphorus gradient. MFG11c (other non-filamentous colonies) were more associated with the nutrient gradient.

Discussion

Nutrients and temperature influenced differently the deep peri-Alpine lakes. SRP and conductivity (as a proxy for the intensity of runoff), and air and water temperature had opposite directions in the NMDS configurations (Fig. 5b, d). The interpretation could not be univocal, because it could be simply linked to the characteristics of the lakes included in the data set. The warmer lakes, Garda and Maggiore, shared oligo-oligo-mesotrophic characteristics, while Big Lake Geneva and Constance were both eutrophic and colder. This study reveals an equivalent importance but a different effect on the phytoplankton community. However, both variables are interconnected variables, as warming affects the stratification of lakes; on the other hand, the deepening and duration of the stratification period impacts the nutrient concentration available for the biotic compartment in lakes (Wetzel 2001; Anneville et al. 2005, George 2010.). Besides difficulties to generalize the results, linked to the

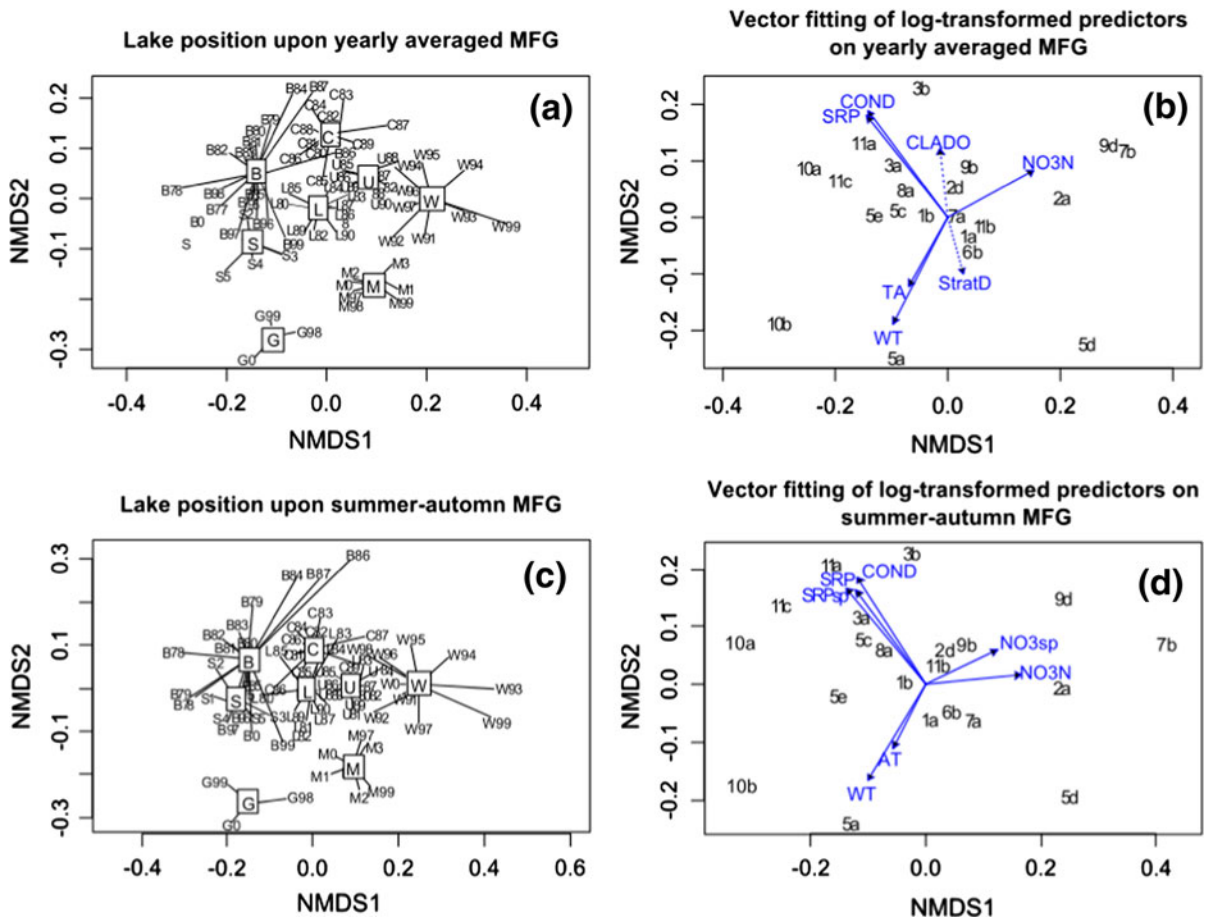


Fig. 5 a–d Output on the NMDS analyses based on yearly averaged MFG (a, b) and on summer–autumn averaged MFG (c, d). The samples belonging to the same lake are labeled at their centroid (G Garda, M Maggiore, W Walen, U Upper Zürich, L Lower Zürich, C Constance, B Big Geneva, S Small Geneva)

(a, c). The environmental variables were fitted, and the significant vectors (*bold* $p < 0.001$, *dotted* $p < 0.01$) show the direction of the environmental gradient and its strengths (length of the vector)

number of available lakes, the analysis allowed to appreciate the strong peculiarities in the composition of phytoplankton in the single lakes. These results support Bleckner's (2005) argument that differences and changes of phytoplankton result not only from the "landscape filter" but also from the so-called internal lake filter (abiotic/biotic interactions and lake history). Therefore, future studies on peri-Alpine lake are advised to further specify the nature and consequences of this "Lake Effect" on the state and behavior of phytoplankton communities, since it can be argued that the phytoplankton community of each lake will respond differently to the effects of eutrophication and climate change in the future (Gerten and Adrian 2001; George et al. 2004).

The eutrophication state based upon phosphorus concentration (OECD 1982) remains a reliable indicator, as higher trophic levels have higher phytoplankton biomass. An exception, however, was Small Lake Geneva, which followed a nonlinear hysteresis pattern (Gawler et al. 1988). Reduced phosphorus levels resulting from lake recovery management do not result in equal levels of reduced phytoplankton biomass. This resilience of total phytoplankton biomass in Small Lake Geneva was already observed in other deep peri-Alpine lakes (Anneville et al. 2002, 2004). Further, it would be interesting to analyze for Small Lake Geneva, either if the route of the phytoplankton community to recovery seems to differ significantly from the route to eutrophication, which

has been seen in shallow lake ecosystems (Ibelings et al. 2007), or if the community change enhanced by eutrophication and re-oligotrophication follows after a resilience time, a reversible trajectory as demonstrated recently in Lake Constance (Jochimsen et al. 2013).

The colonial cyanobacteria (MFG 5) were present in all the considered lakes and with higher frequency in lakes at intermediate and lower altitudes where water temperatures were higher. The filamentous cyanobacteria (Oscillatoriales MFG5a) and other large, mostly non-vacuolated colonies (MFG5c) were related to the increasing temperature. The specific ability of cyanobacteria to adapt to high temperatures has been reported in a number of studies (e.g., Paerl et al. 1985; Robarts and Zohary 1987; Briand et al. 2004; Reynolds 2006). MFG groups are an effective way to assess the ecology of lakes. For example, Lake Garda and Small Lake Geneva were characterized by MFG 10b, colonial filamentous genera, represented by *Mougeotia*. Actually, it was found that in Lake Garda, in the period of its maximum dominance, *Mougeotia* showed higher biomasses after cold winters and deep mixing, that is, after episodes of greater replenishment of phosphorus in the euphotic layers (Salmaso 2010). In summer 2001, the small Lake Geneva showed a massive development of *Mougeotia gracillima* bloom (Lavigne and Druart 2002). Therefore, these results demonstrated that the use of MFGs has a potential advantage, not only in comparison with, but also as complementary to the use of basic taxonomic units to reveal different ecological aspects. Using exclusively a few basic morphological groups, Kruk et al. (2011) stated that phytoplankton composition can be better predicted by a morphological approach. In the case of multiple phytoplankton assemblages recorded in different lakes, MFGs may represent a useful tool to concurrently investigate the evolution of different lakes, overcoming problems related to the comparison of different taxa and to the existence of possible differences in taxonomic accuracy (Salmaso and Padišák 2007; see also Reynolds et al. 2002).

The relationship between air and water temperature has its significance in the light of changing climate in the peri-Alpine region. Air temperature, which is directly affected by global warming, and water temperature were significantly correlated. The use of air temperature as a proxy for water temperature in peri-Alpine lakes, in the uppermost meters of the lake waters and during summer, has been discussed by

Livingstone and Lotter (1998). Moreover, formerly Gallina et al. (2011) were able to demonstrate the capacity of air temperature to affect indirectly the phytoplankton communities in the epilimnion in peri-Alpine lakes. The effect of air temperature on water temperature has been proven to be even stronger in the case of lakes at lower altitudes. An in-depth study of these aspects will require more complete information about the climate and the vertical physical structure of lakes in the Alpine area.

As previously stated, nutrients and conductivity ($\text{NO}_3\text{-N}$, SRP and COND), as well as temperatures (AT and WT), showed a strong link with the configurations of lakes obtained from MFG groups. Cladocerans and the duration of the stratification period had an important role, even though less prominent. Genera, which belong to the larger forms (colonies and filaments) of green algae, followed the phosphorus gradient. Smaller forms, such as the MFG3a (*Chlamydomonas*), were an exception. *Chlamydomonas* is known to be abundant in extremely nutrient-rich waters (Reynolds 2006). Padišák and Tóth (1991) also noticed that these small green algae seem to benefit from the environmental heterogeneity. The temperature gradient mainly pointed toward MFG5a (Oscillatoriales), with the potentially toxic genera *Planktothrix* and *Pseudanabaena* and partly of MFG5d (*Aphanothece*). Under future climate warming scenario, modifications in freshwater communities could favor morphotypes of colonial phytoplankton, especially colonial cyanobacteria (MFG5). Since colonial forms have evolutionary and/or eco-physiological advantages over unicellular forms, with regard to, that is, predation, viral mortality, and specialization (Berdall et al. 2009), it can be hypothesized that colonial forms will become in the future even more dominant in the peri-Alpine region that is very sensitive to short-changes in weather (Thompson et al. 2005). Likewise, Shatwell et al. (2008) showed how warming promoted the colonial filamentous cyanobacteria (Oscillatoriales) in Müggelsee (Germany), a shallow temperate lake. Contrariwise, several studies and ecological rules dealing with the effect of temperature–size relationship forecast that in aquatic systems, warming benefits the small forms (Daufresne et al. 2009; Winder and Hunter 2008). If analyzed more in detail, these considerations contrast only apparently. Large colonial species and filamentous cyanobacteria possessing gas vesicles have the ability, unlike other eukaryotic algae, to overcome the environmental

constrains originated by the increasing water stability, which is an important side effect of higher water temperatures (Walsby et al. 1997). The results presented here confirm Shatwell et al. (2008) rather general arguments and further suggest a strong connection between global warming and the development of cyanobacteria (Shatwell et al. 2008; Paerl and Huisman 2008; Paerl 2009, O'Neil 2011). Additionally, new insights relating warming with mixing regime were highlighted by a recent study using a 40-year data set in Lake Zürich demonstrating that principally the mixing regime was responsible for the seasonal control of the *P. rubescens* population (Posch et al. 2012). The outcome suggests that warmer years lead to weak mixis events, which in one hand increase the N:P ratio favoring the growth of *P. rubescens* and in the other hand prevent the collapse of the gaz vesicles due to the reduced mixing depths, which leads to a reduced pressure executed on the vesicles. These mechanisms are therefore mainly responsible for maintaining and increasing the population of *P. rubescens*. On the other side, it was demonstrated how warmer winters, decreasing the extent of the spring lake overturn and the extent of nutrient replenishment in deep lakes, depressed the growth of cyanobacteria (mostly Planktothrix) during the summer and autumn months (Salmaso 2012). Both these mechanisms contribute to maintain and increase the populations of *P. rubescens*.

In the middle of the temperature and phosphorus gradient, and opposite of the NO_3N gradient, MFG5c included *Anabaena* and *Aphanizomenon*. Both genera are potentially toxic, nitrogen-fixing cyanobacteria (Reynolds 2006). Therefore, these genera are tolerant in nitrogen-poor waters. Interestingly, this study found no cyanobacteria situated along the cold, NO_3N -rich gradient, further supporting the importance of both phosphorus and higher temperature in supporting the growth of this algal group.

During the growth period, nutrients and temperature were the main factors linked to phytoplankton. In contrast, the grazing and the duration of the stratification period did not seem to affect the summer–autumn population. This is in agreement with the PEG model, which indicates that grazing is mostly prevalent during the spring period (Sommer et al. 1986). Overall, these results demonstrate the crucial importance of the concentration of spring nutrients as fertilizers able to affect the phytoplankton composition, not only during

the summer–autumn period but also throughout the year. The nutrient enrichment in spring highly depends on the depth of the mixing layer (Sommer et al. 1986; George 2010), which in turn depends on the climatological/meteorological conditions encountered during winter (Salmaso et al. 2003; Salmaso 2012). Future climate change scenarios, however, predict milder winters with less deep mixing (Perroud et al. 2009). Consequently, this will provide a less nutrient-enriched epilimnion with important effects on the seasonal phytoplankton growth.

Conclusions

As hypothesized, differences in the composition of phytoplankton MFG in the deep peri-Alpine lakes were mainly driven with similar strengths by temperature (air and water) and nutrients (P, N) gradients and secondarily by the gradients of the duration of the stratification period and the grazing by the cladocerans. Cyanobacteria responded differently to these gradients. Oscillatoriales were closely related to higher water temperatures and longer stratification period; Chroococcales and small colonies were found where temperatures were warmer and nitrates more high; lower N-concentrations were linked with a greater presence of large non-vacuolated cyanobacteria colonies and Nostocales. Most notably, during the growth season, nutrients and temperature showed a strong link with the distribution of lakes in the NMDS configurations based on MFGs dissimilarities. In a future scenario, where temperatures in the Alpine region are predicted to increase, it is hypothesized that the effects of global warming will mostly impact cyanobacteria. This study gives strong support to the hypothesis that the fertilization of the epilimnion in deep lakes is a crucial stage in the phytoplankton growth cycle, controlling seasonal development throughout the rest of the year. Furthermore, the results support the existence of specific phytoplankton morpho-functional groups in different lakes, partly unrelated to the climatic and trophic gradients. Future efforts should focus on further defining those factors that can explain these intrinsic differences. In the broader context of research on the effects of climate change, the present study represents a first step toward the knowledge that is needed to model the impacts of climate change on phytoplankton assemblages.

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References

- Ambrosetti W, Barbant L, Rolla A (2006) The climate of Lago Maggiore area during the last fifty years. *J Limnol* 65(Suppl. 1):1–62
- Anneville O, Souissi S, Ibanez F, Ginot V, Druart JC, Angeli N (2002) Temporal mapping of phytoplankton assemblages in Lake Geneva: annual and interannual changes in their patterns of succession. *Limnol Oceanogr* 47:1355–1366
- Anneville O, Souissi S, Gammeter S, Straile D (2004) Seasonal and inter-annual scales of variability in phytoplankton assemblages: comparison of phytoplankton dynamics in three peri-alpine lakes over a period of 28 years. *J Freshw Biol* 49:98–115
- Anneville O, Gammeter D, Straile D (2005) Phosphorus decrease and climate variability: mediators of synchrony in phytoplankton changes among European peri-alpine Lakes. *J Freshw Biol* 50:1731–1746
- Arrigo K (2005) Marine microorganism and global nutrient cycles. *Nature* 437:349–355
- Begert M, Schlegel T, Kirchhofer W (2005) Homogenous temperature and precipitation series of Switzerland from 1864 to 2000. *Int J Climatol* 25:65–80
- Beniston M (2006) Mountain weather and climate: a general overview and a focus on climatic change in the Alps. *Hydrobiologia* 526:3–16
- Beniston M, Diaz HF, Bradley RS (1997) Climatic change at high elevation sites; a review. *Clim Chang* 36:233–251
- Berdall J, Allen D, Braag J, Finkel ZV, Flynn KJ, Quigg A, Rees TAV, Richardson A, Raven JA (2009) Allometry and stoichiometry of unicellular, colonial and multicellular phytoplankton. *New Phytol* 181:295–309
- Bleckner T (2005) A conceptual model of climate-related effects on lake ecosystems. *Hydrobiologia* 533:1–14
- Briand JF, Lebourlangier C, Humbert JF (2004) *Cylindrospermopsis raciborskii* (cyanobacteria) invasion at mid-latitudes: selection, wide physiological tolerance, or global warming. *J Phycol* 40:231–238
- Daufresne M, Lengfellner K, Sommer U (2009) Global warming benefits the small in aquatic ecosystems. *P Natl Acad Sci USA* 106:12788–12793
- Elliot JA, Jones ID, Thackeray SJ (2006) Testing the sensitivity of phytoplankton communities to changes in water temperature on nutrient load, in a temperate lake. *Hydrobiologia* 559:401–411
- Gallina N, Anneville O, Beniston M (2011) Impacts of extreme air temperatures on cyanobacteria in five deep peri-Alpine lakes. *J Limnol* 70(2):186–196
- Gawler M, Balvay G, Blanc P, Druart JC, Pelletier JP (1988) Plankton ecology of Lake Geneva: a test of the PEG-Model. *Arch Hydrobiol* 114:161–174
- George DG (ed) (2010) The impact of Climate Change on European Lakes. Aquatic Ecology Series 4. Springer, New York, pp 339–358. doi:10.1007/978-90-481-2945-4_18
- George G, Marbery SC, Hewitt DP (2004) The influence of the North Atlantic Oscillation in the physical, chemical and biological characteristics of four lakes in the English Lake District. *J Freshw Biol* 49:760–774
- Gerten DR, Adrian R (2001) Differences in the persistency of the North Atlantic Oscillation. *Limnol Oceanogr* 46:448–455
- Huisman J, Matthijs HCP, Visser PM (eds) (2005) Harmful cyanobacteria. Springer, Berlin
- Hutchinson GE (1957) A treatise on limnology, vol 1. Wiley, New York
- Ibelings BW, Mur LR, Walsby AE (1991) Diurnal changes in bouncy and vertical distribution in populations of Microcystis in two shallow lakes. *J Plankton Res* 13:419–436
- Ibelings BW, Portielje R, Lammens E, Noordhuis R, van den Berg MS, Joosse W, Meijer ML (2007) Resilience of Alternative Stable States during the Recovery of Shallow Lakes from Eutrophication: Lake Veluwe as a Case Study. *Ecosystems* 10:4–16
- Intergovernmental Panel on Climate Change (IPCC) (2007) Synthesis report. Contribution of Working Groups I, II and III to the fourth assessment report of the intergovernmental panel on climate change. Core writing team, Pachauri RK, Reisinger A (eds)
- Jochimsen MC, Kümmerlin R, Straile D (2013) Compensatory dynamics and the stability of phytoplankton biomass during four decades of eutrophication and oligotrophication. *Ecol Lett* 16:81–89
- Kruk C, Huszar VLM, Peeters ETHM, Bonilla S, Costa LS, Lürling M, Reynolds CS, Scheffer M (2010) A morphological classification capturing functional variation in phytoplankton. *Freshw Biol* 55(3):614–627
- Kruk C, Peeters ETHM, Van Nes EH, Huszar VML, Costa LS, Scheffer M (2011) Phytoplankton community composition can be predicted best in terms of morphological groups. *Limnol Oceanogr* 56(3):110–118
- Kruskal JB, Wish M (1978) Multidimensional scaling. Sage University Paper series on Quantitative Applications in the Social Sciences, 07–011. Sage Publications, Beverly Hills and London
- Lavigne S, Druart JC (2002) Évolution du phytoplancton du Léman. Rapp Comm int prot eaux Léman contre pollut. Campagne 2001:71–84
- Lavigne S, Cordonier A, Gallina N, Perfetta J (2006) Évolution du phytoplancton du Petit Lac. Campagnes 2001–2005. Rapp. Comm int prot eaux Léman contre pollut. Campagne 2005:101–116
- Legendre P, Legendre L (1998) Numerical ecology, 2nd English edition. Elsevier Science, Amsterdam
- Litchman E, Klausmeier CA (2008) Trait-based community ecology of phytoplankton. *Annu Rev Ecol Evol Syst* 39:615–639
- Livingstone DM, Lotter AF (1998) The relationship between air and water temperatures in lakes of the Swiss Plateau: a case study with paleolimnological implications. *J Paleolimnol* 19:181–198

- Lund JWG, Kipling C, Lecren EO (1958) The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. *Hydrobiologia* 11:143–170
- Lung WS, Paerl HW (1988) Modeling green-blue algal blooms in the Lower Neuse River. *Water Res* 22:895–905
- Morabito G, Ruggio D, Panzani P (2002) Recent dynamics (1995–1999) of the phytoplankton assemblages in Lago Maggiore as a basic tool for defining association patterns in the Italian deep lakes. *J Limnol* 61(1):129–145
- Moss B, McKee D, Atkinson D, Collings SE, Eaton JW, Gill AB, Harvey I, Hatton K, Heyes T, Wilson D (2003) How important is climate? Effects of warming, nutrient addition and fish on phytoplankton in shallow lake microcosms. *J Appl Eco* 40:782–792
- Organisation for Economic Co-operation and Development (OECD) (1982) Eutrophication of waters. Monitoring, assessment and control. Organisation for Economic Cooperation and Development, 193 pp
- Oksanen J, Blanchet FG, Kindt R, Legendre P, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2011) vegan: Community Ecology Package. R package version 1.17–10. <http://CRAN.R-project.org/package=vegan>
- Padisák J, Tóth LG (1991) Some aspects of the ecology of the subdominant green algae in a large nutrient limited shallow lake (Balaton, Hungary). *Arch Protistenkunde* 139:225–242
- Paerl HW, Huisman J (2008) Blooms like it hot. *Science* 320:57–58
- Paerl HW, Huisman J (2009) Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. *Environ Microbiol Rep* 1:27–37
- Paerl HW, Paul VJ (2012) Climate change: links to global expansion of harmful cyanobacteria. *Water Res* 46:1349–1363
- Paerl HW, Bland PT, Bowles ND, Haibach ME (1985) Adaptation to high intensity, low wavelength light among surface blooms of the cyanobacterium *Microcystis aeruginosa*. *Appl Environ Microbiol* 49:1046–1052
- Paul VJ (2008) Global warming and cyanobacterial harmful algal blooms. In: Hudnell KH (ed) *Cyanobacterial harmful algal blooms: state of the science research needs series*, vol 619. Springer Advances in biology and medicine, New York, pp 239–257
- Perroud M, Goyette S, Martynov A, Beniston M, Anneville O (2009) Simulation of multi-annual thermal profiles in deep Lake Geneva: a one-dimensional lake-model intercomparison study. *Limnol Oceanogr* 55:1574–1594
- Posch T, Köster O, Salcher MM, Pernthaler J (2012) Harmful filamentous cyanobacteria favoured by reduced water turnover with lake warming. *Nat Clim Chang* 2:809–813
- R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>
- Reynolds CS (2006) *Ecology of phytoplankton, ecology, biodiversity and conservation series*. Cambridge University Press, Cambridge
- Reynolds CS, Walsby AE (1975) Water blooms. *Biol Rev* 50:437–481
- Reynolds CS, Huzar V, Kruk C, Naselli-Flores L, Melo S (2002) Towards a functional classification of the freshwater Phytoplankton. Review. *J Plankton Res* 24:417–428
- Roberts RD, Zohary T (1987) Temperature effects on photosynthesis capacity, respiration, and growth rates of bloom-forming cyanobacteria. *New Zeal J Mar Fresh* 21:391–399
- Rott E (1981) Some results from phytoplankton counting intercalibrations. *Schweiz Z Hydrol* 43:34–63
- Ryding SO, Rast W (1989) The control of eutrophication in lakes and reservoirs. UNESCO and Parthenon Publishing Group, Paris
- Salmaso N (2010) Long-term phytoplankton community changes in a deep subalpine lake: responses to nutrient availability and climatic fluctuations. *Freshw Biol* 55:825–846
- Salmaso N (2011) Interactions between nutrient availability and climatic fluctuations as determinants of the long term phytoplankton community changes in Lake Garda, Northern Italy. *Hydrobiologia* 660:59–68
- Salmaso N (2012) Influence of atmospheric modes of variability on the limnological characteristics of a deep lake south of the Alps. *Clim Res* 51:125–133
- Salmaso N, Padisák J (2007) Morpho- Functional Groups and phytoplankton development in two deep lakes (Lake Garda, Italy and Lake Stechlin, Germany). *Hydrobiologia* 578:97–112
- Salmaso N, Mosello R, Garibaldi L, Decet F, Brizzio MC, Cordella P (2003) Vertical mixing as a determinant of trophic status in deep lakes: a case study from two lakes south of the Alps (Lake Garda and Lake Iseo). *J Limnol* 62(Suppl 1):33–41
- Salmaso N, Buzzi F, Garibaldi L, Morabito G, Simona M (2012) Effects of nutrient availability and temperature on phytoplankton development: a case study from large lakes south of the Alps. *Aquat Sci* 74:555–570
- Schopf JW (2000) The fossil record: tracing the roots of the cyanobacterial lineage. In: Whitton BA, Potts M (eds) *The ecology of cyanobacteria*. Kluwer Academic Publishers, Dordrecht, pp 13–15
- Shatwell T, Köhler J, Nicklisch A (2008) Warming promotes cold-adapted phytoplankton in temperate lakes and opens a loophole for Oscillatoriales in spring. *Glob Chang Biol* 14:1–7
- Sivonen K, Jones G (1999) Cyanobacterial toxins. In: Chorus I, Bertram J (Eds) *Toxic cyanobacteria in water: a guide to public health consequences, monitoring and management*. The World Health Organization. ISBN 0–419–23930–8. E&FN Spon, London, UK, pp 41–111
- Sommer U, Gliwicz ZM, Lampert W, Duncan A (1986) PEG-model of Seasonal Succession of Planktonic Events in Fresh Waters. *Arch Hydrobiol* 106:433–471
- Stich HB, Brinker A (2011) Oligotrophication outweighs effect of global warming in a large, deep, stratified lake ecosystem. *Glob Chang Biol* 16:877–888
- Straile D (2000) Meteorological forcing of plankton dynamics in a large and deep continental European lake. *Oecologia* 122:44–50
- Thompson R, Kameniki C, Schmidt R (2005) Ultra sensitive Alpine lakes and climate change. *J Limnol* 64:139–152
- Utermöhl H (1958) Zur Vervollkommnung der quantitativen Phytoplankton Methodik. *Mitteilungen der Internationalen Vereinigung für Limnologie* 9:1–38

- Vollenweider RA, Kerekes J (1982) Eutrophication of waters. Monitoring, assessment and control. OECD Cooperative programme on monitoring of inland waters (Eutrophication control), Environment Directorate, OECD, Paris
- Walsby AE, Hayes PK, Boje R, Star LJ (1997) The Selective advantage of buoyancy provided by gas vesicles for planktonic cyanobacteria in the Baltic Sea. *New Phytol* 136:407–417
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ (2002) Phylogenies and community ecology. *Annu Rev Ecol* 33:475–505
- Weithoff G (2003) The concepts of “plant functional types” and “functional diversity” in lake phytoplankton- a new understanding of phytoplankton ecology? *Freshw Biol* 48:1669–1675
- Wetzel RG (2001) *Limnology: lake and river ecosystems*, 3rd edn. Academic Press, San Diego
- Williamson CE, Saros JE, Vincent WF, Smol JP (2009) Lakes and reservoirs as sentinels, integrators and regulators of climate change. *Limnol Oceanogr* 54:2273–2282
- Winder M, Hunter DA (2008) Temporal organization of phytoplankton communities linked to chemical and physical forcing. *Oecologia* 156:179–192
- Zuur AF, Ieno EN, Smith GM (2007) *Analysing ecological data*. Springer, New York