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Winter and spring mixing depths affect the trophic status and composition of phytoplankton in the northern meromictic basin of Lake Lugano

Marco SIMONA

Ufficio Protezione e Depurazione Acque - Sezione Protezione Aria, Acqua e Suolo, Riva Paradiso 15, CH-6900 Paradiso (Switzerland)
e-mail: marco.simona@ti.ch

ABSTRACT

The trophic state of Lake Lugano is still too high to be acceptable, despite extensive recovery measures undertaken in recent decades which have resulted in a reduction of the external phosphorus load to the deepest of the lake's basins (northern basin; Z_{max}=286 m) to fairly acceptable values. Since meromixis was established in the middle of last century, the deep hypolimnion of the northern basin (the layer between ca *100 m and the bottom) has contained high quantities of nutrients (especially phosphorus) which are a major potential source of internal load. When there are particularly strong winter mixing events, a portion of this phosphorus reserve is redistributed along the upper water column (0-100 m). The impact of meteo-climatic conditions on the plankton biocenosis were analysed using data collected in the northern basin (Gandria station) during the three-year period 1998-2000. The phytoplankton composition, which is typical of eutrophicated waters, shows marked interannual variations, also depending on the degree of mixing of the waters at the start of the vegetative period. Though there is no steady pattern of typical dominant species / master species in the lake, there is a seasonal succession characterised by a marked development of diatoms in spring, and a predominance of chlorophyceans and cyanobacteria in summer and autumn. Under present conditions, the mechanisms of internal replenishment of nutrients towards the euphotic layer, due to the phenomena of late winter and spring mixing, constitute a significant source of nutrients for the spring and summer growth of phytoplankton. On the other hand, pronounced mixing phenomena, like those occurring in the two-year period 1999-2000, can reduce the hypolimnetic nutrient reserves and cause a decrease in the trophic potential of the basin, contrasting with an increase in algal biomass in the euphotic zone.*

Key words: deep lakes, eutrophic lakes, phytoplankton, mixing depth

1. INTRODUCTION

Lake Lugano has been the object of many limnological studies since the end of the nineteenth century. Early research into the plankton populations included the studies of zooplankton by Pavesi (1880) and of phytoplankton by Steiner (1913). Research intensified throughout the twentieth century, especially after the second world war, when the first signs of the eutrophication process were appearing in the lake (Polli & Simona 1992).

In 1972, the International Commission for the Protection of Swiss-Italian Waters (CIPAIS) began to coordinate limnological research on the water of lakes Maggiore and Lugano, common to both countries, with the adoption of a long-term plan to monitor their trophic evolution and assess the impact of the algal nutrient load on the two lakes. In 1980, Canton Ticino (CH) took over the limnological programme involving Lake Lugano and its tributaries, appointing the former Environmental Studies Laboratory (LSA, now UPDA), of the Air, Water and Soil Protection Department (SPAAS) to implement it. At the same time (1978-81) the former Italian Institute of Hydrobiology in Pallanza (Italy) (now the Institute of Ecosystem Study, CNR-ISE) conducted a comparative study of the major deep subalpine lakes (Maggiore, Lugano, Como, Iseo, Garda), to assess their trophic state in the light of the changes which had taken place in their watersheds during the previous decades (Ambrosetti *et al*. 1983). Linked with these studies is a project conducted in the framework of the Working Group on the Deep Southern Subalpine Lakes (QuAlps and GLaP projects; Mosello & Salmaso 2000; Ruggiu 2002). This project, which includes our study, has the aim of comparing the phytoplankton communities of the large lakes south of the Alps, which, despite their location in a common geographical and climatic context, have very different trophic states. The specific objectives of this paper include i) a description of the recent (1998-2000) composition and structure of phytoplankton in the deeper basin of Lake Lugano (northern basin) and ii) a study of the influence of climatic evolution and lake mixing dynamics on the selection of the dominant phytoplankton species.

2. STUDY SITE

Lake Lugano is situated on the border between Switzerland and Italy. It occupies a valley originating from the river erosion of a canyon of the Tertiary period, profoundly reshaped during the Alpine glaciations of the Pleistocene (Niessen 1987). The watershed (624 km^2) is made up of calcareous rocks, gneiss and por-

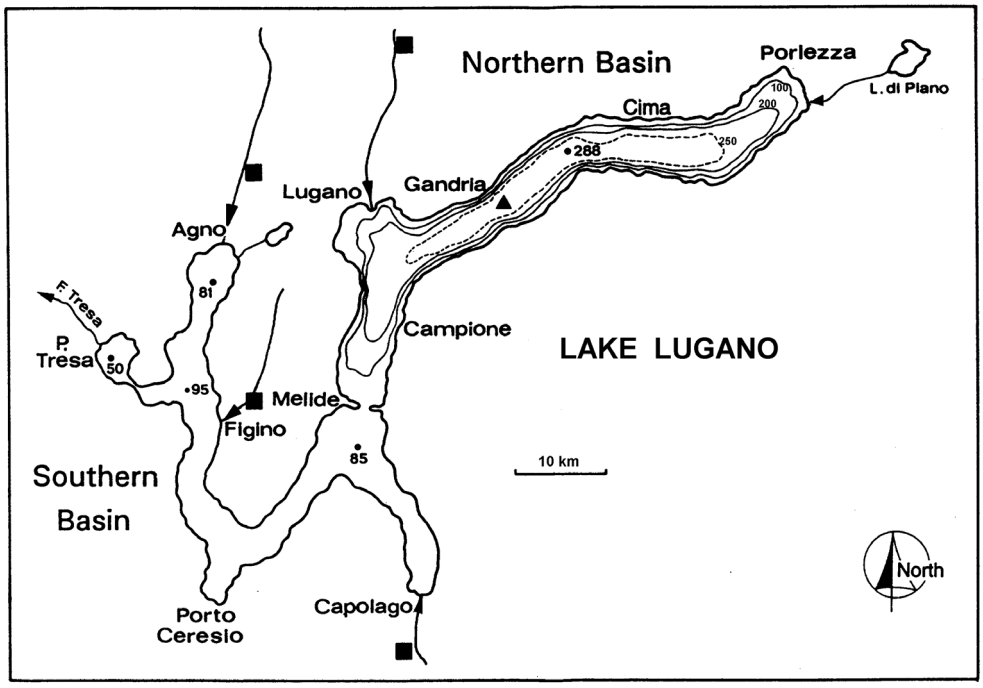

Fig. 1. Bathymetric map of Lake Lugano. The filled triangle and the filled squares indicate respectively the sampling site in the northern basin and the wastewater treatment plants.

Tab. 1. Morphological and hydrological characteristics of Lake Lugano.

Lake basin		Northern	Southern	Ponte Tresa
lake area	(km^2)	27.5	20.3	1.1
maximum depth	(m)	288	95	50
mean depth	(m)	171	55	33
lake volume	(km^3)	4.69	1.14	0.03
theoretical renewal time	(y)	12.3	1.4	0.04
Watershed				
land area	(km^2)	269.7	290.3	5.6
total area	(km^2)	297.2	607.8	614.5

phyry. Due to the pre-alpine climate and the configuration of the land, the lake tributaries have the character of torrential streams. Glacial action has divided the lake into three sub-basins, each with very different geo-morphological and hydrological characteristics. Figure 1 shows the bathymetric map and the location of the sampling station in the northern basin; table 1 summarises the main morphological and hydrological data of the whole lake.

The northern basin reaches its maximum depth (288 m) off the small town of Gandria. The small surface of its catchment area, compared to its water volume, determines a long theoretical water renewal time (12.3 years). The condition of meromixis characterising this basin was triggered by an increase in eutrophication, and enhanced by its great depth, which makes water circulation even more difficult (Wüest *et al*. 1992).

A more detailed description of the lake is reported in Barbieri & Polli (1992).

3. METHODS

Limnological monitoring of the northern basin of Lake Lugano has been regularly performed since 1980, and since 1983 samples have been taken at least monthly in the station of Gandria. The data in this study refer to the three-year period 1998-2000. Throughout this period the environmental variables were measured fortnightly (physical and chemical parameters) or monthly (algal nutrients), while the plankton community evolution was studied on the basis of 16 annual samples.

The physical characteristics of the whole water column were measured every metre using a multiparameter probe; the following parameters were measured: temperature, conductivity, pH, dissolved oxygen and light transmittance. Water transparency was measured by Secchi disk (SD), and photosynthetic radiation (PAR)

Tab. 2. Air temperature, water temperature and mixing depth in Lake Lugano.

Year		1998	1999	2000
Mean yearly air temp.	(°C)	12.5	12.6	13.0
Mean winter air temp. (Dec-Feb)	(°C)	5.3	3.9	4.3
Max. mixing depth	(m)	55	78	86
Water temp. at the overturn	(°C)	6.3	5.6	5.6
Max. water temp. (Aug. 0.4 m)	(°C)	26.0	24.3	24.0

Tab. 3. Correlation coefficients (*r*) among the untransformed (lower-left triangular matrix) and log transformed (upper-right triangular matrix) values of pH, percent saturation of oxygen, conductivity, algal nutrients (P, N, Si), Secchi disk transparency, chlorophyll-*a*, phytoplankton density and biovolume, measured in the epilimnetic (0-20 m) layer at Gandria in the years 1998-2000. (**Bold type** correlations are significant at $p < 0.05$; number of cases : n = 72; density and biovolume: n = 48).

	pH	O_2 (%)	Cond (20°C)	RP	NO_3-N	SiO_2-Si	Secchi	Chl-*a*	Density	Biovolume
pH	-	**0.82**	**-0.42**	**-0.45**	**-0.52**	**-0.59**	**-0.55**	**0.39**	**0.29**	**0.34**
O_2 (%)	**0.79**	-	-0.15	**-0.35**	**-0.46**	**-0.71**	**-0.39**	**0.26**	0.16	**0.32**
Cond (20°C)	**-0.42**	-0.10	-	**0.77**	0.15	-0.11	**0.46**	-0.19	**-0.46**	-0.08
PO_4-P	**-0.56**	**-0.44**	**0.77**	-	0.09	**0.26**	0.21	-0.13	-0.15	0.07
NO_3-N	**-0.53**	**-0.49**	0.10	0.00	-	**0.32**	**0.71**	**-0.38**	**-0.54**	**-0.48**
SiO_2-Si	**-0.59**	**-0.69**	-0.06	**0.34**	**0.41**	-	0.04	-0.21	0.30	-0.13
Secchi	**-0.58**	**-0.39**	**0.42**	**0.25**	**0.68**	0.11	-	**-0.60**	**-0.69**	**-0.79**
Chl-*a*	**0.28**	0.10	-0.14	-0.14	**-0.35**	-0.22	**-0.53**	-	0.24	**0.79**
Density	0.26	0.27	-0.23	-0.18	**-0.38**	0.02	**-0.39**	0.00	-	**0.41**
Biovolume	0.19	0.14	-0.05	-0.03	**-0.49**	-0.12	**-0.72**	**0.81**	0.28	-

by underwater quantum sensor (LiCor 192SA); the euphotic depth (Z_{eu}) was considered operationally as the depth at which $I_z=0.01\times I_0$ (where I_z and I_0 are the light intensities at the depth Z and at the surface, respectively). Chemical analyses were performed on water samples collected at 16 discrete depths (covering the whole water column). They included determination of dissolved inorganic carbon, algal nutrients (total and reactive phoshorus (RP, TP), nitrate nitrogen and ammonium, reactive silica), dissolved oxygen, and substances produced under anoxic conditions (e.g., CH_4, HS^-).

Water samples for chlorophyll-*a* and phytoplankton analyses were collected at the integrated depth from 0 to 20 m with a Schröder-sampler (Schröder 1969). Chlorophyll-*a* was also measured at 11 different depths in the euphotic layer. Zooplankton were analysed on samples collected in the 0-50 m layer by net hauls (with 95 µm mesh). Chlorophyll-*a* was determined by spectrophotometry after extraction in 90% ethanol (DEV 1986). Phytoplankton were determined and counted by inverted microscopy on subsamples preserved in acetic Lugol's solution (Leitz Diavert and Leica DM IL microscopes), following Sournia (1978). Algal biomass was calculated by multiplying the value of cell density with specific biovolumes, approximated to simple geometrical solids (Rott 1981). Crustacean zooplankton were counted with a stereoscope (Wild M3). Zooplankton biomass (dry weight) was calculated by applying the length-weight relationship proposed by Dumont *et al*. (1975). Correlations between phytoplankton abundance and chemical variables (Tab. 3) were calculated according to Salmaso (2002).

The Shannon diversity index (H') was calculated using the natural logarithm of the individual algal biovolumes of each sample (cf. Magurran 1988).

Meteorological and hydrological data were supplied by the Federal Office of Meteorology and Climatology (METEOSWISS) and by the Swiss National Hydrological and Geological Survey.

Further details on the sampling and chemical analytical methods used may be found in the annual reports on eutrophication research in Lake Lugano (LSA 1990).

4. RESULTS

4.1. Meteorological and hydrological characteristics

Figure 2 reports the monthly trend of air temperature and precipitation, measured at the weather station of Lugano. The meteorological trend over the three investigated years shows a high degree of variability. As regards air temperature, 1998 was very mild from January to March and particularly cold in autumn (November); the 1999 values were close to the long term average during the whole year, and the values for 2000 were continuously above the average, except for the month of July.

Precipitation was slightly lower than the long term average in 1998 (1508 mm), slightly higher in 1999 (1699 mm) and among the highest values ever recorded in 2000 (2149 mm). In 1998 and 1999 monthly precipitations were always higher than 100 mm between April and October, whereas the rainfall distribution during 2000 was always very irregular, with extreme peaks (>300 mm) in July, October and November.

4.2. Thermal regime and euphotic depth

During summer the lake showed a marked thermal stratification, reaching the highest temperature values in August, and with a metalimnion at about 15 m. In the 0-50 m layer, the lowest temperatures were measured in February (*ca* 6 °C; Fig. 3).

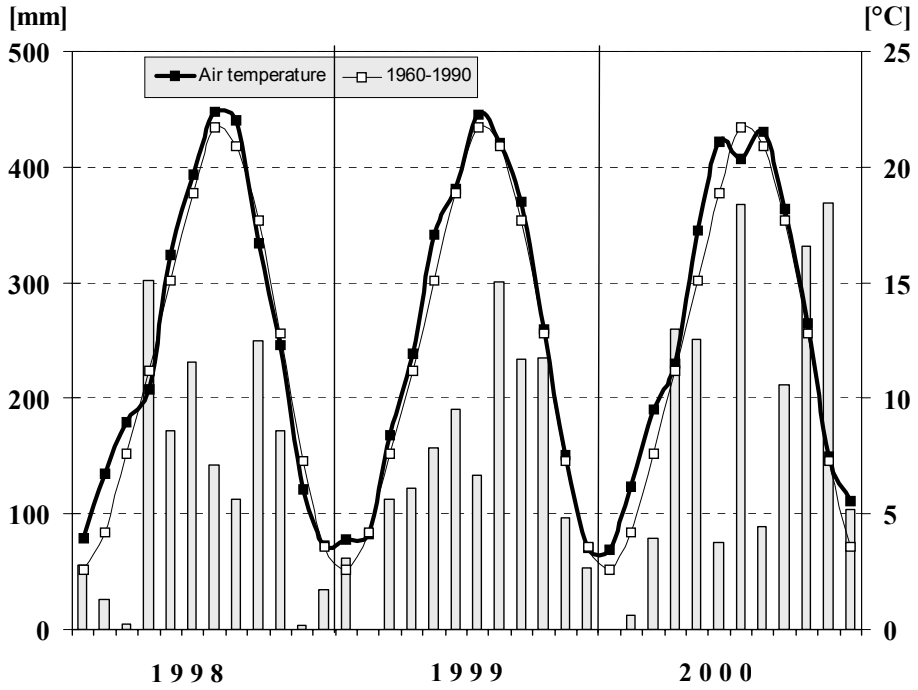

Fig. 2. Monthly average values of precipitation (bars, mm) and air temperature (line, °C) measured at the weather station of Lugano-Biblioteca Cantonale (data: Meteoswiss).

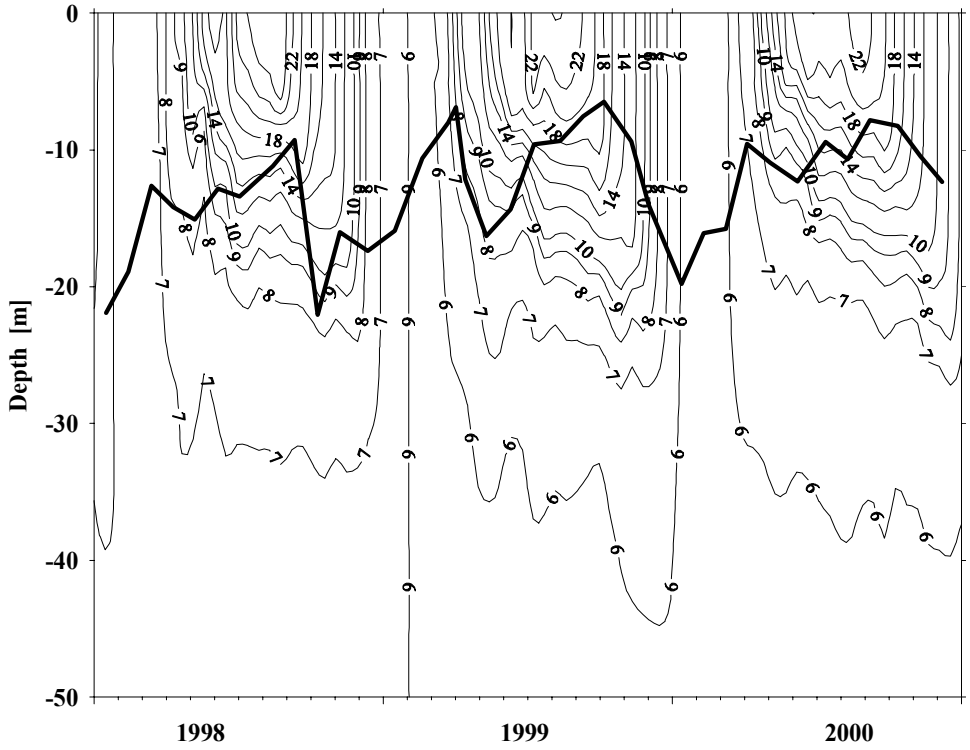

Fig. 3. Thermal regime (°C) and euphotic depth (m) of Lake Lugano (Gandria).

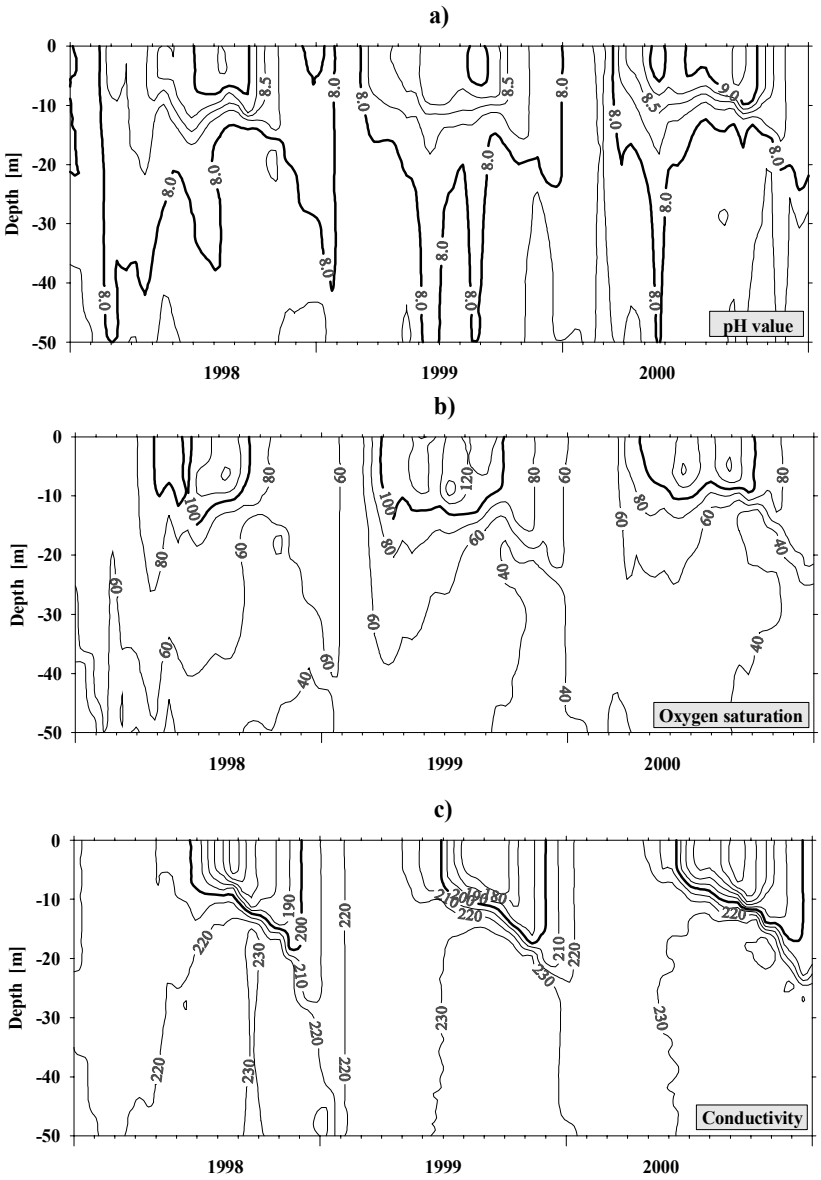

Fig. 4. Seasonal fluctuations of (**a**) dissolved oxygen, (**b**) pH and (**c**) conductivity in the 0-50 m layer of Lake Lugano (Gandria).

As shown by Ambrosetti *et al*. (1983), the heat budget of a lake depends largely on the difference between the mean temperatures of the atmosphere and the water, as well as on the wind regime and solar radiation. In particular, the trend of the values in the winter period (December-February) is decisive for the winter mixing. The data recorded during the investigated period show that, despite the steady increase in mean annual values of atmospheric temperature over the last two decades (LSA 1998), the colder winters of 1998-1999 and 1999-2000 caused a progressive cooling of the water column and an increase of the winter and spring mixing depth (Tab. 2). In 1998 the mean winter air temperature was 5.3 °C; at the same time, there was a mixing of the water column to 55 m at a temperature of 6.3 °C. In the two following years there was a sharp decrease in the mean winter air temperature (3.9 °C in 1999 and 4.3 °C in 2000), which caused a greater deepening of the mixed layer, to 78 m (1999) and 86 m (2000), with a water temperature of 5.6 °C in both years (Tab. 2).

High euphotic depth values (around 20-22 m) were observed on three occasions (January 1998, October 1998 and January 2000). An important clear-water phase occurred in May 1999 (Z_{eu}=16 m). During the vegetative period (March-October) the productive layer generally reached 10-15 m depth; however, during strong algal developments (e.g., March and September 1999) Z_{eu} decreased to 6.5-7.0 m.

4.3. Water chemistry

The isoplethes of pH, oxygen saturation and conductivity in the upper water column (0-50 m) over the three years are shown in figure 4. The annual fluctuations of these variables were mainly determined by

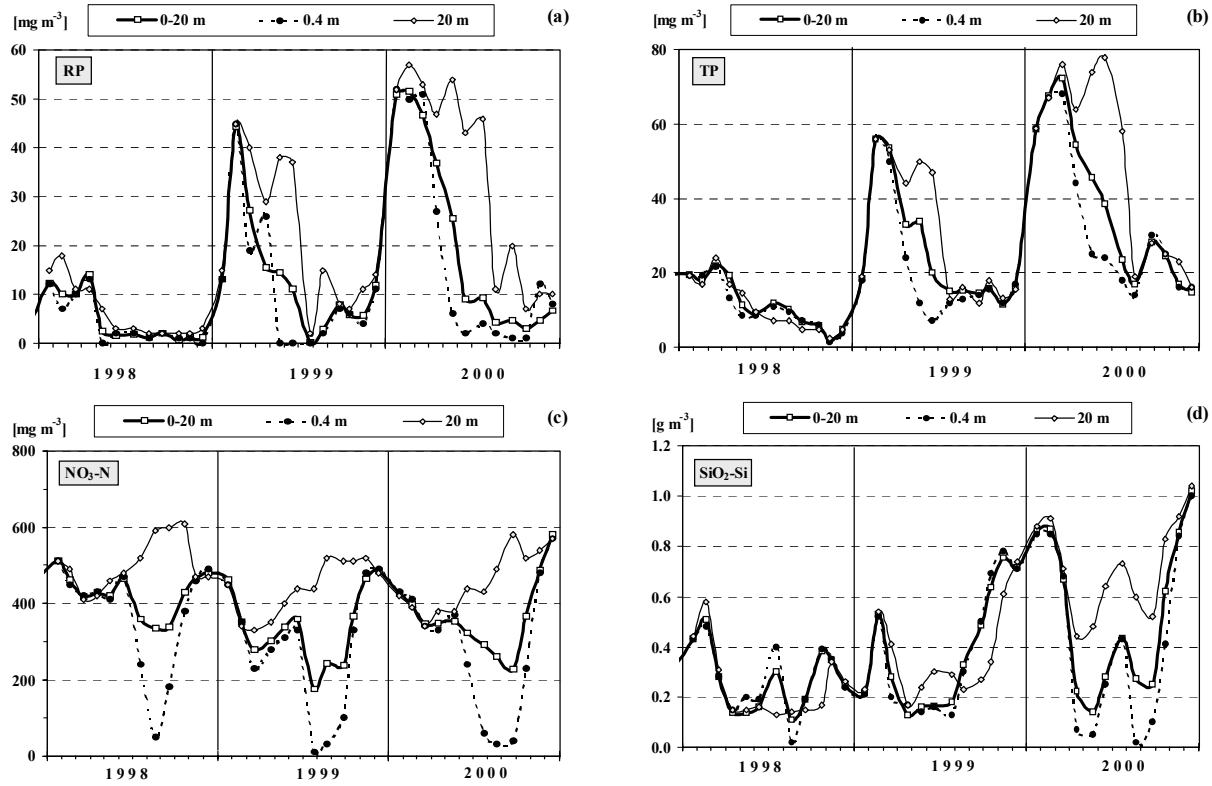

Fig. 5. Seasonal fluctuations of (**a**) reactive phosphorous (RP), (**b**) total phosphorous (TP), (**c**) nitrate nitrogen (NO_3-N) and (**d**) reactive silica (SiO_2-Si) in the 0-20 m layer of Lake Lugano (Gandria).

physical (mixing and stratification) and biological (planktonic activity) processes.

At the surface, the highest pH values (>9) were measured in the summer period, generally between July and September; in 2000, high values were also measured in May and from June to October (Fig. 4a). In the euphotic layer, pH values decreased below 8.0 only during the winter mixing period (January-February).

The epilimnion is characterised by marked oxygen supersaturation from April-May to September; maximum values (120-130%) were observed at a depth of around 5-10 m (Fig. 4b). In the northern basin of Lake Lugano the waters below 100 m are completely anoxic (Barbieri & Simona 1997). For this reason, at the beginning of the vegetative period the years characterised by a deeper winter mixing showed low saturation values in the surface waters (49% in 1999 and 44% in 2000) compared to the years with mild winters (64% of O_2 saturation in 1998). At 50 m dissolved oxygen never exceeded 60% saturation.

Owing to their common dependence on algal photosynthesis, pH and O_2 (% saturation) showed a significant correlation - after normalisation - with algal abundance (table 3, upper right triangular matrix).

Conductivity in the epilimnion decreased progressively beginning from the spring months (Fig. 4c); the lowest values were observed in August and September (146, 161 and 147 µS cm^{-1} in 1998, 1999 and 2000, respectively). The decrease of conductivity in the calcareous waters of the deep southern subalpine lakes is linked to the precipitation of calcium carbonate, which is mainly caused by algal CO_2 depletion during summer stratification (Salmaso & Decet 1998). Depending on the strength of the vertical mixing, the layer delimited by the 230 µS cm^{-1} isopleth indicated an increasing bottom-up supply of solutes in 1999 and 2000. Correspondingly, during the winter overturn the conductivity values in the epilimnion were around 217 µS cm^{-1} in 1998 and 227 µS cm^{-1} in 1999 and 2000.

The seasonal changes of the algal nutrients (nitrogen, phosphorous and silica) in the upper water column (0-20 m) showed different patterns during the three years (Fig. 5). Owing to the meromictic conditions of the northern basin and the different winter climatic conditions (Tab. 2), from 1998 to 2000 the amplitude of the recycling of the nutrient-rich deep waters varied widely, with a strong impact on the trophic conditions in the epilimnetic layers (see section 4.7).

Reactive phosphorus (RP) underwent a drastic depletion after the spring algal development (Fig. 5a). During the period of thermal stratification (May-September) the concentrations at the surface and in the 0-20 m layer were generally below 5 and 10 µg P l^{-1}, respectively. The variable phosphorus supply from the deepest layers to the epilimnion after the winter overturn led to different initial RP concentrations in the three years;

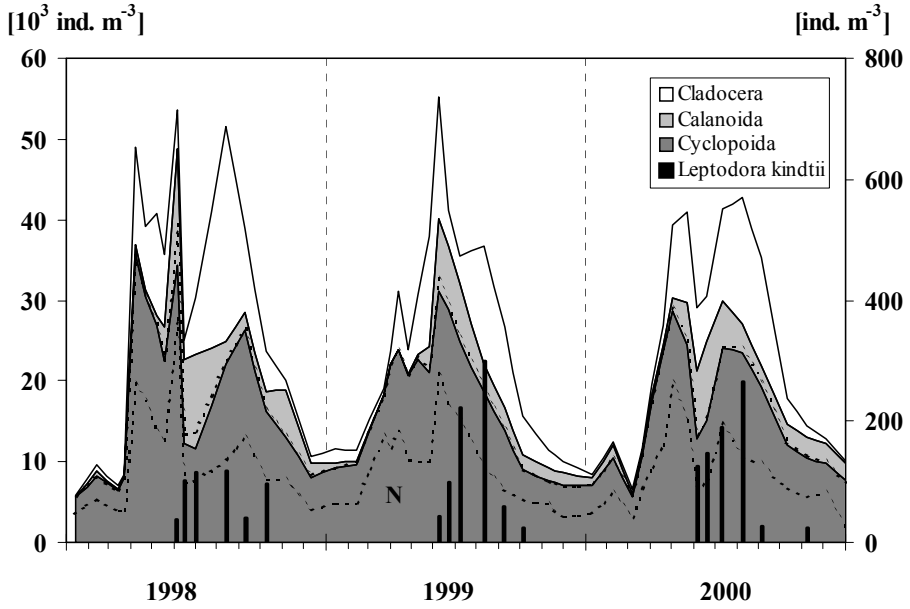

Fig. 6. Seasonal fluctuations of the crustacean zooplankton in Lake Lugano (Gandria). The area below the dotted line indicates the contribution of nauplii (N). The right axis shows the density values recorded for *Leptodora kindtii* (vertical bars).

very low values were observed in 1998 (14 µg P l^{-1}), whereas a marked increase was recorded in 1999 (44 µg P l^{-1}) and in 2000 (52 µg P l^{-1}). The temporal development of total phosphorus (TP) closely followed that of reactive phosphorus (Fig. 5b). Maximum concentrations of total phosphorous during the spring overturn were 22, 56 and 72 µg P l^{-1} in 1998, 1999 and 2000, respectively.

Inorganic nitrogen in the epilimnion was mainly present as nitrate [NO_3-N]. This compound showed a regular temporal pattern (Fig. 5c); the maximum concentrations in the 0-20 m layer were not observed during the spring overturn, but in late autumn (1998: 0.48 mg N l^{-1}; 1999: 0.49 mg N l^{-1}; 2000: 0.58 mg N l^{-1}). A marked depletion in the 0-20 m layer occurred during the summer, with minimum concentrations of 0.33 mg N l^{-1} (August 1998), 0.17 mg N l^{-1} (July 1999) and 0.23 mg N l^{-1} (September 2000). At the same time the surface values (measured at 0.4 m) fell below the limits of detection (Fig. 5c).

As with other nutrients, the availability of silica is dependent on internal recycling induced by winter circulation (peaks in February), as well as on external inputs originating in the catchment basin. In spite of the extent of the deep mixing in winter 1998/1999, concentrations of silica remained relatively low, because of its rapid consumption by a massive diatom development which started in November 1998.

4.4. Zooplankton

Density values of the crustacean zooplankton are reported in figure 6. In the three years studied the development phases began around mid-April and continued until early October.

The numerically greatest component is that of the cyclopoid copepods, also because of the major contribution of small-sized larval stages (nauplii); represented primarily by *Cyclops* cf. *abyssorum*, as well as *Thermocyclops crassus* and *Mesocyclops leuckarti*, this group reaches peaks between 29,000 and 34,000 ind m^{-3}. A single species of calanoid copepod, *Eudiaptomus gracilis*, is present, and reaches its maximum development in June and July (9000-14,000 ind m^{-3}).

The principal cladocerans are *Daphnia hyalina*, which reaches its maximum development from April to June (up to 16,000 ind. m^{-3} in 1999), and *Diaphanosoma brachyurum*, with maxima in August and September (up to 24,000 ind m^{-3} in 1998); *Eubosmina longirostris* was observed exclusively in autumn 2000 (*ca* 1000 ind. m^{-3}). The only carnivorous cladoceran in Lake Lugano is *Leptodora kindtii*, which develops regularly from June to October (up to 300 ind m^{-3} in 1999).

4.5. Phytoplankton density and water transparency

Lake Lugano contains high quantities of phytoplankton, which can strongly limit the penetration of light into the water column (see Fig. 2). Generally speaking, the maximum Secchi disk values were measured in January (9.4-13.5 m), when algal production values are low and the vertical mixing of the water column is high, and in May (7.5-11.2 m), when grazing activity is high. The lowest transparency values were recorded in March and April (2.6-6.6 m), and from August to October (2.5-3.3 m), in correspondence with major phases of algal development (diatoms and cyanophyceans/chlorophyceans, respectively). Euphotic layer depth values (Z_{eu}), calculated on the basis of PAR at-

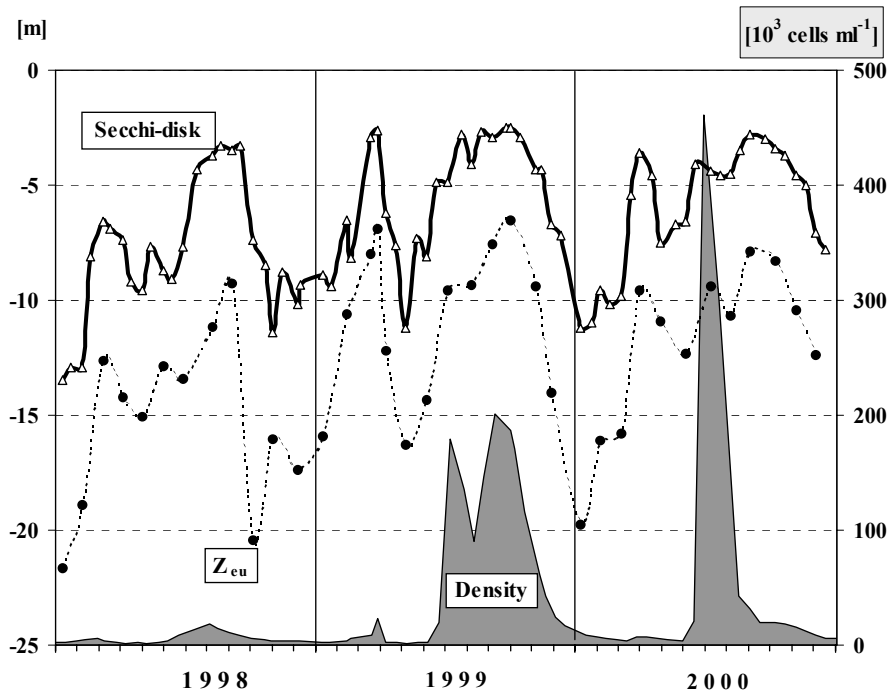

Fig. 7. Total density of phytoplankton and water transparency in Lake Lugano (Gandria). The contribution of ultraplankton and nanoflagellates is negligible.

tenuation measurements on the profile (see 4.2), show a similar trend. The data collected at the station of Gandria during the three investigated years reveal that the Z_{eu} depth values are closely linked to Secchi disk values (SD):

$$Z_{eu} = 4.1 \times SD^{0.6}; \quad r^2 = 0.88; \quad n = 37$$

It must be emphasised that this relationship is optimally applicable when the particulate matter is distributed homogeneously in the productive layer (winter-spring), while it may be less precise in periods of marked stratification of the algal populations (summer-autumn, see paragraph 4.6.).

The integrated samples (layer 0-20 m) for the three years considered show very different density values: peaks did not exceed 25,000 cells ml^{-1} in 1998, but reached 201,000 cells ml^{-1} in 1999, and 460,000 cells ml^{-1} in 2000. All the highest density values (>100,000 cells ml^{-1}) are linked to the development of colonies of Chroococcales (*Aphanothece*, *Aphanocapsa* and *Woronichinia*), of very small cell size (maximum cell length 1-3 µm; Fig. 7).

4.6. Seasonal time course of chlorophyll a and phytoplankton biovolume

The high degree of correlation between algal biomass and chlorophyll-*a* in the euphotic layer (Tab. 3) enables us to use the chlorophyll values measured at discrete depths along the vertical profile to monitor the space-time development of the phytoplankton biovolume (Fig. 8). In the three years of the study the highest chlorophyll concentrations (>10 mg m^{-3}) were measured in late winter-spring and late summer, and between May and June in the last two years (deep epilimnion: 10-15 m). There were marked variations in maximum concentrations between each year, relatively small in 1998 (15 mg m^{-3} in March and September), and distinctly higher in 1999 (34 mg m^{-3} in April) and 2000 (37 mg m^{-3} in October).

The trend of chlorophyll-*a* values measured on the integrated samples collected in the 0-20 m layer (Fig. 9a) also highlights the two chlorophyll peaks in 1999 (25 mg m^{-3}; April) and 2000 (23 mg m^{-3}; October). The fortnightly sampling frequency means that we have a detailed temporal trend of chlorophyll-*a*, showing further peaks >10 mg m^{-3} in 1998 (in March, August and November), 1999 (in January), and 2000 (in April). Altogether, the seasonal trend appeared to be rather irregular, and strongly influenced by meteoclimatic events in each year. Figure 9a also illustrates the trend of the chlorophyll-*a*: algal biovolume ratio in the integrated samples (0-20 m). The values are generally in the range 5 to 10 µg mm^{-3}, except for two periods: May-June 1998 (low biovolume values, high water transparency and chlorophyll maxima at depth), and September-October 1999 (bloom of cyanobacteria, cf. *Woronichinia* sp.).

The principal fraction of the phytoplankton biovolume in Lake Lugano is made up of cyanobacteria (Cyanoprokaryota) and diatoms (Bacillariophyceae); over the last ten years there has been an increase in the contribution of other algal groups, especially chloro-

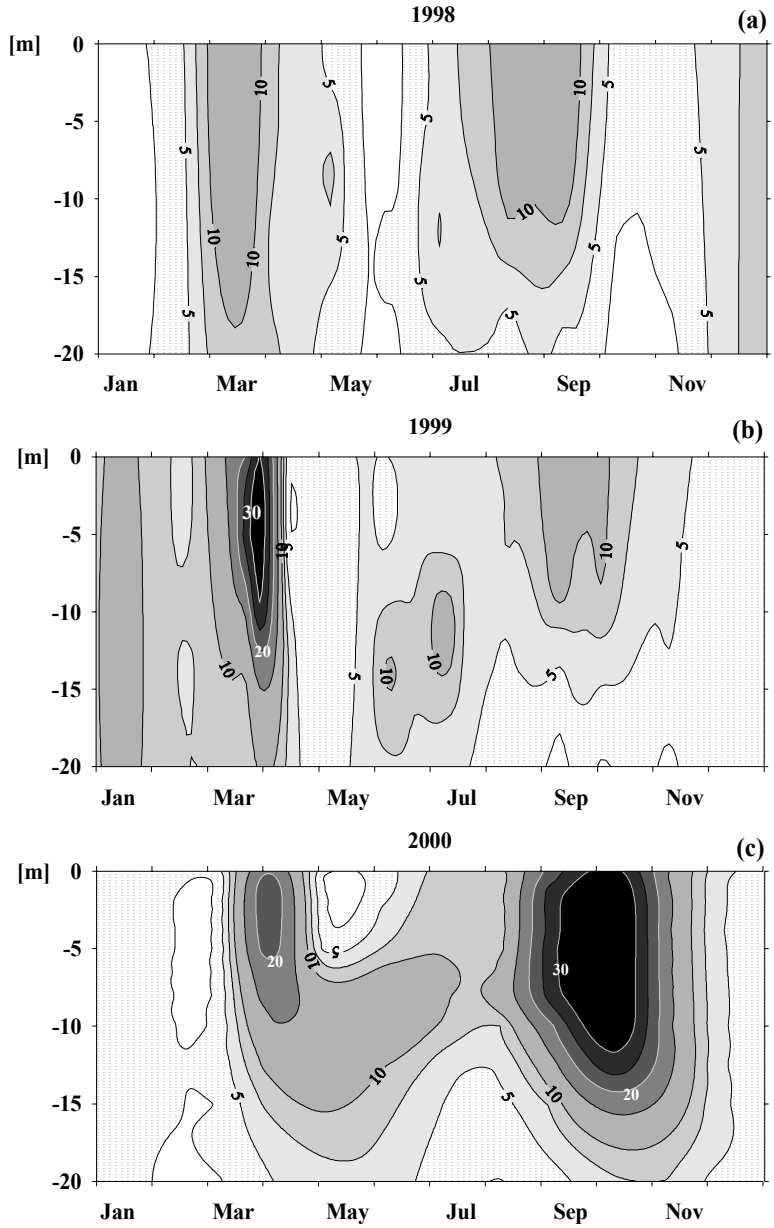

Fig. 8. Temporal development of the vertical distribution of chlorophyll-*a* in Lake Lugano (Gandria) in (**a**) 1998, (**b**) 1999 and (**c**) 2000.

phyceans (Barbieri & Simona 2001). A characteristics common to the phytoplankton in the three years was the development of diatoms in the late winter and spring months, though the 1999 development occurred a couple of months earlier than in 1998 and 2000 (Figs 9b, d). The summer groupings are more differentiated than those of the spring, but also show greater variability. Chlorophytes were more abundant in 1998 and 2000, while cyanobacteria presented their seasonal maxima in summer and autumn 1999 and 2000, and, again in the last two years, a large xanthophytes (*Tribonema* sp.) population was recorded towards the beginning of June. A high peak of conjugatophytes (mainly *Mougeotia* sp.) was also recorded in 2000. Other taxonomic groups which developed for brief periods with high percentages of biomass include the cryptophytes (up to 74% in May 1998).

During the maximum development of phytoplankton, the greatest contribution to the total biovolume is usually made by a limited number of species, with a consequent drop in the degree of ecological diversity of the community. In this connection, figure 9b shows the temporal evolution of the Shannon Diversity Index (H'). The index ranges between maxima of around 2.9-3.2 (summer-early autumn) and minima of around 1.4-1.6 (generally autumn-winter); in 1999 the Shannon Index dropped below 1.0 on two occasions, in February and in October-November, when there was a high development of *Tabellaria fenestrata* and colonies of Chroococcales, respectively (section 4.7).

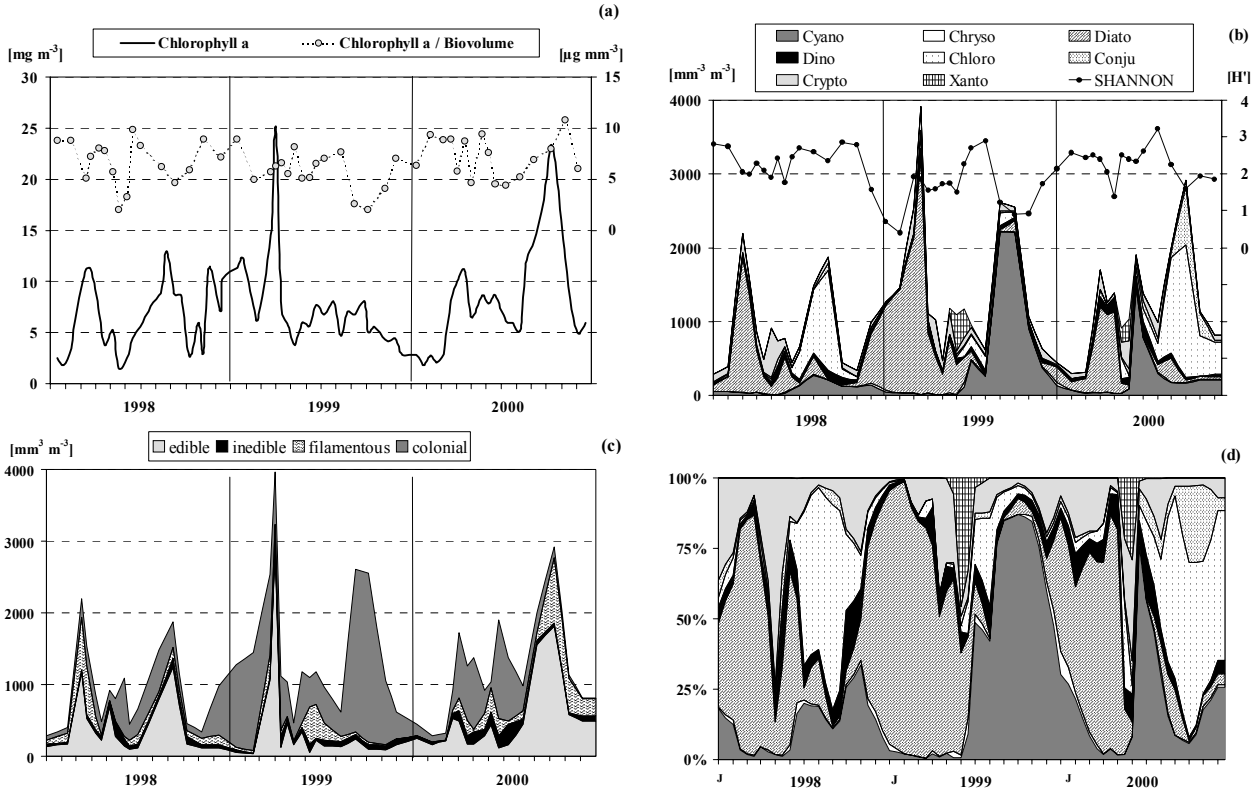

Fig. 9. Temporal evolution of phytoplankton in the 0-20 m layer of Lake Lugano (Gandria). (**a**) chlorophyll-*a* and chlorophyll:biovolume ratio; (**b**) biovolume subdivided by the main taxonomic groups and Shannon diversity; (**c**) phytoplankton subdivided into four groups based on their susceptibility to grazing; (**d**) percentage contribution of the different taxonomic groups to total biovolume. CYANO, Cyanprokaryota; CHRYSO, Chrysophyceae; BACIL, Bacillariophyceae; DINO, Dinophyceae; CHLORO, Chlorophyceae; CONJU, Conjugatophyceae; CRYPTO, Cryptophyceae; XANTO, Xantophyceae.

As regards the edibility characteristics of the phytoplankton (Fig. 9c), the taxa found were subdivided into four categories according to their degree of susceptibility to grazing, using the same criteria as Salmaso (2002). The principal fractions are represented by poorly edible colonial forms of cyanobacteria (*Snowella*, *Woronichinia*, *Aphanothece*) and diatoms (*Tabellaria*, *Asterionella*, *Aulacoseira*), and by edible forms of diatoms (small Centrales) and coccal chlorophyceans (*Oocystis*, *Sphaerocystis*, *Coelastrum*). The edible component of phytoplankton exhibits its maximum peaks in March-April and August-September (in 2000 until October), and undergoes high grazing pressure by herbivorous zooplankton throughout the vegetative period, first by cladocerans (in April-May: *Daphnia hyalina*), then diaptomids (in June-July: *Eudiaptomus gracilis*), and lastly by cladocerans again (August – September: *Diaphanosoma brachyurum*; figure 6 and section 4.4).

4.7. Dominant phytoplankton species

The dynamics of the phytoplankton community was analysed in detail by monitoring the temporal evolution of the main species present in the 0-20 m layer, defined for each sample according to a criterion of relative dominance (all the species which make up 80% of the total biovolume; see Ruggiu, 1983) and one of absolute dominance (all the species which reach a biovolume of at least 50 mm^3 m^{-3}). The list of the species identified for each sample is given in table 4 along with the corresponding biovolume values. According to their percent contribution to the 80% biovolume, the dominant species were subdivided into three categories (following Morabito *et al*. 2002): dominant (>10%), sub-dominant (between 5% and 10%) and important (<5%). The annual number of dominant species varies from a minimum of 27 (1999) to a maximum of 41 (2000). The high interannual variability is confirmed by the fact that the community was characterised significantly by only 14 species, which were common to all three years of the study, on the basis of the dominance criteria described above (Tab. 4., in bold). A further 10 species were present with significative peaks (>150 mm^3 m^{-3}) in only one or two out of the three years, and were totally absent in the other or others (i.e. *Snowella lacustris* and *Coelastrum polychordum* in 1998; *Tabellaria fenestrata* in 1998 and 1999; *Asterionella formosa* and *Oocystis* sp. in 1998 and 2000; *Aphanothece* sp., Chroococcales (cf. *Woronichinia* sp.) and *Tribonema* sp. in 1999 and 2000; *Aphanocapsa* sp. and *Mougeotia* sp. in 2000).

Tab. 4a. 1998. Biovolumes (BV) of phytoplankton in the 0-20 m layer at Gandria (mm^3 m^{-3}). The values reported indicate **dominant** (BV>10%), sub-dominant (5%<BV<10%), or important (BV<5%) species. Species marked with # are present in all three years; * values do not contribute to 80% of total biovolume.

1998	15/01	12/02	13/03	23/03	09/04	21/04	07/05	19/05	05/06	16/06	02/07	13/08	10/09	09/10	06/11	11/12
Cyanoprokaryota																
# *Aphanizomenon flos-aquae*	16									**49**	**69**				**65**	**110**
Chroococcus dispersus											18					
Oscillatoria redekei	17															
Oscillatoria sp.		14														
# *Planktothrix rubescens*	15	26								19		46	143	**75**	31	
Snowella lacustris											31	**209**		28		
Bacillariophyceae																
# *Aulac. islan*. ssp. *helvetica*		**80**	**711**	**657**	**142**											
Asterionella formosa	22	14	186	**187**	37											
Cyclotella ocellata												**223**				
# *Cyclotella radiosa*			**316**	**276**	**129**	38								14		
# *Fragilaria crotonensis*	26	37	* 54	68	**242**	**173**	73									
# *Stephanodiscus neoastraea*		37	**529**	101												
# *S. parvus / minutulus*	25							**116**								
Tabellaria fenestrata								**96**	**461**	**163**	**23**				**37**	**642**
Dinophyceae																
Gymnodinium helveticum						25	48	52	31	15			85	**77**	33	**37**
Peridinium cinctum / willei								**79**	52	31	37					
Chlorophyceae																
Coelastrum polychordum												120	**202**	23		
# *Eudorina elegans*										13				23	13	
Oedogonium sp.											33					
Oocystis sp.												**254**	**600**	25		
# *Pandorina morum*		19									53			13	16	
Phacotus lenticularis												27				
Scenedesmus costatus												29				
S. ecornis / linearis													56			
# *Sphaerocystis schroeteri*										13	**194**	**175**	61			
Ulothrix sp.											18					
Conjugatophyceae																
Closterium aciculare	13															
Cosmarium laeve													82			
Staurastrum paradoxum								69								
Cryptophyceae																
# *Cryptomonas* sp. (medium)	**31**	25	106		64	**104**	**266**	**160**	62		33		36	28	32	
# *Cryptomonas* sp. (large)	**54**	**54**			**103**	**67**	**346**	44						38	31	
# *Rhodomonas* sp. (small)	10	19	* 75						23	23	33			15	20	
# *Rhodomonas* sp. (medium)	10		* 62							35						

Tab. 4b. 1999. Biovolumes (BV) of phytoplankton in the 0-20 m layer at Gandria (mm^3 m^{-3}). The values reported indicate **dominant** (BV>10%), sub-dominant (5%<BV<10%), or important (BV<5%) species. Species marked with # are present in all three years; * values do not contribute to 80% of total biovolume.

1999	14/01	18/2	23/3	01/04	13/04	27/04	10/05	26/05	09/06	23/06	09/07	11/08	09/09	05/10	09/11	01/12
Cyanoprokaryota																
# *Aphanizomenon flos-aquae*										72	**183**	18				
Aphanocapsa sp.											34	16				
Aphanothece sp.											**214**	**110**	80	* 52		
div. Chroococcales												**65**	**2036**	**2116**	**873**	**364**
# *Planktothrix rubescens*												43				
Haptophyceae																
Chrysochromulina sp.										34	28					
Chrysophyceae																
Mallomonas sp.										32						
Bacillariophyceae																
# *Aulac. islan*. ssp. *helvetica*			**283**	223	72											
# *Cyclotella radiosa*			229	183												
# *Fragilaria crotonensis*														* 139		
# *Stephanodiscus neoastraea*			* 208	* 116												
# *S. parvus* / *minutulus*			252	**1956**												
Synedra ulna																40
Tabellaria fenestrata	**1124**	**1355**	**1116**	**684**	**704**	**463**	**249**	**666**	**390**	**319**	**97**					
Dinophyceae																
Gymnodinium helveticum				* **68**	**122**		17				41	56				
Peridinium cinctum / *willei*									* 58							
Chlorophyceae																
Carteria sp.				224												
# *Eudorina elegans*											37	16				
# *Pandorina morum*										72	56	30				
Scenedesmus ecornis / linearis												15				
# *Sphaerocystis schroeteri*												**74**				
Cryptophyceae																
# *Cryptomonas* sp. (medium)							**69**	71			54	43	* 57			**66**
# *Cryptomonas* sp. (large)				66		**339**	45	**152**		49		17				27
# *Rhodomonas* sp. (small)			223			53										27
# *Rhodomonas* sp. (medium)			* 68	* 58												
Rhodomonas sp. (large)				* 136												
Xantophyceae																
Tribonema sp.								66	**500**	**384**	32					

Tab. 4c. 2000. Biovolumes (BV) of phytoplankton in the 0-20 m layer at Gandria (mm^3 m^{-3}). The values reported indicate **dominant** (BV>10%), sub-dominant (5%<BV<10%), or important (BV<5%) species. Species marked with # are present in all three years; * values do not contribute to 80% of total biovolume.

2000	11/01	08/02	07/03	21/03	03/04	19/04	02/05	23/05	06/06	20/06	11/07	08/08	05/09	10/10	08/11	05/12
Cyanoprokaryota																
# *Aphanizomenon flos-aquae*									43	204		**60**	33			
Aphanocapsa sp.										177	**170**	22				
Aphanothece sp.										**397**	**177**					
Chroococcus dispersus												22				
div. Chroococcales	**131**	**61**	24	29						**601**	**384**	**141**	73			
# *Planktothrix rubescens*														* 77	**153**	**199**
Snowella lacustris										56		21				
Haptophyceae																
Chrysochromulina												20				
Chrysophyceae																
Mallomonas caudata	31															
Uroglena skujae										57						
Bacillariophyceae																
# *Aulac. islan*. ssp. *helvetica*				46	**183**	**213**										
Asterionella formosa		19	**56**	**162**	**574**	76										
Cyclotella ocellata													192			
# *Cyclotella radiosa*			14										33			
Cyclotella sp.													35			
Cyclotella sp. (small)								58								
# *Fragilaria crotonensis*				40	**274**	**573**	**974**	59				40				
# *Stephanodiscus neoastraea*	**154**	10	23	39		50										
# *S. parvus / minutulus*	16	**69**	**95**	**278**		52	* 53									
Synedra ulna	19															
Dinophyceae																
Ceratium hirundinella											40		36			
Gymnodinium helveticum		12		44	87	68	77		75	* 56	135	21				33
Gymnodinium sp. (small)		11														
Peridinium cinctum / willei		10					84	52								
Chlorophyceae																
Carteria sp.					73											
Coelastrum polychordum													42	* 62		
# *Eudorina elegans*								31			62					
Oocystis sp.												71	**1038**	**1612**	**469**	**398**
# *Pandorina morum*								**198**			42					
Phacotus lenticularis												72				
Scenedesmus costatus													65			
# *Sphaerocystis schroeteri*												41				
Conjugatophyceae																
Mougeotia sp.												38	53	**768**	**293**	23
Staurastrum paradoxum									79		39	20				
Staurastrum punctulatum										75	40					
Cryptophyceae																
# *Cryptomonas* sp. (medium)		19	**14**	88	97			73	**237**		54	**115**				
# *Cryptomonas* sp. (large)								**95**	61			38				
# *Rhodomonas* sp. (small)	11	**29**	22						61			26				
# *Rhodomonas* sp. (medium)			17	**30**	59							30				
Rhodomonas sp. (large)					61											
Xantophyceae																
Tribonema sp.								**190**	**293**							

Tab. 5. Trophic parameters for the characterisation of Lake Lugano. *: parameters used by OECD 1982.

		1998	1999	2000
*Secchi-disk, average	(m)	8.1	5.5	6.3
*Secchi-disk, minimum (month)	(m)	3.3 (IX)	2.5 (X)	2.8 (IX)
*Chlorophyll-*a*, average (0-20 m)	(mg m^{-3})	6.5	7.5	8.7
*Chlorophyll-*a*, maximum (month)	(mg m^{-3})	13.0 (VIII)	25.1 (IV)	23.4 (X)
*Total phosphorus, average (0-20 m)	(mg P m^{-3})	12	25	39
Total phosphorus, overturn (0-20 m)	(mg P m^{-3})	22	56	67
Total phosphorus, overturn (0-100 m)	(mg P m^{-3})	52	71	76
Total phosphorus, overturn (100-286 m)	(mg P m^{-3})	294	274	226
Total phytoplankton biovolume, average	(cm^3 m^{-3})	0.84	1.45	1.23

In the study period the greatest seasonal development of the community was by groups of different species. In 1998 the highest biovolume peaks (between 529 and 711 mm^3 m^{-3}) were reached by *Aulacoseira islandica*, *Stephanodiscus neoastraea*, *Tabellaria fenestrata* and *Oocystis* sp. (Tab. 4).

Apart from *Tribonema* sp. and the colonies ascribable to the order of the Chroococcales, the highest biovolume peaks in the two years (1999-2000) characterised by a greater extension of the spring mixing – and therefore higher nutrient replenishment – were of different species. As in 1998, in 1999 the genus *Stephanodiscus* (*parvus*/*minutulus* group) and the species *T. fenestrata* were identified with much higher peaks (1956 and 1355 mm^3 m^{-3}, respectively); in the same way, *Oocystis* sp. was also found in 2000, with a peak of 1612 mm^3 m^{-3}. Unlike in the previous two years, the spring diatom development in 2000 was no longer almost exclusively by *T. fenestrata* and *Stephanodiscus* spp., but also by *Asterionella formosa* and *Fragilaria crotonensis*. Moreover, there was also a large development of *Mougeotia* sp. (Tab. 4) in 2000.

4.8. Trophic parameters

Table 5 gives the trophic parameters used by the OECD (1982) for the trophic classification of lakes. In consideration of the lake's meromictic characteristics, the table also shows the mean phosphorus values measured in the layers between 0-20 m, 0-100 m and 100 m-bottom (286 m) when the spring mixing was at its maximum extent. Lastly, the mean annual values of phytoplankton biovolume were also calculated. The results highlight a significative deterioration in the surface water quality from 1998 to the two-year period 1999-2000, with a significative increase in TP concentrations in the epilimnion and in the algal biomass values (chlorophyll and phytoplankton biovolumes). At the same time, due to greater mixing with the surface waters, TP concentrations in the deep hypolimnion dropped sharply.

4.9. Influence of winter mixing on the phytoplankton community

Under the present conditions of meromixis and high nutrient concentrations in the deep hypolimnion, the development of plankton populations in the northern basin of Lake Lugano is largely influenced by the intensity of the winter mixing (and thus by the meteoclimatic characteristics each year), which has a profound effect on the replenishment of nutrients in the euphotic layers during and after the beginning of the spring phytoplankton growth.

At the beginning of 1998, due to the weak winter circulation, the reactive phosphorus content in the 0-20 m layer was extremely low (around 10 mg P m^{-3}, cf. Fig. 5); this undoubtedly contributed to limiting phytoplankton development during the vegetative period, lowering the annual mean total biovolume to the minimum values for the whole period studied (0.84 cm^3 m^{-3}; Tab. 5). Throughout 1998, biovolume maxima never exceeded 2 cm^3 m^{-3}, with the most abundant species (apart from a strong development of *Oocystis* sp. in August-September) being spring (*A. islandica* and *S. neoastraea*) and late-spring/winter diatoms (*T. fenestrata*).

The winter of 1998-1999, on the other hand, was particularly severe, with one of the deepest water mixings of the last 20 years (78 m; Tab. 2), leading to a marked nutrient enrichment in the surface layers (Tabs 2 and 5). Compared with the previous year, concentrations of total phosphorus at the circulation increased from 52 to 71 mg P m^{-3} in the 0-100 m layer, and from 22 to 56 mg P m^{-3} in the 0-20 m layer (Tab. 5). Favoured by the early start of the winter circulation and the good conditions of solar radiation, a massive development of winter diatoms (*Tabellaria fenestrata*: absolute dominance for 8 consecutive months; Tab. 4) began to appear as early as November 1998; during the winter months these had already consumed part of the nutrients coming from the deep layers. The quantity of nutrients still available at the start of the vegetative period was however sufficient to support two later major phases of development characterised by the dominance of centric diatoms in April (*Stephanodiscus parvus*/*minutulus*; total phytoplankton biovolume: 4.0 cm^3 m^{-3}) and of Chroococcales in October (cf. *Woronichinia* sp.; total biovolume: 2.6 cm^3 m^{-3}).

The 1999-2000 winter was also characterised by very low temperatures and by an even deeper mixing of the water column (Tabs 2 and 5). The initial TP con-

centrations exceeded the levels of the previous year (76 mg P m^{-3} in the 0-100 m layer), but the process of replenishment of the nutrients from the deep layers began later, preventing a repeat of the exceptional phytoplankton development of winter 1998-1999. The greater availability of nutrients in the epilimnion (67 mg P m^{-3} in the layer 0-20 m) was then exhibited in an increasing rise of total biovolume values throughout the vegetative period. Compared with those of the two previous years, the spring maxima of diatom biovolume in 2000 were not only of lesser importance than other algal groups, but were also caused by different species (*Asterionella formosa* and *Fragilaria crotonensis*). During this year, the summer and late summer-autumn populations were dominated by cyanobacteria (cf. *Woronichinia* sp.) and green algae (*Oocystis* sp. and *Mougeotia* sp.), respectively, with corresponding total biovolumes ranging between 1.7 and 2.9 cm^3 m^{-3}.

5. DISCUSSION

Results from the three-year study 1998-2000 reveal the existence of a high degree of interannual variability of the algal populations in the northern basin of Lake Lugano. Seasonal cyclicity occurs for phytoplankton only at the level of the main taxonomic groups, with a development in late winter and spring of large pennate and centric diatoms, in summer of chlorophyceans, and in summer-autumn of cyanobacteria. At species level, however, there is some difficulty in defining a group of associations as typical or as master species (according to Salmaso 2002). Seasonal succession depends to a large extent on allogenic factors which regulate nutrient replenishment (precipitation, thermal regime, climatic evolution and winter mixing) and autogenic factors (e.g. self-shading, competition, grazing).

The productive layer of the northern basin of Lake Lugano remains in a high trophic state. This situation derives less from an excessive external load (which has currently fallen to almost acceptable values following urban sewage treatment measures)(Barbieri & Simona 2001) than from the algal nutrients which have accumulated in the deep layers (100-286 m), linked to the meromixis of the water column.

The nutrient pool recirculated into the euphotic layer at the end of the winter mixing forms a major reserve of nutrients available for phytoplankton growth. The phosphorus concentrations measured during the three years of the study in the 0-20 m layer (expressed both as annual mean and as values at circulation) reveal an increase in trophic level corresponding to the increase in the mixing depths in 1999 and 2000 (see also Tab. 2); the same effect is also seen in the 0-100 m layer. In the three years, the trophic state descriptors show that the productive layer (0-20) of the northern basin of Lake Lugano went from a condition of (oligo)mesotrophy in 1998 to one of meso-eutrophy in 1999-2000. In a parallel trend, TP concentrations in the deep layers (100-286 m) decreased progressively from 1998. At present, though, we do not have enough data to say with any certainty if the observed trend will continue. The key factor is the evolution of the climate in the next few years, especially as regards the coldest months. However, if the trend were to continue, we might see the start of a slow process of consumption of the nutrient reserves accumulated in the deep layers, via bottom-up transport. This in turn might lead to conflicting effects: if there were a progressive recovery of the overall trophic state of the lake, there might be a slowing down in the recovery of the trophic state of the surface layers.

Evidence of the marked resilience of the lake to a reduction of the nutrient pool in the deep hypolimnion in meromictic conditions is provided by the fact that, while the major recovery measures undertaken since the mid-seventies have reduced the external load from over 150 to 30 t P y^{-1}, with TP concentrations in the 0-100m layer falling from 145 to the current 50-70 µg P l^{-1}, there has also been a marked increase in P content in the deep hypolimnion (100 m-bottom: from 145 to the current 225-295 µg P l^{-1}) (Barbieri & Simona 1997, and Tab. 5).

The reduction of phosphorus in the top 100 m resulted in a sudden, dramatic decrease of phytoplankton biomass in the northern basin at the beginning of the 90s. A comparison of mean values calculated on two 8-year periods (1981-88 and 1989-1996; Barbieri & Simona 1997) shows a striking drop in algal biovolume (-60%; from 16.0 to 6.4 g m^{-2}) and chlorophyll-*a* in the 0-20 m layer (-40%; from 12.8 to 8.0 µg l^{-1}), accompanied by an increase in transparency (+30%; from 4.2 to 6.0 m) and a net increase in zooplankton biomass (copepods + cladocerans), both herbivores (+60%) and carnivores (+10%). In the three years of our study zooplankton continued to exert strong pressure on the edible fraction of phytoplankton in the vegetative period, thus favouring the development of filamentous and colonial species. Clearwater episodes occurred in May-June every year, though to varying extents (see Fig. 8).

The consequent improvement in water transparency has enabled the phytoplankton to exploit the nutrients in the deep epilimnion, especially during the phase of thermal stratification, when the surface concentrations of P, N and Si (Fig. 5) tend to become limiting. In the thermal stratification period the environmental conditions at the lower limit of the euphotic zone and at the thermocline are more favourable for algal species which prefer conditions of low light, low temperatures, low turbulence and a high nutrient level (Figs 3 and 5). The vertical chlorophyll profiles measured during the summer-autumn stratification (Fig. 8) highlight the presence of a major phytoplankton population even at depth, close to the thermocline (10-15 m).

Despite the improvement in the underwater light regime, for most of the year the depth of light penetration still remains lower than the depth of the sampled layer (0-20 m). Consequently, the biovolume values are often

"diluted" on a water column of a depth up to three times greater than the productive layer, assuming values similar to those of lakes with a lower trophic level but a greater euphotic layer, such as Garda (Salmaso 2002) or Maggiore (Morabito *et al*. 2002).

While the technique of integrated sampling on the water column means that the phytoplankton populations can be monitored properly even in situations of high spatial heterogeneity (for instance, during thermal stratification), it is also true that its use should be adapted to the trophic conditions of each waterbody. Future research should include a comparison between lakes with different trophic levels: not only on layers of a predetermined thickness (which, in studies on deep subalpine lakes, is generally between 0 and 20 m), but also on the layer actually involved in primary production (which could approximately correspond to the layer between the surface and the lower limit of the euphotic zone).

A major element common to the two years characterised by a deeper extension of the mixed layer was the development of a greater algal biomass in the productive layer. On the other hand, the high variability in the development of the dominant species in the three years of the study as well as in the two years (1999-2000) when there was a deeper extension of the mixed layer prevents the formulation of definite generalisations about the species able to respond positively to episodes of higher fertilisation of the surface waters. This result is different from that found in Lake Garda during the 90s. In that lake, the importance of the spring circulation in fertilising epilimnetic waters was statistically confirmed through an analysis of the whole set of data available from 1991 to 2000 (Salmaso *et al*. 2000; 2002). The results were similar to those found in this study on Lake Lugano, in so far as they showed the clear impact on the trophic variables of the mixing depth and lake volumes involved at the spring overturn, with positive effects on epilimnetic phosphorus, chlorophyll-*a* and total algal biovolumes, and negative effects on water transparency. However, the effect of the impact of the mixing depth on phytoplankton was more regular and predictable than in Lake Lugano. In particular, during the two years of complete overturn and complete fertilisation of the epilimnetic waters (which took place in the two years 1999-2000), the community showed a greater development of cyanobacteria (*Planktothrix rubescens*) and *Mougeotia* sp.

6. CONCLUSIONS

The limnological studies conducted regularly since the 80s on the phytoplankton community of Lake Lugano have made it possible not only to characterise in detail its composition and dynamics, but also to interpret the trophic evolution of the lake in relation to the recovery interventions carried out on its watershed. Despite the marked reduction of the external anthropogenic load, the current trophic level of the two lake basins is still too high to be acceptable. In particular, very considerable quantities of nutrients are still accumulated in the deep hypolimnetic layers of the meromictic northern basin. At the moment, also in view of the drastic reduction in nutrients which followed recovery operations, the meteoclimatic events of the winter and spring months and the intensity of nutrient recycling from the deepest towards the surface layers form a complex of factors which are decisive in controlling the trophic level of the lake.

The choice of the three years from 1998-2000 as a period of comparison between the major deep lakes in the southern prealpine area was especially significant in this connection, as it was possible to evaluate the behaviour of the pelagic biocenosis under very different environmental conditions: weak winter circulation and strong summer heating of the surface waters (1998), early winter cooling and deep circulation of the water (1999), deep winter circulation and abundant summer-autumn precipitation (2000). This variety of situations has highlighted the great variability of the plankton population, within which no typical succession emerges at the level of dominant species, but only of the three main algal groups: diatoms in spring, chlorophyceans and cyanophyceans in summer and autumn. A response of the phytoplankton to the greater fertilisation of the epilimnetic waters in 1999 and 2000 can be seen in the massive development of individual species such as *Tabellaria fenestrata* (winter-spring 1999), *Asterionella formosa* and *Fragilaria crotonensis* (spring 2000), *Tribonema* sp. (June 1999 and 2000), Chroococcales (cf. *Woronichinia* sp.; summer 1999 and autumn 2000), *Oocystis* sp. and *Mougeotia* sp. (autumn 2000).

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