

Phytoplankton assemblages in two sub-basins of Lake Como

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ABSTRACT

This paper reports the results of a two-year study on the chemical characteristics and phytoplankton assemblages in the western (Como) and eastern (Abbadia Lariana) sub-basins of Lake Como. The data were collected from September 1997 to August 1999 in the frame of an investigation financed by the Provincial Administration of Como and Lecco. Over the period of study TP concentrations ranged between 6-46 $\mu\text{g P l}^{-1}$ at Abbadia, and 5-50 $\mu\text{g P l}^{-1}$ at Como. Reactive phosphorus ranged between 6-31 $\mu\text{g P l}^{-1}$ at Como, and 6-25 $\mu\text{g P l}^{-1}$ at Abbadia. By the end of the study, 85 taxa belonging to six algal groups were identified. Chlorophyta (Chlorophyceae and Conjugatophyceae) (30) were the best represented, followed by Bacillariophyceae (23), Cyanoprokaryota (8), Cryptophyceae (6), Chrysophyceae (6) and Dinophyceae (6). The time variation of chlorophyll *a* (0.5-9.72 $\mu\text{g l}^{-1}$), phytoplankton density (177-64925 cell. ml^{-1}) and biovolume (21-6665 $\text{mm}^3 \text{m}^{-3}$) showed the same trend, with the lowest and maximum values recorded during winter and from spring to summer, respectively. In order to compare the seasonal succession in the two sub-basins, cluster analysis and non-metric multidimensional scaling ordination were used jointly. Multivariate analysis showed i) a substantial homogeneity in the time seasonality of the dominant phytoplankton assemblages in the two sub-basins and ii) a clear differentiation of summer phytoplankton from the other seasonal phases. From a purely quantitative point of view, there were dissimilarities between the two stations. The western sub-basin showed a greater algal production than Abbadia, especially in spring and summer. Despite the strong reduction of TP since the 1980s, the results of investigations carried out during the 1990s indicated a substantial stability of phytoplankton. It is emphasised that a reduction in biomass and shift in species composition will be possible only by assuring a severe control of the nutrient loads.

Key words: phytoplankton, Lake Como, deep lakes

1. INTRODUCTION

In origin the deep southern subalpine lakes were oligotrophic; successively, they underwent a progressive eutrophication as shown by the increase in nutrient concentrations and by palaeolimnological studies (Guilizzoni *et al.* 1982; Mosello & Giussani 1997). In the early 1970s, the studies carried out on Lake Como demonstrated a strong dominance of few species, mainly belonging to cyanobacteria (*Planktothrix rubescens* and *Gomphosphaeria lacustris*) (Braga 1972). In the late 1970s, total phosphorus concentrations at spring overturn reached their maximum (80 $\mu\text{g P l}^{-1}$) (Ambrosetti *et al.* 1983). In this period the phytoplankton assemblages were dominated by *Stephanodiscus hantzschii* in spring, and by *Planktothrix rubescens* and *Gomphosphaeria lacustris* in summer (Barbanti *et al.* 1986).

During the 1980s, the reduction of nutrient loads, following the abatement of phosphorus in detergents, caused a TP decrease in the Como basin, from 71 $\mu\text{g P l}^{-1}$ in 1986 (Mosello *et al.* 1991) to 40 $\mu\text{g P l}^{-1}$ measured at spring overturn, in 1992.

In 1994 the ARPA (Regional Environmental Protection Agency of Lombardy Region) Department of Lecco, with the cooperation of CNR Istituto Italiano di Idrobiologia (presently Istituto per lo Studio degli Ecosistemi) started an investigation on phytoplankton structure and dynamics in two stations located in the

eastern basin: Abbadia Lariana and Lierna (Buzzi 1995). This paper reports the results obtained between September 1997 and August 1999 at the stations of Como (western basin) and Abbadia Lariana (eastern basin). The research, financed by the Provinces of Como and Lecco, was carried out in the frame of a collaboration among University of Milan and the ARPA Departments of Lecco, Como and Sondrio. The data were elaborated by a common protocol in the frame of a research project devoted to the study of the trophic evolution of the deep southern subalpine lakes (Mosello & Salmaso 2000).

2. STUDY AREA

Lake Como is the deepest Italian lake (410 m, in front of Argegno; Fig. 1); its surface and water volume are 146 km^2 and 22.5 km^3 , respectively.

The catchment area covers 4522 km^2 , most of which is formed by calcareous rocks, especially dolomite, with marl and sandstone. Owing to its shape, resembling an upside-down "Y", Lake Como may be subdivided in three sub-basins, i.e. the Western, the Eastern and the Northern basins (Fig. 1). The bathymetric and the hydrological characteristics of the Western and Eastern basins, which are the objects of this paper, are very different. The western branch is separated from the rest of the lake by an underwater ridge and has a water renewal time of 8.3 years. The eastern branch, with a regular

bottom and the presence of the outlet at its southern edge, has a lower renewal time. The water renewal time of the whole lake has been estimated in 12.8 years (Buzzi *et al.* 1997).

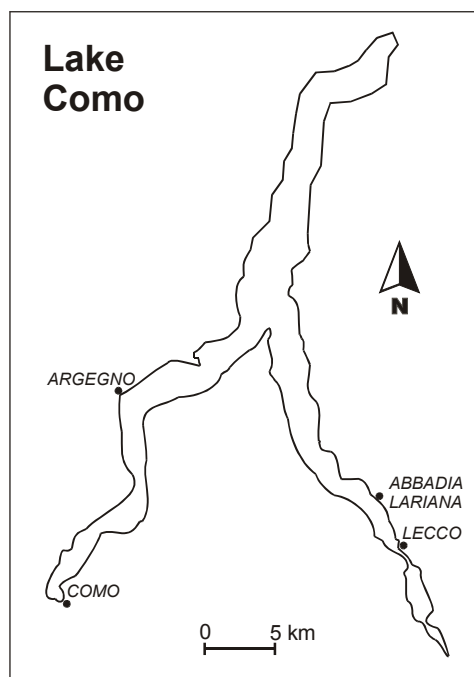


Fig. 1. Map of Lake Como and location of the sampling stations.

Lake Como is oligomictic, with the spring mixing typically involving the first 150–200 m, a complete turnover being rare (Ambrosetti & Barbanti 1992). In 1999 a complete mixing of the water column was observed at the deepest point (Argegno).

The climate of this area is intermediate between middle-European and northern-Mediterranean; annual precipitations are mainly concentrated in spring and autumn.

3. METHODS

Monthly samplings were carried out in the stations of Como ($Z_{\max} = 100$ m) and Abbadia Lariana ($Z_{\max} = 135$ m) from September 1997 to August 1999; each sampling date at Como was shifted of 1 or 2 weeks in respect of the corresponding sampling at Abbadia. Integrated samples for phytoplankton analyses were obtained from the layer 0–20 m by mixing sub-samples collected every two meters with a Ruttner bottle. In the two stations, two subsamples were fixed with acetic Lugol's solution and formaldehyde, respectively. In order to identify small centric diatoms, aliquots of sub-samples fixed in formaldehyde were oxidised with hydrogen peroxide and then mounted on glass slides. The subsamples fixed in Lugol's solution were analysed with an inverted microscope (Leica IMDL), following the Utermöhl technique (Utermöhl 1958). The smallest

algae (including ultraplankton, up to 4 μm) were identified at 400 $\times$, whereas the less abundant and larger organisms were determined at 200 $\times$, until 400 individuals for the most abundant species were reached. Phytoplankton biovolume was estimated from density data and measurements of specific cell volume obtained approximating cell shapes to simple geometrical solids (Rott 1981).

Species were identified following the series Süsswasserflora von Mitteleuropa (established by A. Pascher) and Das Phytoplankton des Süßwassers (established by G. Huber-Pestalozzi). The taxonomy of Oscillatoriales was based on the updating by Anagnostidis & Komárek (1988).

Chlorophyll-*a* was determined by spectrophotometry (Lorenzen 1967) after filtration of the 0–20 m integrated samples on Whatman GF-F glass-fiber filters, disruption of the filters with a grinder and 24 h extraction in 90% acetone.

In the two stations, samples for chemical analyses were collected at 0, 2.5, 5, 10, 20, 30, 50, 80 and 100 m; further samples at 135 m were collected at Abbadia Lariana. Soluble reactive and total phosphorus (SRP, TP), nitrate and ammonium nitrogen ($\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$) were measured following standard methods (A.P.H.A., A.W.W.A and W.E.F., 1995). The analytical procedures are described in Mosello *et al.* (1999). Dissolved oxygen and temperature profiles were obtained *in situ* using a multiparametric WTW probe. Values of the chemical variables in the upper 20 m were estimated averaging the single values obtained from samples collected at discrete depths.

Water transparency was measured with a Secchi disk without the aid of a bathyscope. The euphotic depth (Z_{eu}) (Talling 1971) was estimated from Secchi disk transparency (Z_s) as suggested in Tilzer (1988), using the relationship:

$$Z_{\text{eu}} = 5.02 \times Z_s^{0.70}$$

Major phytoplankton seasonal modifications in the two stations were evaluated from the changes inside the assemblages of the dominant species, namely those species which, at least once during the whole seasonal cycle, contributed to build up 80% of the total community biovolume. Moreover, in order to evaluate the annual phytoplankton cycle in the two sub-basins during 1998, cluster analysis (average linkage) and non-metric multidimensional scaling ordination (NMDS) were used jointly (Salmaso 1996). Both techniques were applied to a dissimilarity matrix obtained from the calculation of Bray-Curtis index (Bray & Curtis 1957) after transformation of the original data by double square root.

4. RESULTS

4.1. Physical parameters

In the upper 20–30 m, a pronounced stratification was observed in the two stations from July to October

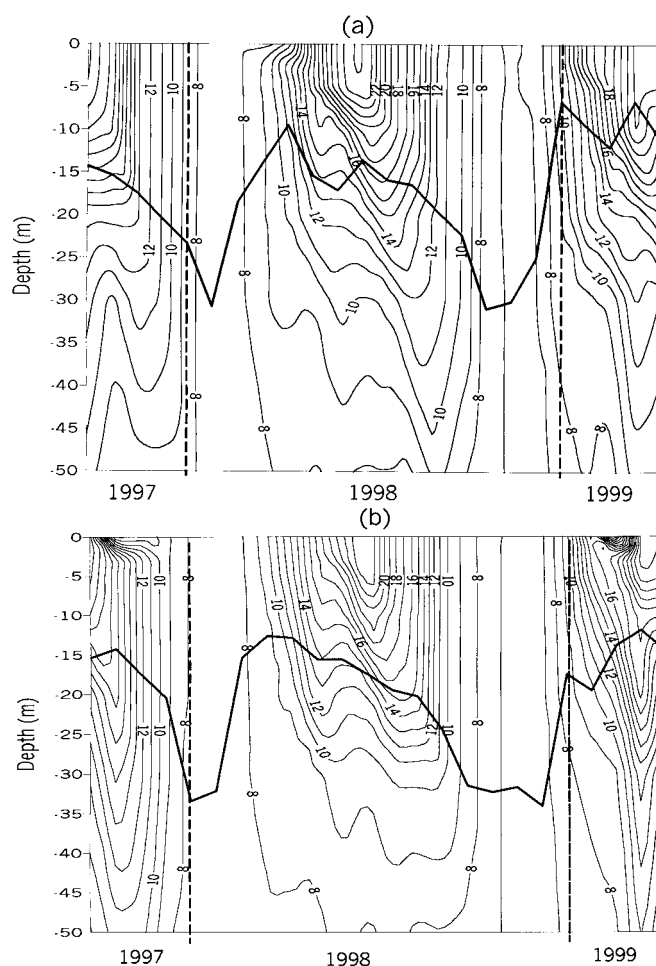


Fig. 2. Isopleths of temperature (°C) with superimposed seasonal variation of the euphotic depth (m) at Como (a) and Abbadia Lariana (b).

(Fig. 2). In the sampled layers (0–100 m at Como and 0–135 m at Abbadia) a complete homogenisation took place from January to March. Maximum water temperatures in the stations of Como and Abbadia were observed in August (24.6 and 23.5 °C, respectively).

The lowest values of transparency (1.5 m) were recorded in April and July 1999 in the western basin (Fig. 3d); the highest value (15 m) was recorded in January 1998 in the eastern basin. The limit of the euphotic zone was between 15–30 m during the autumn and winter months, and between 6.6–15.0 m in spring and summer. The thickness of the mixed layer (Z_m) exceeded Z_{eu} during the colder months, whereas Z_{eu} exceeded Z_m in summer, from June to September.

4.2. Chemical characteristics

The time course of oxygen (percent saturation) and pH were parallel, even along the depth gradient in the epilimnion, with maximum values in summer and minimum in the coldest month (Figs 4a, b). In October 1997 the lowest pH (7.3) and dissolved oxygen saturation (13%) values were recorded in the metalimnetic

zone at Como (30 m). The highest pH in the western basin was recorded, at 5 m depth, in August 1998 (9.3); in the eastern basin the maximum values (9.0) were recorded at the surface, in July and August 1999.

Temporal variations of conductivity at Abbadia Lariana (Fig. 4c) were similar to the changes in alkalinity values, suggesting an impact of the precipitation of calcium carbonate caused by algal CO₂ depletion during summer. In the western basin conductivity was probably influenced, from May to July 1998, by conspicuous loads of industrial waste, common in this basin; this could be indicated by the high NH₄-N concentration recorded in July 1998 (160 µg N l⁻¹) and in the high annual mean computed in 1998 (52.2 µg N l⁻¹).

In the layer 0–20 m, annual average values of total phosphorus concentrations in 1998 were 27.4 and 15.6 µg P l⁻¹ in the western and eastern basins, respectively; the minimum and maximum values during the entire period of study were 17.2–42.6 and 4.1–36.6 µg P l⁻¹ at Como and Abbadia Lariana, respectively (Fig. 4d). Reactive phosphorus ranged between 2.5–30.2 µg P l⁻¹ at Como, and 2.5–27.4 µg P l⁻¹ at Abbadia Lariana.

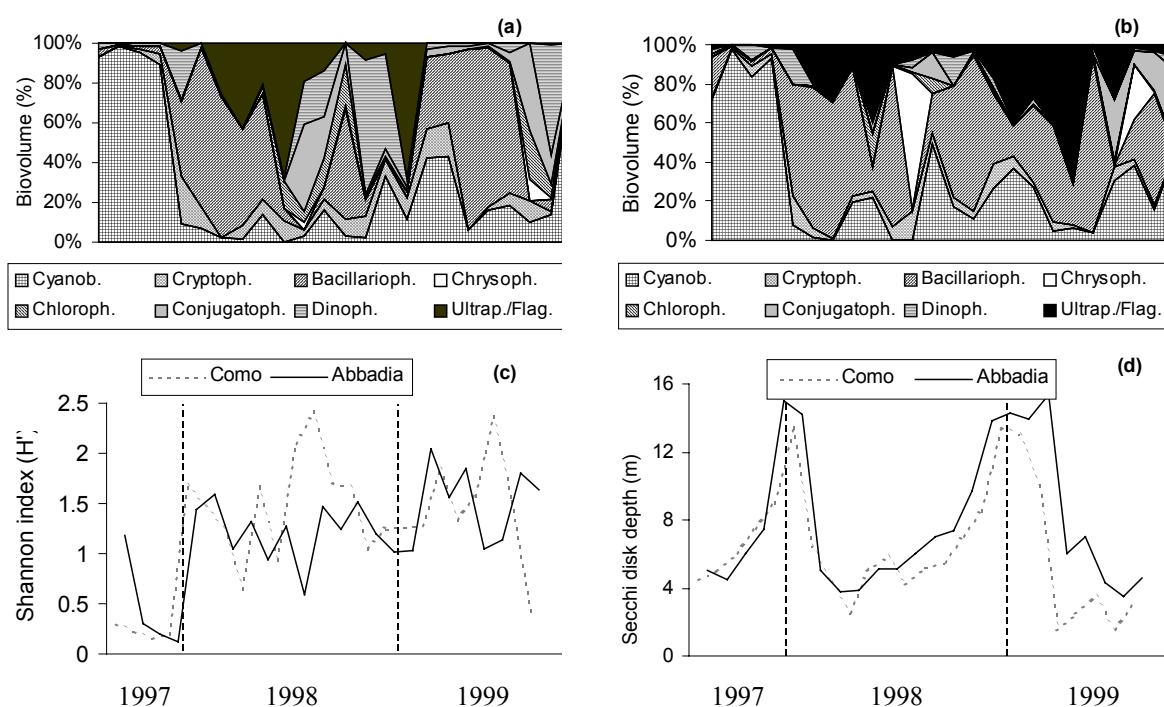


Fig. 3. Changes in the percentage contribution of phytoplankton groups to total biovolume at Como (a) and Abbadia (b). The temporal variations of the diversity index and transparency are reported in (c) and (d).

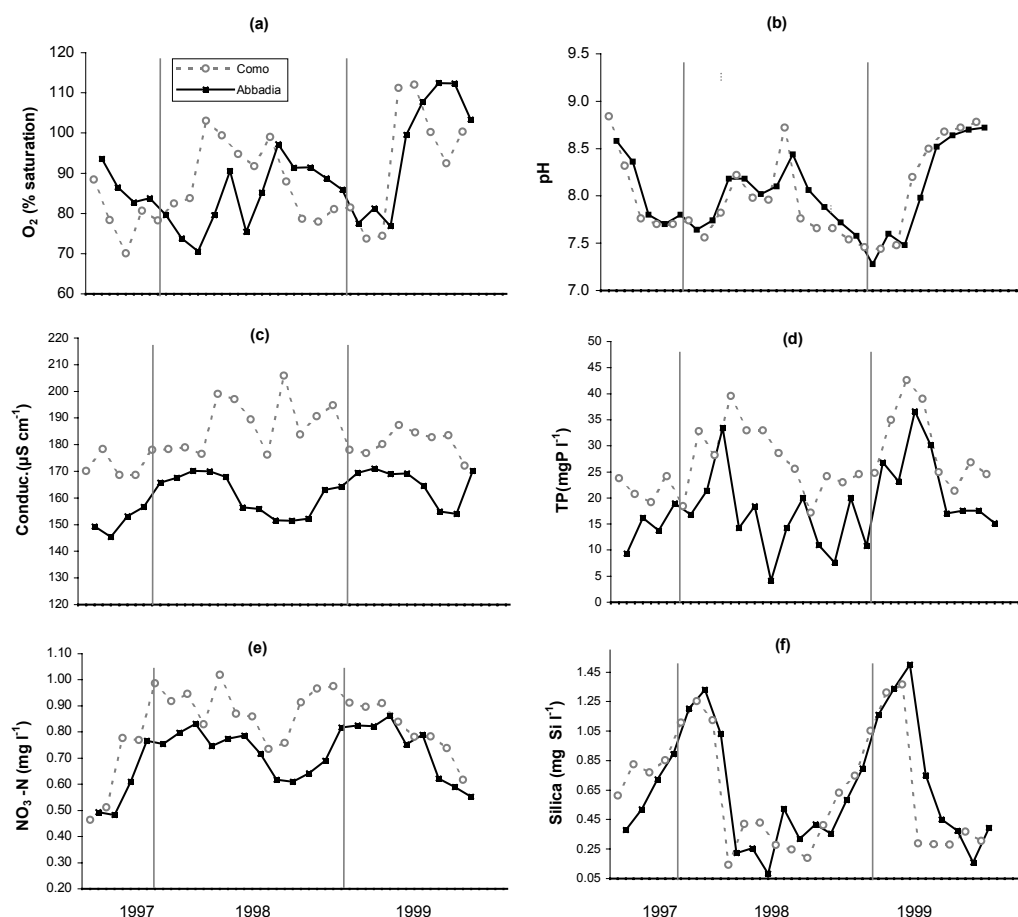


Fig. 4. Temporal variation of dissolved oxygen (a), pH (b), conductivity (c), total phosphorus (d), nitrate nitrogen (e) and reactive silica (f) in the layer 0-20 m.

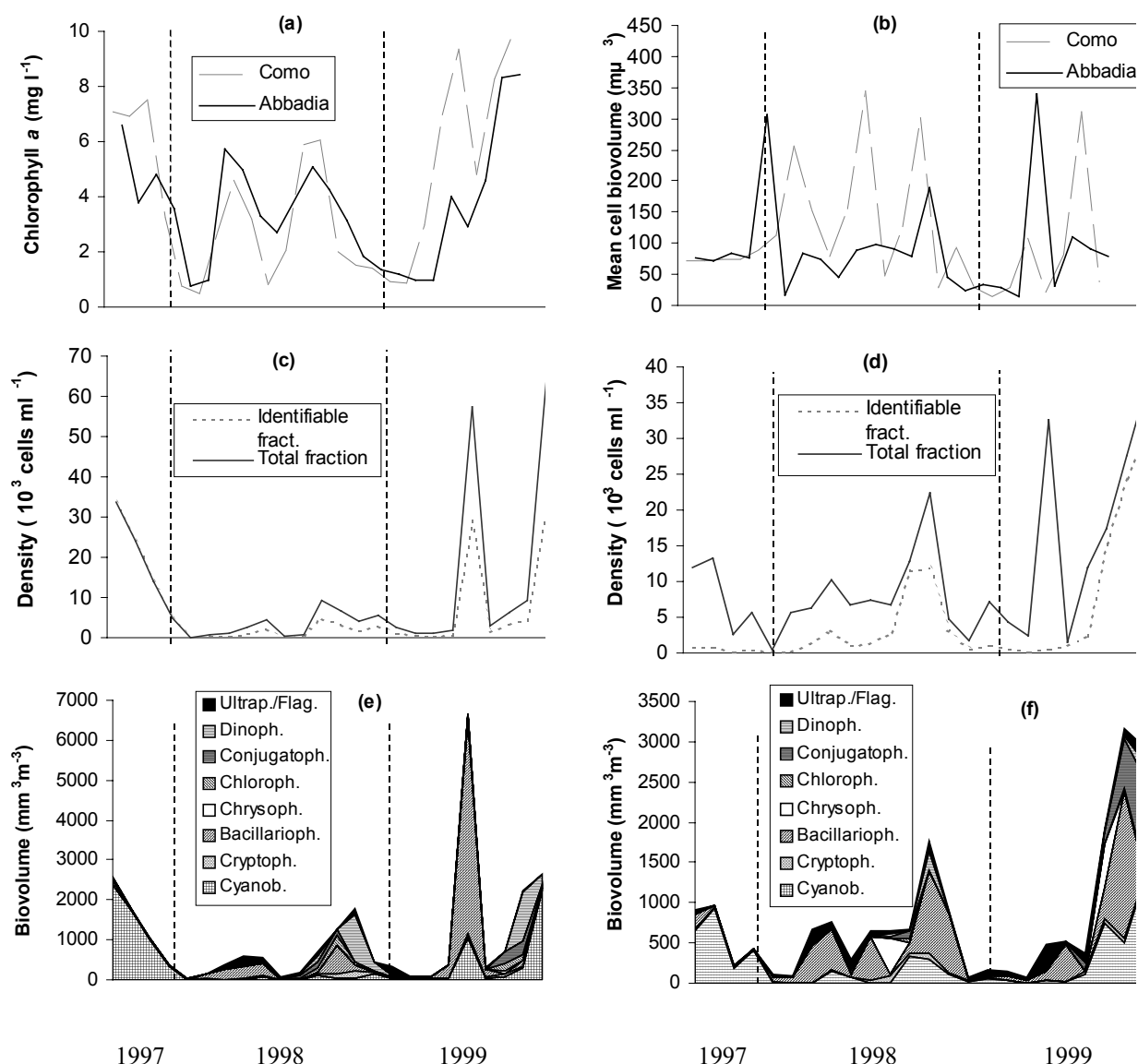


Fig. 5. Temporal variations of chlorophyll-*a* (a) and mean cellular biovolume (b) in the two sampling stations. Phytoplankton density and biovolume at Como (c, e) and Abbadia (d, f).

Minimum concentrations of $\text{NO}_3\text{-N}$ were recorded in September 1997, in the western basin (Fig. 4e), during the maximum development of cyanobacteria. All in all, $\text{NO}_3\text{-N}$ concentrations in the layers 0-20 m ranged between *ca* 0.46-1.0 mg N l^{-1} ; however, at the surface, minimum $\text{NO}_3\text{-N}$ concentrations reached a value of 0.25 mg N l^{-1} (Como, 2 September 1997). Annual mean values in 1998 were 0.90 and 0.74 mg N l^{-1} in the western and eastern basins, respectively.

Silica concentrations in the layer 0-20 m were lowest from late spring to mid summer. Minimum and maximum values were recorded at Abbadia Lariana in June 1998 (0.084 mg l^{-1}) and March 1999 (1.5 mg Si l^{-1}). At the surface, minimum Si concentrations were recorded in June 1998, at Abbadia Lariana (0.01 mg Si l^{-1}).

4.3. Density, biovolume and chlorophyll-*a*

Figure 5a shows the temporal variations of chlorophyll-*a* in the two sampling stations. The lower concentrations at Abbadia Lariana were recorded in winter (with a minimum of 0.8 $\mu\text{g l}^{-1}$ in January 1998); the maximum concentration was recorded during August 1999 (8.4 $\mu\text{g l}^{-1}$); the annual mean in 1998 was 3.2 $\mu\text{g l}^{-1}$. The western basin exhibited seasonal variations of chlorophyll-*a* similar to the eastern one, but with the minimum and maximum values occurring in February 1998 (0.5 $\mu\text{g l}^{-1}$) and August 1999 (9.7 $\mu\text{g l}^{-1}$); the annual mean in 1998 was 2.6 $\mu\text{g l}^{-1}$.

Phytoplankton biovolume and density values are reported in figures 5e-f, c-d. In general, the seasonal evo-

Tab. 1. List of the dominant taxa, common to both stations, that have contributed at least in one occasion to the 80% biovolume of all the determined taxa, peaks of biovolume of each species and species frequency in both stations over the total phytoplankton biovolume.

	Dominant taxa		Biovolume mm ³ m ³		Frequency %	
	Abbadia	Como	Abbadia	Como	Abbadia	Como
CYANOBACTERIA						
<i>Planktothrix rubescens</i>	+	+	961	2177	79	96
<i>Gomphosphaeria lacustris</i>	+	+	162	22	25	29
<i>Limnothrix</i> sp.	+	+	55	244	75	83
CHLOROPHYCEAE						
<i>Eudorina elegans</i>		+		59		4
<i>Pediastrum boryanum</i>		+		71		4
<i>Sphaerocystis Schroeteri</i>		+		10		8
<i>Nephrocitium agardhianum</i>		+		49		8
CONJUGATOPHYCEAE						
<i>Mougeotia</i> sp.	+	+	1006	257	46	33
<i>Staurastrum gracile</i>	+			224		29
CHRYSTOPHYCEAE						
<i>Dinobryon sociale</i>	+	+	443	4	8	4
<i>Uroglana americana</i>	+		540		4	
BACILLARIOPHYCEAE						
<i>Asterionella formosa</i>	+	+	183	4720	75	33
<i>Fragilaria crotonensis</i>	+	+	1784	559	92	83
<i>Tabellaria fenestrata</i>	+	+	534	75	29	17
<i>Stephanodiscus parvus</i>	+	+	289	138	38	25
<i>Aulacoseira islandica</i>	+	+	136	250	42	29
<i>Aulacoseira</i> cfr. <i>ambigua</i>	+		78		21	
<i>Cyclotella comensis</i>	+		75		13	
<i>Synedra acus</i>	+	+	52	22	29	8
<i>Melosira varians</i>	+	+	43	50	21	17
CRYPTOPHYCEAE						
<i>Rhodomonas minuta</i>	+	+	61	85	71	100
<i>Cryptomonas erosa</i>	+		18		38	
<i>Cryptomonas ovata</i>		+		13		21
DINOPHYCEAE						
<i>Ceratium hirundinella</i>	+	+	1179	1231	42	46
<i>Peridinium</i> sp.		+		53		4
<i>Gymnodinium</i> sp.	+		1		13	

lution of phytoplankton abundance shows a trend comparable to that of chlorophyll-*a*. In particular, chlorophyll-*a* and biovolume showed a significant correlation during the whole study period ($r=0.55$, $P<0.05$ at Como and $r=0.79$, $P<0.05$ at Abbadia).

The highest biovolume at Como was recorded in April ($6665 \text{ mm}^{-3} \text{ m}^{-3}$), during a high development of *Asterionella formosa*; annual mean values in 1998 and during the entire study period were 531 and $1053 \text{ mm}^{-3} \text{ m}^{-3}$, respectively. The maximum density value, recorded in August 1999 ($64925 \text{ cell ml}^{-1}$), was also due to a strong contribution of ultraplankton (Fig. 5d). In the eastern basin (Fig. 5f) maximum biovolume and density values ($2994 \text{ mm}^{-3} \text{ m}^{-3}$ and $37560 \text{ cell ml}^{-1}$) were recorded in August 1999, during a high development of *Fragilaria crotonensis*; annual mean values in 1998 and during the entire study period were 559 and $792 \text{ mm}^{-3} \text{ m}^{-3}$, respectively.

In 1998, and during the whole study period, the mean cellular biovolumes, obtained from the ratio between total biovolume values and total density values (Fig. 5b), were $62\text{--}111 \text{ }\mu\text{m}^3$ at Como, and $95\text{--}91 \text{ }\mu\text{m}^3$ at

Abbadia Lariana, respectively. The differences among the mean biovolume in the two stations are mainly due to different contributions of the ultraplanktonic cells.

The mean chlorophyll-*a* content per unit biovolume ranged between $1\text{--}37$ and $2\text{--}23 \text{ pg mm}^{-3}$ in the western and eastern basins, respectively.

4.4. Composition and species dynamics

By the end of the study period, 85 taxa belonging to six groups were identified. Chlorophyta (Chlorophyceae and Conjugatophyceae) (30) were the best represented, followed by Bacillariophyceae (23), Cyanoprokaryota (8), Cryptophyceae (6), Chrysophyceae (6) and Dinophyceae (6).

The dominant taxa, identified in the two stations, are listed in table 1. This table of this table reports the species that, starting from the most abundant, have contributed at least in one occasion to the 80% biovolume of all the determined taxa; for every species, biovolume peaks are indicated together with the occurrence (in percent) of each species in the whole study period and in the two stations.

At least two species, *Fragilaria crotonensis* and *Planktothrix rubescens*, have continuously characterised, with high biovolume values, the phytoplankton assemblage. Other species, like *Tabellaria fenestrata* and *Mougeotia* sp. in the western basin, and *Asterionella formosa* in the eastern basin, were less frequent, showing a single, conspicuous peak during their annual development.

The seasonal evolution of some selected dominant taxa (cf. Tab. 1) is reported in figure 6. During the complete thermal homogenisation of the water column (January and February), the dominant taxa in the western basin were *Fragilaria crotonensis* and *Rhodomonas minuta* in 1998, *Planktothrix rubescens*, *Fragilaria crotonensis* and *Aulacoseira islandica* in 1999. In the eastern basin the situation was different only in 1999, when *Melosira varians* and *Aulacoseira* cf. *ambigua* gave an important contribution to the phytoplankton assemblage.

During early spring, *A. formosa* and *F. crotonensis* were the most abundant species; in the station of Como, in April 1999, *A. formosa* reached the highest biovolume value recorded in this study ($4720 \text{ mm}^{-3} \text{ m}^{-3}$). Other taxa, such as *A. islandica* and *A. cf. ambigua* gave a minor contribution to the assemblage. At Abbadia Lariana *Stephanodiscus parvus* was the dominant species in March and April 1998.

In late spring and early summer, with the start of thermal stratification, a transition occurred from a community dominated by diatoms to more diversified assemblages; Chlorophyceae (*Sphaerocystis Schroeteri* and *Pediastrum boryanum*) and Conjugatophyceae (*Staurostrum gracile* and *Mougeotia* sp.) were the most abundant taxa in the western basin. In May and June 1998, in the eastern basin, *P. rubescens*, *T. fenestrata* and *Carteria globosa* were the most important species; in 1999 there was a bloom of *Uroglena americana*, with densities up to $300,000 \text{ cell ml}^{-1}$ along the littoral zone.

In the early and middle summer period, with stable water column stratification, phytoplankton assemblages at Como showed a different development in 1998 and 1999. In 1998 many species (such as *S. gracile*, *Mougeotia* sp., *Ceratium hirundinella*, *Nephrocitium agardhianum* and many others) contributed to 80% biovolume, especially in August, when the diversity index reached its maximum value (Fig. 3c).

Small Cyanobacteria belonging to Chroococcales (e.g. *Gomphosphaeria lacustris* and *Aphanocapsa* sp.) were abundant in this period. In 1999 *P. rubescens*, (82% of total biovolume in August), *C. hirundinella* and *Mougeotia* sp. dominated the algal community. In 1999, the same dominant species found at Como were noticed also at Abbadia Lariana, with the addition of *P. rubescens*, *G. lacustris* and *Dinobryon sociale*.

During late summer the assemblages were characterised by a high development of *P. rubescens* in 1997

($2314 \text{ mm}^{-3} \text{ m}^{-3}$ in September), and *F. crotonensis* and *C. hirundinella* in 1998.

As mixing depth increased, the autumn and early winter assemblages were mainly constituted by three species, i.e. *P. rubescens*, *Rhodomonas minuta* and *Limnithrix* sp.

4.5. Seasonal evolution of the algal assemblage in 1998

The dendrogram obtained by cluster analysis indicates a similar pattern of phytoplankton succession in the two stations (Fig. 7). The highest hierarchical level denotes a separation of the summer samples from all the others. The single seasons can be identified at a lower level of dissimilarity. Winter (W) and spring (SP) samples were grouped in single clusters, while summer (S1 to S4) and autumn (A1 and A2) were subdivided into sub-groups.

By the NMDS technique I could reveal a chronological ordination of the different groups identified by cluster analysis (Fig. 8; the "stress" of the configuration equals to 0.17). In particular, along the first axis of the two dimensional configuration, the summer samples are distinguished from the others; by contrast, the differences among the winter, spring and autumn groups are less evident.

The most important feature of the samples belonging to the winter group (W) was the low biovolume. This group is characterised by a weak dominance of *F. crotonensis*, *A. islandica*, *R. minuta* and *Melosira varians*.

The spring group was strongly dominated by diatoms. At Abbadia, the centric diatom *Stephanodiscus parvus* was the main taxon, followed by *A. islandica*; at Como, large colonial diatoms, mainly *A. formosa*, followed by *Fragilaria crotonensis*, dominated the assemblages.

After the stabilisation of the water column, large diatoms progressively decreased in favour of other taxa. In this period the distance between the groups in the NMDS configuration increased, indicating a strong intensification of the assemblage turnover (Fig. 8). Both cluster analysis and NMDS indicate that in summer the differences between the assemblages of the two stations were at their maximum.

The first summer phase includes the samples of June (S1, Como; S2, Abbadia). S1 was characterised by *S. Schroeteri* and *R. minuta*, while in S2 *T. fenestrata* was the main taxon. Similarly, the algal assemblages of the two mid-summer groups (S3, S4; July-August) were rather different in the two stations, even though, in general, both were characterised by a similar development of chlorophytes. The station of Abbadia, in July, was dominated by *D. sociale*, while *S. gracile* and *C. hirundinella* gave an important contribution to the assemblage at Como. In August, *P. rubescens* and *Mougeotia* sp. gave the main contribution to the biovolume in the stations of Abbadia and Como, respectively.

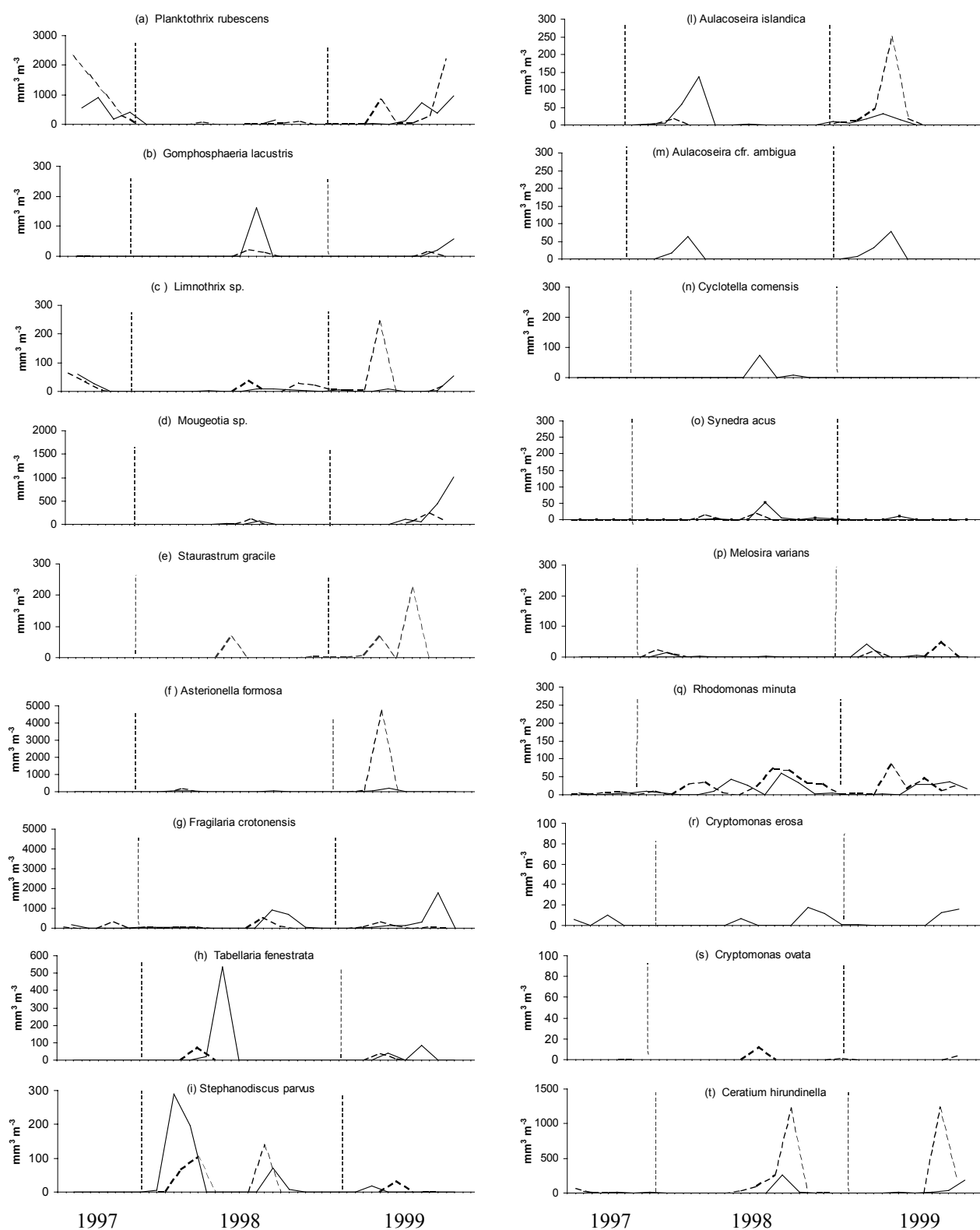


Fig. 6. Temporal variations of biovolume for selected dominant species of the groups Cyanobacteria (a-c), Conjugatophyceae (d-e), Bacillariophyceae (g-p), Cryptophyceae (q-s) and Dinophyceae (t). Broken line: Como St.; solid line: Abbadia St.

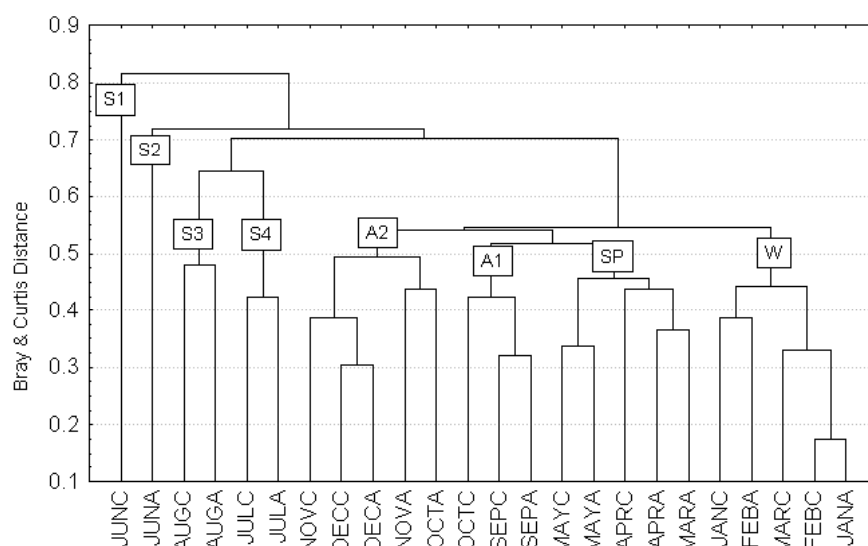


Fig. 7. Dendrogram showing the results of the classification of samples from Lake Como. The samples are named according to the month and the station (C=Como, A=Abbadia Lariana).

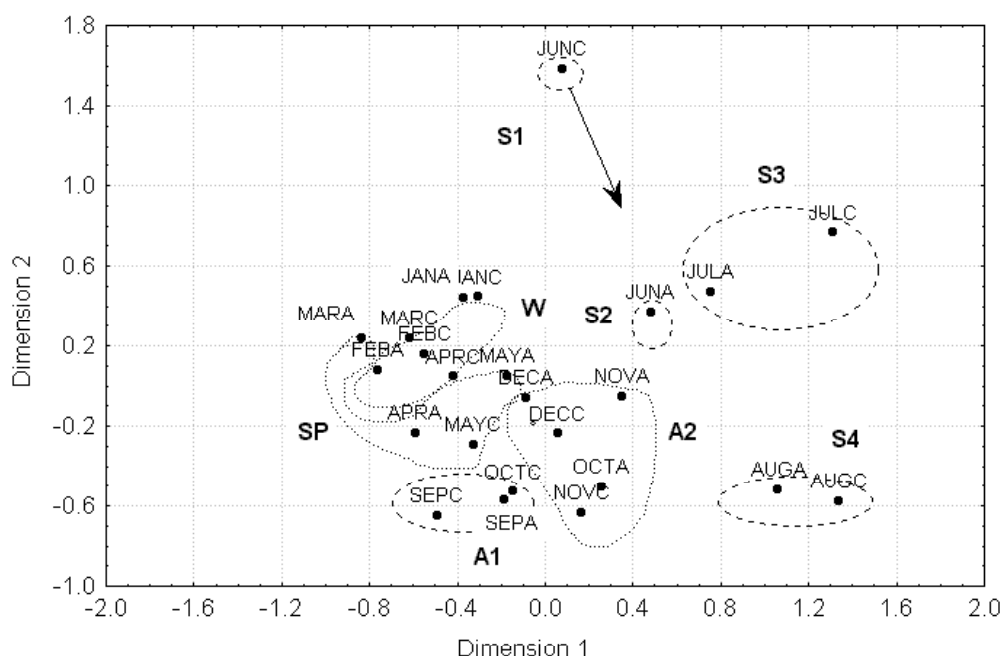


Fig. 8. Ordination of samples in the two-dimensional NMDS configurations. Groups are numbered as in figure 7. The arrow shows the direction of the succession.

The early autumnal phase (A1) was dominated, with high biovolume, by *F. crotonensis*, *P. rubescens* and *C. hirundinella*. The late autumn group (A2) stood out for a progressive decrease of biovolume and the appearance of *Limnotherix* sp. and *A. islandica*.

5. DISCUSSION

The seasonal development of phytoplankton is strictly associated with the temporal variations of some important environmental factors. It is known that during

winter, with the lowest values of Z_{eu}/Z_m ratio, low algal growth is due, to low irradiance and water temperature, as well as to the dilution of algal cells along the water column. The increasing of illumination with the progress of winter, the high availability of nutrients and high water column turbulence are a group of factors which strongly support the development of large colonial (*Asterionella* and *Fragilaria*) and medium-large centric diatoms (*Stephanodiscus* and *Aulacoseira*). Many diatoms have in general low threshold under minimum

light (cf. Sommer 1987) favouring growth in well mixed waters; moreover, large diatoms can maintain large overwintering vegetative populations which may rapidly grow and become dominant after the winter months (cf. Reynolds 1984). The decrease of turbulence, resulting from water column stabilisation, and the exhaustion of silica are important factors for the decline of large diatoms (Sommer 1987); however, owing to the dependence of diatom populations from the net rate of increase (nutrient dependent) and losses (sinking and mortality), it is difficult to ascertain the relative impact of these two factors. Many studies show that cultured diatoms can grow until Si is reduced to *ca* 5 $\mu\text{g Si l}^{-1}$ (Reynolds 1984). In this investigation (cf. Fig. 4f), minimum concentrations of silica in the layer 0-20 m (0.084-0.144 mg Si l^{-1}) are still suitable for diatom growth, but probably not enough to maintain a positive net balance in a progressively stabilised water column (cf. Salmasso 2000). *Tabellaria fenestrata* was the last diatom to develop with large biovolumes before summer; this was probably favoured also by the photosynthetic properties of this species, which is adapted to light intensities apparently inhibitory for the low light adapted species like *Fragilaria* and *Asterionella* (Reynolds 1984).

The summer period is characterised by intensifying thermal stratification which reduces the uptake of nutrients from the hypolimnion and determines a rapid segregation of resources along the water column, with major niche differentiation in early and mid summer. During these months, sinking, grazing losses and nutrient depletion assume a more critical role in controlling community composition. Some morphological and behavioural adaptations like small size, motility (flagellated organisms) density reduction (mucilaginous colonies) and buoyancy control (e.g. cyanobacteria) should be seen primarily as mechanisms prolonging the residence times of algal populations in the upper illuminated layers. Many of the taxa that develop during the summer months (e.g. many Chlorococcales, *G. lacustris*, *C. hirundinella*, *D. sociale* and *P. rubescens*) share a few of these adaptations. In particular, *P. rubescens* is homogeneously vertically distributed during circulation and exhibits a metalimnetic accumulation during the summer months. This is due to its ability to regulate its vertical position, and favoured by its adaptation to conditions of low irradiance (Lampert & Sommer 1997). These properties allow a strong dominance of this species in late summer and autumn, when the progressive mixing of the water column determines a strong rearrangement of the community, with the disappearance of Chroococcales and the sporadic reappearance of *Fragilaria*.

From late summer to spring, multivariate analysis revealed a substantial homogeneity in phytoplankton evolution between the two sub-basins. Only during early summer the assemblages were less homogeneous. The different evolution of phytoplankton in the west and east

basins during thermal stratification, and after the decline of large diatoms, reflects a different rate of change in the communities. However, this situation was likely amplified by the different sampling calendar in the two stations.

The peaks and the average values of biovolume, transparency and chlorophyll-*a* at Como indicate a greater algal production than at the station of Abbadia, especially in spring and summer. According to the PEG model (Sommer *et al.* 1986), the development of abundant summer phytoplankton should be a function of nutrient availability during the spring months. TP concentrations at spring overturn in 1998 and 1999 were similar in the two sub-basins; on the contrary, during the rest of the year, TP concentrations were often lower at Abbadia. Considering the different physiographic properties of the two sub-basins, the differences of algal production between the two stations may be the consequence not only of nutrient availability, but also of hydrological events. This aspect, coupled with a clear classification and quantification of industrial loads discharged in the western basin (cf. section 4.2), should be faced by future environmental and limnological investigations in Lake Como.

The lower algal biovolumes (Figs 5e, f), and the apparently smaller utilization of N-NO₃ (Fig. 4e) during the spring and summer months in 1998, testify a smaller algal development than in 1997 and 1999. In this connection a lower development of *Planktothrix rubescens* in the western basin should be noted. However, the lower algal biomasses observed in 1998 do not seem linked to a different availability of TP (cf. Fig. 3d). Physical factors should also be considered in an in-depth analysis (e.g. hydrology, meteorological events).

Referred to the whole study period, biovolume composition in the western basin was dominated by cyanobacteria (50%), followed by diatoms (26%) and Cryptophyceae (12%). In the eastern basin, diatoms were the most abundant (35%), followed by cyanobacteria (31%), ultraplankton (8%) and Chrysophyceae (5%). The mean biovolume values were lower in 1998 (531 and 559 $\text{mm}^3 \text{m}^{-3}$ at Como and Abbadia, respectively) than during the entire period (1053 and 792 $\text{mm}^3 \text{m}^{-3}$). All in all, these values fall within the interval 500-2000 $\text{mm}^3 \text{m}^{-3}$ defined by Rott (1984) as characteristic of mesotrophic lakes.

The most recent study on the phytoplankton of Lake Como was carried out from February to October 1997 in three stations located in the western basin (Bettinetti *et al.* 2000). Compared to the present work, the results revealed a common dominance of *P. rubescens* in late summer, autumn and early winter, and of *R. minuta* in late autumn and winter. Spring was characterized by the same diatom assemblage as in the present work, with some differences in relative abundances: in spring 1997 the most abundant diatom was *Stephanodiscus hantzschii*, whereas in the spring of 1998 and 1999 the

dominant diatoms were *A. formosa* and *F. crotonensis*. Other species, such as *A. islandica*, gave a lower contribution to phytoplankton biovolumes.

In the present investigation, two biovolume maxima (in spring and late summer) were found. Bettinetti *et al.* (2000) recorded only one maximum value in autumn; moreover, the phytoplankton biovolume and density values recorded by these authors were generally higher than those found in the present study; this was also observed in September and October 1997, the two months sampled in the course of both investigations. These differences may depend, at least in part, on to the different sampled layers, i.e. 0-10 metres (Bettinetti *et al.* 2000) and 0-20 metres (present study).

In the eastern basin the most recent studies were made by Chiaudani & Premazzi (1993) and Buzzi (1995). A comparison with these two papers is not reliable; in the first case a different approach was used to determine phytoplankton abundance; in the second case, samples were collected with a lower sampling frequency. However, species like *F. crotonensis*, *P. rubescens* and *R. minuta* were the most important in the assemblages described in the two mentioned papers, just as in the present one.

6. CONCLUSIONS

Since the 1980s a decrease of TP concentrations in the water column of Lake Como was recognised (from ca 75 $\mu\text{g P l}^{-1}$ down to 40-50 $\mu\text{g P l}^{-1}$ in the first half of the 1990s; Mosello *et al.* 1997, 1999, 2001). The lower algal nutrient availability caused a significant decrease of some dominant species such as *Microcystis aeruginosa* and *Melosira granulata*, which are usually associated with eutrophic environments. In the second half of the 1990s, the decrease of TP came to an end, and phytoplankton communities did not undergo major changes, as confirmed by a study on sedimentary diatoms (Marchetto & Bettinetti 1995).

The present nutrient concentrations in the two sub-basins are around 35 $\mu\text{g TP l}^{-1}$ (Mosello *et al.* 1999, 2001). However, a considerable amount of phosphorus is sequestered in the deep hypolimnion, thus deferring complete or higher replenishment of nutrients in the euphotic layers until years of complete or more extended episodes of vertical mixing. With favourable environmental conditions (e.g. enhanced water column stability), the high trophic potential of Lake Como may be suitable for the development of cyanobacterial blooms. In August 2000, a bloom of *M. aeruginosa* developed in the entire western branch, with a maximum density of 300,000 cell ml^{-1} (ARPA-Lombardia; unpublished Technical Report).

Despite the strong reduction of TP since the 1980s, the results of investigations carried out during the 1990s indicated a substantial stability of the phytoplankton assemblage. This is in accord with the statement by Sas (1989) on the recovery pattern observed in deep lakes

after the reduction of phosphorus. At present, Lake Como is in the phase where the dominant species are adapting to reduced resource levels. In the future, a reduction in biomass and shift in species composition should be observed, provided that a severe control of the nutrient loads discharged into the lake will be adopted.

Future studies on the algal communities should become an indisputable feature in the management of Lake Como, because of phytoplankton populations rearrange their biomass and composition in reply to changing nutrient levels and trophic conditions. However, the knowledge of meteorological and hydrological data is a necessary step to identify the most relevant factors influencing the seasonal alternation of the dominant phytoplankton species.

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