Effects of climatic fluctuations and vertical mixing on the interannual trophic variability of Lake Garda, Italy

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Abstract

A linked chain of causal factors—namely, winter air temperature, spring lake temperature, extent of the spring lake overturn, and extent of surface nutrient enrichment—had significant effects on the annual development of phytoplankton structure and biomass in Lake Garda, a large (49×10^9 m³), deep (350 m) lake located south of the Alps. The relationship between the winter climate and the North Atlantic Oscillation (NAO) was unclear, probably because of the location of the lake, which was on the border between different centers of action of the NAO (the Mediterranean region and central and northern Europe). Soon after the major enrichment episodes, conjugatophytes and large diatoms developed with higher biovolumes during April, whereas from midsummer to midautumn, the cyanobacteria and, more irregularly, the conjugatophytes were more important. In two other deep southern subalpine lakes (Iseo and Lugano), the interannual variations in the extent of spring vertical mixing, nutrient replenishment, and phytoplankton development were closely related because of the common effects of winter climate on the subalpine region. The effect was proportionally more evident in the two meromictic and more eutrophic lakes, Iseo and Lugano, because of the higher nutrient content in their hypolimnia.

External nutrient loads and the consequent overall content of algal nutrients do not exclusively control the trophic status of a lake. Other factors, such as morphometry, hydrology and in-lake hydrodynamics, climatic conditions, and food-web structure, also have a major influence on the development of algal biomass and species composition (Ryding and Rast 1989). Identification of the most relevant factors and mechanisms affecting the trophic evolution in different typologies of lakes is crucial for correct interpretation of the modifications observed in the chemical and biotic characteristics as well as for identification of the most efficient recovery strategies.

Large, deep lakes belong to a well-defined typology (Tilzer and Serruya 1990). Depending on their maximum depth, morphology, and climatic location, they may undergo complete circulation every year (holomictic lakes) or show a constant stratification (meromictic lakes), whereas those lakes characterized by variable temporal periods of incomplete mixing, interspersed with occasional events of complete mixing during cold winters, are classified as oligomictic (Wetzel 2001). In oligomictic and meromictic lakes, the vertical distribution of nutrients and many chemical characteristics of the deep waters are influenced by the microbial decomposition of the algal biomass and by the duration of the segregation of the hypolimnion from the surface waters (Salmaso and Decet 1998). In these lakes, the extent of vertical mixing at the end of the winter months represents an important factor in determining the fraction of algal nutrients that may be recycled from the deep waters to the surface. At the beginning of the year, the mixing processes affecting the water masses may have a strong influence on algal production in successive months. The late winter and early spring months therefore may be considered to delimit the most critical period within the annual evolution of a deep lake. In this context, the climatic evolution during the coldest months and the water-mixing dynamics represent a complex of factors that are essential for interpretation of the interannual variations of the trophic status in oligomictic and meromictic lakes. On the other hand, despite the acknowledged importance of spring mixing events in deep lakes, the quantitative significance of these events has been poorly investigated (Goldman and Jassby 1990).

The deep lakes located south of the Alps (lakes from east to west: Garda, Iseo, Como, Lugano, and Maggiore; Fig. 1A) constitute one of the largest freshwater supplies in Europe. Because of their great depth, ranging from 251 m (Iseo) to 410 m (Como), the deep southern subalpine lakes are oligomictic (lakes Garda, Como, and Maggiore; Salmaso and Decet 1998; Ambrosetti and Barbanti 1992), either tending toward meromixis (Lake Iseo; Garibaldi et al. 1999) or being completely meromictic (Lake Lugano; Barbieri and Mosello 1992).

The limnological investigations carried out during the 1990s in the largest of the deep southern subalpine lakes (Lake Garda) showed a significant interannual variability in the chemical and biotic characteristics of the trophogenic layers, with conditions ranging from oligomesotrophy to mesotrophy (Salmaso 2002). Important year-to-year variations in the nutrient concentrations and phytoplankton were also documented in Iseo and Lugano (Salmaso et al. 2003*a*). In previous studies, Salmaso et al. (2003*b*) and Simona (2003) suggested that a key role was being played by the winter climatic conditions and spring vertical mixing in controlling
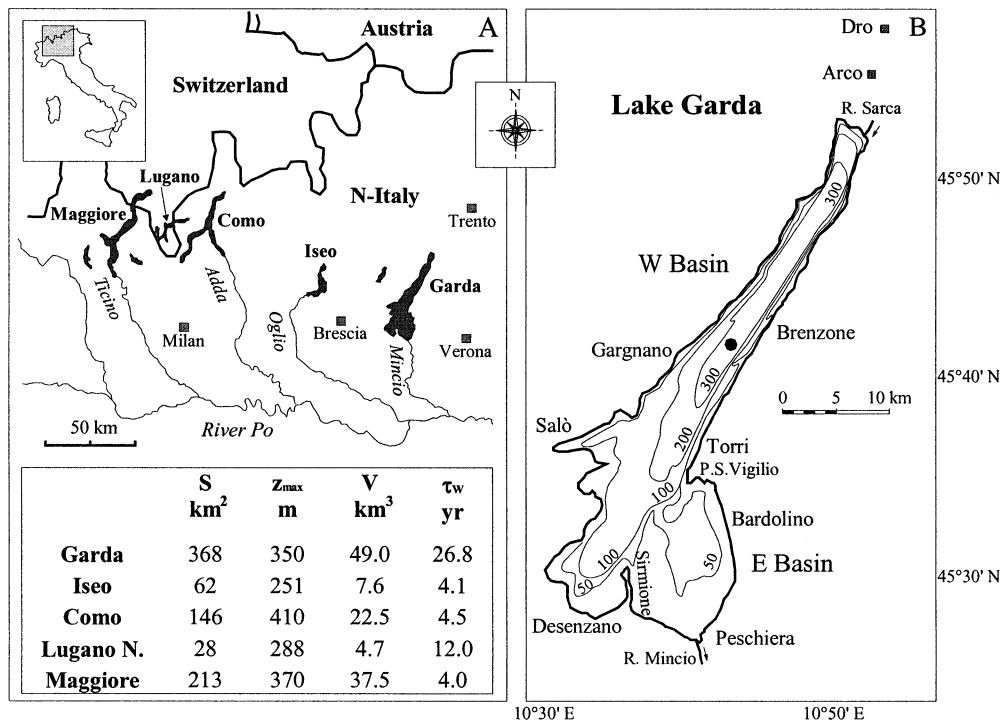
Fig. 1. (A) Geographic location and morphometric characteristics of the deep southern subalpine lakes in Northern Italy (data from Ambrosetti and Barbanti 1992). S, lake surface area; z_{max}, maximum depth; V, lake volume; τ_w, theoretical water renewal time. (B) Bathymetric map of Lake Garda (From IRSA 1974, modified) and location of the sampling station (circle).

the year-to-year variations of the trophic status in the deep southern subalpine lakes.

The objective of the present study was to provide interpretative elements essential for explaining the causes of the interannual differences of the trophic characteristics observed in the large, oligomictic Lake Garda. The study analyzes the relationships between climatic fluctuations during the winter months, the extent of the spring vertical water mixing and phosphorus fertilization, and phytoplankton composition and structure. Finally, the hypothesis of a common effect of the winter climate on the mixing regimes and spring fertilization of the deep southern subalpine lakes was investigated using a subset of coherent temporal data recorded in the lakes Garda, Iseo, and Lugano.

Methods

Study site—The geographic location of the deep southern subalpine lakes, their morphometric characteristics, and the bathymetric map of Lake Garda are reported in Fig. 1. These lakes present some common morphologic features. They are narrow, elongated, and delimited laterally by steep sides; their bottoms are generally flat. Their thalwegs are roughly north–south oriented, with the exception of the N-basin of Lake Lugano (east–west).

Lake Garda is the largest Italian lake (Fig. 1B). The main inflow is the river Sarca, at the northern edge of the lake; other tributaries are less important and mainly flow toward the western and northern shores. The outflow, with an average discharge of 58 m^3 s^{-1}, is the river Mincio, at the

southern edge of the lake. Compared with the other deep southern subalpine lakes, Lake Garda has a long theoretic water renewal time (27 yr) because of its low ratio of catchment area to lake volume and its low annual rainfall (790–1,150 mm; Istituto di Ricerca sulle Acque [IRSA] 1974). On the basis of bathymetric values, Lake Garda can be divided into two basins separated by an underwater ridge connecting the Sirmione peninsula with Punta S. Vigilio. The western basin is the larger and deeper of the two. In its northern part, the shores are steep and the bottom extends for >20 km at depths ranging from 300 m to 350 m. The shallower eastern basin has a maximum depth of 81 m and represents only a small portion of the lake's overall volume (<7%). Details of the catchment and the lake have been reported by IRSA (1974).

Field program and laboratory analyses—Samples normally were collected every 4 weeks between 1991 and 2003 in the deepest zone of the lake (western basin, off Brenzone; Fig. 1B). Detailed and continuous chemical analyses have been performed since 1995; in the years before 1995 chemistry was determined only irregularly and on a limited number of variables and samples. In 1995, water samples for chemical analysis (including dissolved oxygen) were collected at the surface and at depths of 20, 100, and 200 m. From 1996 onward, further samples were collected at 150 m and 300 m and, since 1997, at 60 m; additional samples to determine oxygen were collected at depths of 10 m and 250 m and at ~1 m above the bottom. Oxygen was fixed in the field and determined in the laboratory by titration (io-

dometric method; American Public Health Association [APHA] et al. 1989). From 1995 to 2000 and from 2002 to 2003, the chemical analyses were carried out by the Veneto Region Environment Protection Agency (ARPAV, district of Belluno) following standard methods (APHA et al. 1989); the analytical procedures have been described in detail by Salmaso et al. (1997) and by Salmaso and Decet (1998). In March 2001 and from August to December 2001, the chemical analyses were carried out by the CNR-ISE (Institute of Ecosystem Study, Pallanza) and by the Department of Chemical Processes of Padova University, respectively. The chemical methods and results were checked and verified in the framework of different projects (e.g., Mosello et al. 1995) and with regular, annual intercalibrations.

Water samples for chlorophyll *a* (Chl *a*), dry weight, and phytoplankton analyses were collected in the euphotic layer (depth, 0–20 m) from June 1992; in the preceding period, the analyses were carried out on samples collected only on the surface. The statistical analyses take into consideration the biological data recorded exclusively within the 0–20-m layer from January 1993 to December 2003. The concentration of Chl *a* was determined by spectrophotometry after filtration on Whatman GF-C glass-fiber filters, disruption of the filters with a grinder, and 24-h extraction in 90% acetone. Dry weight was determined following Salmaso and Decet (1998). Phytoplankton analysis was carried out on subsamples preserved in acetic Lugol's solution. Algal cells were counted on Zeiss Axiovert 135 and IM35 inverted microscopes. A detailed description of the procedures used in the field and laboratory has been reported by Salmaso (2002).

Transparency was estimated, with the aid of a bathyscope, using a Secchi disk.

Since 1991, measurements of temperature, oxygen, pH, and conductivity have been carried out in the water column using underwater multiparametric probes (Idronaut Ocean Seven 401 from 1991 to 1997 and Seacat SBE 19-03 as of January 1998). The resolution of the temperature probes is 0.001°C or less. Before taking the measurements, the probes were conditioned for at least 30 min in the surface waters. The whole sequence of depth profiles of pH, conductivity, and oxygen was used for determining the time and extent of mixing in Lake Garda. The depth of the spring mixing was taken to be the maximum point at which an upper layer of almost-uniform values for the selected variables met a lower layer of rapidly changing values (Goldman and Jassby 1990). The reported values of mixing depths represent only approximate estimates because of their dependence on the sampling frequency and on nonperfect synchrony (in some years) in depth and time changes of all the selected variables. Previously published estimates of mixing depth in 1992–1993 (180 m) and in 1998 (170 m) were checked and corrected with slightly different estimates (190 m and 150 m, respectively). Lake volumes were calculated by means of polynomial interpolation of discrete depth (Z, in m) and volume (V, in m^3 × 10^6) data tabulated by IRSA (1974): $V = (3.295 × 10^2)Z - (7.509 × 10^{-1})Z^2 + (6.025 × 10^{-4})Z^3$ ($r^2 \approx 1$). This function was used to estimate the volume-weighted average values of the temperature between 0 m and 100 m and the volume-weighted average concentrations of total phosphorus (TP) and dissolved oxygen in selected layers.

Climatic data—Mean daily air temperatures were obtained at the Agricultural Institute of San Michele all'Adige (Section of Agrometeorology). The meteorological station is located at Arco (91 m a.s.l.), which is ~5 km away from the northern border of the lake. In some cases (particularly from the end of 2000 to 2002), missing observations were replaced with the corresponding measurements made at Dro (123 m a.s.l.), which is 5 km north of Arco (Fig. 1B). A comparison of the daily temperatures recorded in the two stations from the end of 1999 to 2003 showed that the two series gave practically the same results ($r \approx 1$). Finally, the data were checked with those obtained at the Trento station (194 m a.s.l.), which is ~25 km north of Arco, showing the existence of a high correspondence between the two datasets ($r = 0.96$, $p < 0.01$).

The local climatic conditions were related to large-scale climatic phenomena influencing the European regions, namely the north–south dipole pattern found over the Atlantic Ocean (North Atlantic Oscillation [NAO]). A seasonal, station-based NAO index representative of the winter conditions (December–February; NAO_w) was obtained from the website of the U.S. National Center for Atmospheric Research (Climate and Global Dynamics Division, Climate Analysis Section; Hurrell 1995; Hurrell et al. 2003). The index expresses the difference of sea-level pressure between Ponta Delgada, Azores, and Stykkisholmur/Reykjavik normalized relative to the period 1865–1984.

Data analyses—Before correlation analyses, the annual averages of the physical, chemical, and biological variables were linearly detrended for selected subperiods under examination. This transformation makes it possible to compute correlations representing mechanistic relationships at the annual time scale, avoiding spurious correlations originating from the presence of temporal trends (cf. Chatfield 1991). However, the comparison of the correlations obtained with the detrended and nondetrended series gave essentially similar results.

Analysis of variance was used to test for differences between the means of selected variables. In the case of heterogeneity of the variances (checked by the Bartlett's test at $p < 0.05$), the computations were carried out on the log-transformed variables.

Statistical analyses were conducted with Systat 10.2 (Systat Software, Inc.) and Statistica 5.1. (Statsoft, Inc.).

Results

Climatic fluctuations and their impact on the lake thermal structure and mixing—The temporal evolution of the hypolimnetic temperatures recorded since spring 1990 are reported in Fig. 2A. Episodes of cooling of the deepest waters were identified in spring 1991, March 1999, and February–March 2000. The coarse sampling interval during winter 1990–1991 makes it difficult to state the month during which the cooling occurred in 1991. In the deepest layer (depth, 300 m to bottom), the decrease of the temperature values on these three occasions ranged from 0.1°C (1991) to 0.37°C (1999). In the period between the cooling episodes (spring 1991 to late winter 1998) and from spring 2000, the hypo-
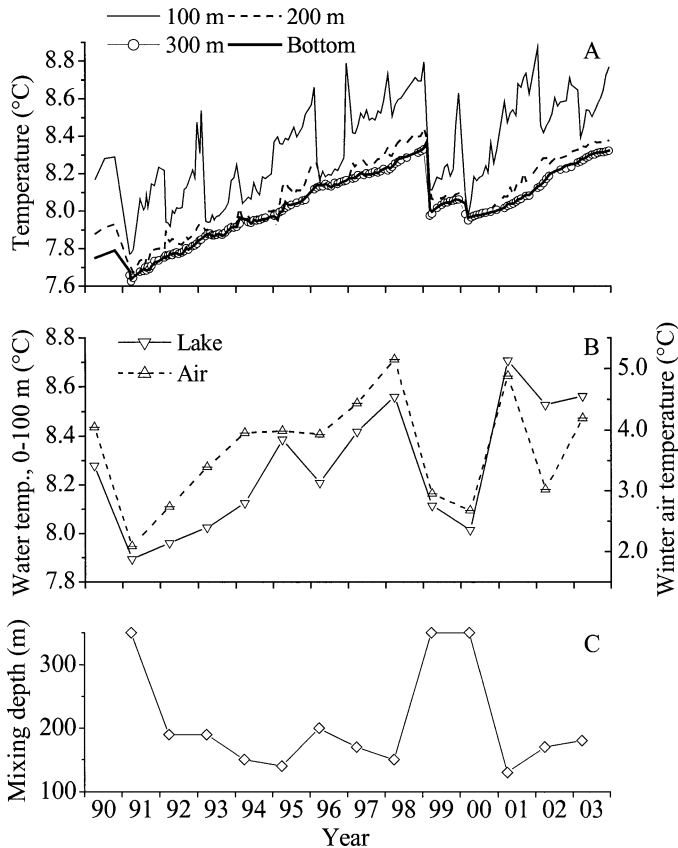
Fig. 2. (A) Hypolimnetic temperatures from April 1990 to December 2003. The original series of data (1991–2003) has been integrated with the temperatures measured during 1990 by Provincia Autonoma di Trento (1991). (B) Volumetrically weighted spring minimum lake temperatures between 0 m and 100 m (T_{0-100}) and average winter (December–February) air temperatures from 1990 to 2003 (T_W). As for T_W, the years in the graph refer to the months of January and February; the minimum lake temperature in 1990 was computed on the basis of two measures carried out on 10 April at 50 m and 100 m. (C) Spring mixing depths (Z_{SMix}).

limnion underwent progressive warming, with temperatures in the layer below 200 m increasing at a speed of 0.09–0.10°C yr^{-1}.

The alternation of periods of gradual warming with short events of cooling is strongly linked to the long-term evolution of the winter climatic conditions. Figure 2B shows the temporal evolution of the mean winter air temperatures at the Arco meteorological station (T_W). The figure also shows the minimum mean values of temperature recorded every year in the lake from 0 to 100 m (T_{0-100}). In the period under consideration, these values always occurred between the second half of February and the beginning of April. The 0–100-m layer underwent homogeneous cooling every year and, thus, may be considered to represent the part of the lake that is most affected by the climatic events during the limnological winter.

The analysis of the vertical, physical, and chemical profiles recorded since 1991 with the multiparametric probes allowed association of the larger hypolimnetic cooling episodes observed in 1991, 1999, and 2000 with complete cir-

Table 1. Correlation coefficients, r, between the descriptors of winter climatic conditions, spring mixing depths, and spring epilimnetic total phosphorus concentrations in Lake Garda. The correlations refer to the years from 1991 to 2003 (with the exception of the correlations including TP_S, 1995–2003). All calculations are based on linearly detrended data. Values are significant at $p < 0.01$ (**), $p < 0.05$ (*), and $p < 0.10$ (+).

	T_W	T_{0-100}	Z_{SMix}	TP_S
NAO_W	−0.42	−0.51+	0.45	0.33
T_W		0.82**	−0.77**	−0.85**
T_{0-100}			−0.84**	−0.80**
Z_{SMix}				0.81**

culations of the lake. The complete overturn episodes were also confirmed by the results of the laboratory analyses on the discrete samples (*see next section*). In the remaining years, the spring mixing depths ranged from 130 to 200 m (Fig. 2C).

Table 1 summarizes the relationships between the NAO index, T_W, the spring lake temperatures, and the mixing depths. The table also reports the correlation coefficients between the above variables and the concentrations of TP at maximum overturn (TP_S; *see next section*). The spring lake temperatures were strongly ($p < 0.01$) correlated with the T_W. The NAO_W was negatively correlated with the winter air and the spring lake temperatures, although the relationship was significant ($p < 0.1$) only for T_{0-100}. The extent of spring water mixing (Z_{SMix}) showed a strong negative ($p < 0.01$) correlation with the air and lake temperatures and no significant correlation ($p > 0.10$) with the NAO_w.

Temporal dynamics of oxygen and phosphorus—The effects of oligomixis on the long-term temporal evolution and vertical distribution of the chemical variables became particularly evident in the case of oxygen and phosphorus (Fig. 3). From 1996 onward (the period with a sufficient number of chemical analyses in the whole water column), the average concentrations of oxygen in the deep hypolimnion (depth, 200 m to bottom; Fig. 3A) and at the bottom of the lake were always greater than 6 and 4 mg L^{-1}, respectively.

Hypolimnetic TP showed a mirror-like temporal dynamic compared with oxygen (Fig. 3B). In years of incomplete mixing (1996–1998 and 2001–2003), the annual average concentrations of TP in the layer from 200 m to the bottom were 32.5 ± 0.5 μg L^{-1} (mean ± 1 SEM); these concentrations were more than threefold as high as those measured in the layer from 0 m to 20 m (9.5 ± 0.4 μg L^{-1}). In contrast, during years with a complete overturn, TP concentrations at the end of the winter months assumed homogeneous values in the whole water column. The temporal evolution of the mean concentrations of TP in the trophogenic layers (depth, 0–20 m) during the maximum overturn of the lake (i.e., between February and March; TP_S), is shown in Fig. 3C. In the period under examination (1995–2003), and with the exclusion of 2002, the mean spring TP concentrations during incomplete overturn remained <15 μg L^{-1}, reaching values of 19 and 16 μg L^{-1} in the years of complete circulation (1999 and 2000, respectively). Overall, the fluctuations of
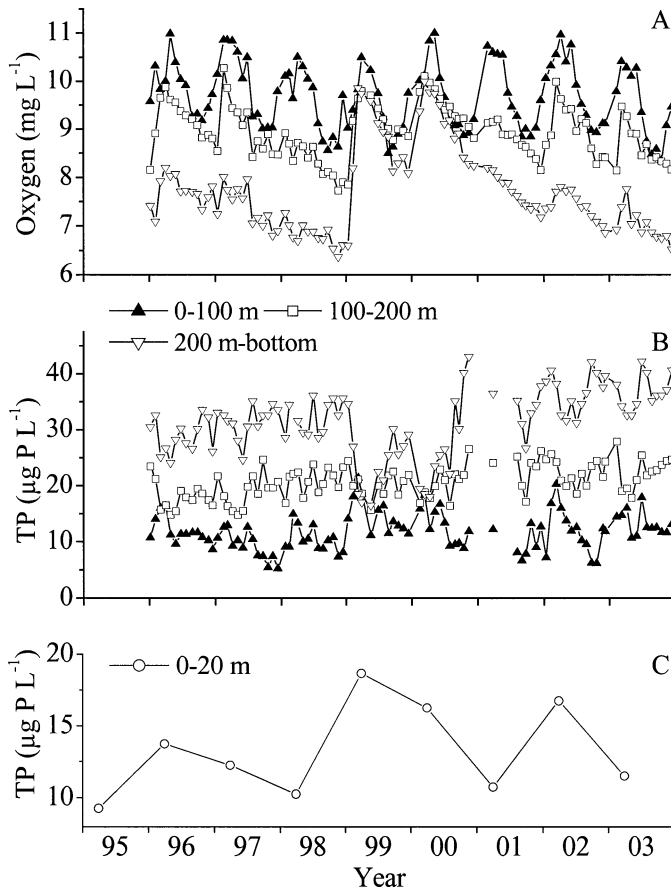
Fig. 3. Average concentrations of (A) oxygen and (B) total phosphorus from January 1996 to December 2003 in three selected layers. (C) Average (February–March) concentrations of total phosphorus (TP_S) from January 1995 to December 2003 in the trophogenic layer.
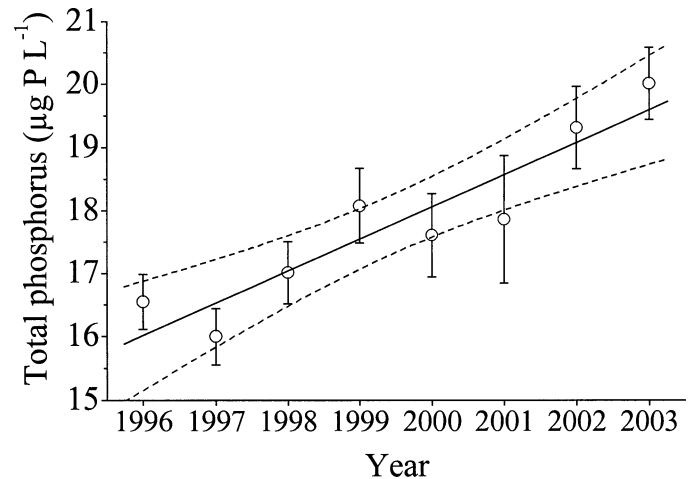

Fig. 4. Annual average values of the volumetrically weighted concentrations, from 0 m to the bottom, of total phosphorus from 1996 to 2003. A linear regression, with 95% confidence limits, has been fitted to the series ($r^2 = 0.86$, $p < 0.01$). The vertical bars indicate the standard errors of the means.

TP_S were strongly determined by the interannual variations in the intensity of lake cooling and mixing. In fact, TP_S showed a strong negative relationship with the T_W and with the minimum spring lake temperatures and a strong positive relationship with the spring mixing depths (Table 1). The NAO index had only a marginal, nonsignificant influence on TP_S. As for the other nutrients, the effect of the last two circulation events was more evident on silica and less on nitrates, which during incomplete mixing showed less marked vertical concentration gradients (data not shown; Salmaso and Decet 1998).

A further inspection of Fig. 3B shows a slight but appreciable tendency of phosphorus to increase in the hypolimnetic layers. The increase was discernible considering the mean concentrations of TP before and after the two overturn episodes (1999–2000) in the layers from 100 m to 200 m (19.3 ± 0.4 and 22.5 ± 0.5 μg L^{-1}, respectively) and from 200 m to the bottom (30.8 ± 0.5 and 36.0 ± 0.6 μg L^{-1}, respectively). The tendency for phosphorus in the lake to increase was confirmed by looking at the temporal evolution of the mean concentrations of TP in the whole water column from 1996 to 2003 (Fig. 4). In the period under examination, the concentrations increased significantly ($r^2 = 0.86$, $p < $

0.01) from 16 to 17 up to 20 μg L^{-1} (i.e., at a rate of 0.4–0.5 μg L^{-1} yr^{-1}). This increase, however, did not seem to affect the TP concentrations in the surface layers ($r^2 = 0.09$, $p > 0.1$; Fig. 3C).

Interannual variations in the trophic descriptors and phytoplankton—Figure 5 reports the annual evolution of some important trophic parameters in Lake Garda. As for the phytoplankton, the figure shows the annual variations for two selected groups, showing a more interpretable temporal pattern compared with the other classes (cyanobacteria and Conjugatophyceae; see the following discussion).

The annual averages of TP were always indicative of moderate trophic status (Fig. 5A). The biological variables (Fig. 5B,D–G) showed high (but not exclusive) values during the complete overturns in 1999 and 2000. The transparency showed contrasting features, with small values in two of the three years of circulation (1991 and 2000; Fig. 5C). The high average transparencies recorded in the middle of the 1990s, with values near ultraoligotrophy, were strongly influenced by the maximum values recorded during spring overturn (up to 27.5 m between March and April 1996). These high seasonal transparencies were favored by the dispersal of the algal cells down to the bottom of the mixed layer, as shown by occasional fluorometric profiles of chlorophyll *a* recorded up to 1997.

The influence of the winter climatic fluctuations (NAO$_W$, T_W, and $T_{0–100}$), Z_{SMix}, and the replenishment of nutrients (TP_S) on the group of variables represented graphically in Fig. 5B–G was analyzed by computing the correlation coefficients reported in Table 2. As for the second group of variables (phytoplankton and transparency), the series used in the computations represent the average values of a subset of data from the period potentially affected by the spring overturn—that is, between its concluding phases (March) and the time preceding the next hypolimnetic mixing (December). The NAO index was only weakly and not signifi-
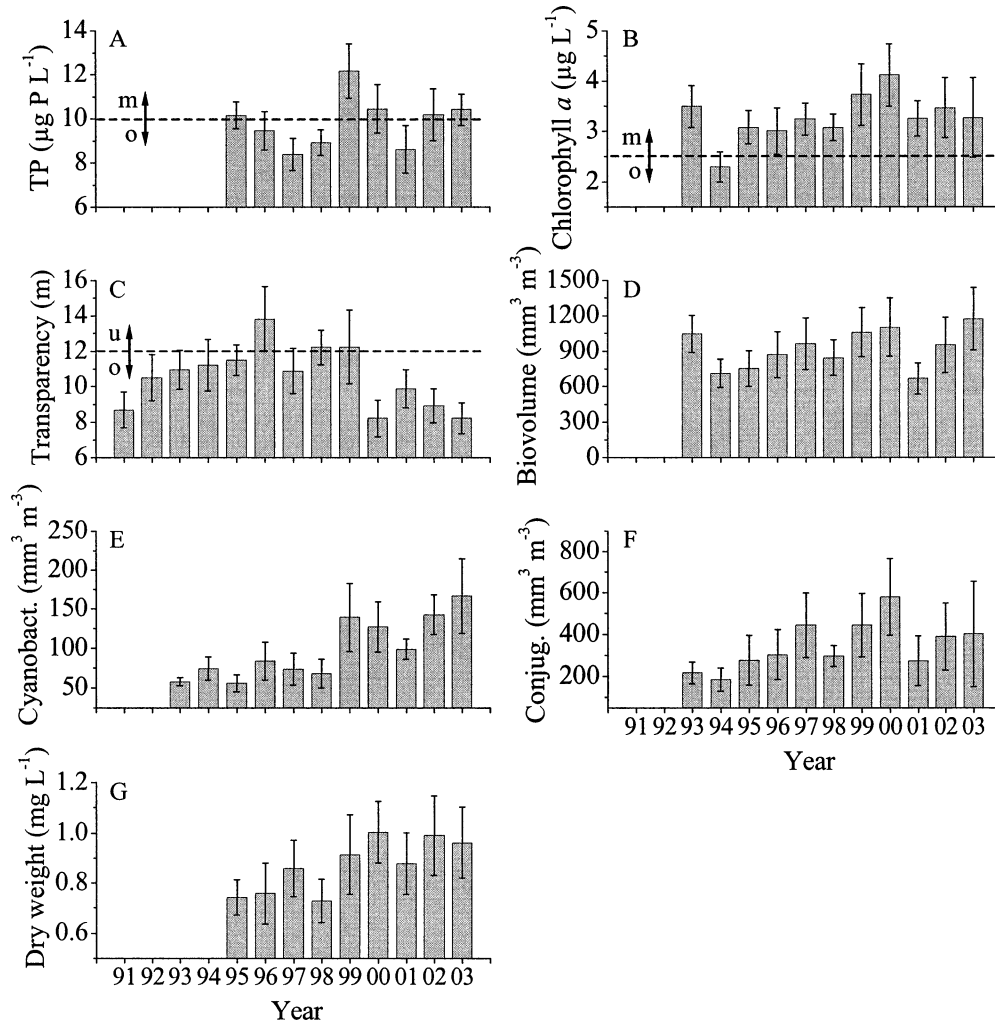
Fig. 5. Annual average values (January–December; depth, 0–20 m) of (A) total phosphorus, (B) Chl *a,* (C) Secchi disk depth, (D) total phytoplankton biovolume, (E) biovolume of cyanobacteria, (F) biovolume of conjugatophytes, and (G) dry weight. For each trophic parameter (A–C), the graphs report the boundary values for trophic categories (OECD 1982). The vertical bars indicate the standard errors of the means. m, mesotrophy; o, oligotrophy; u, ultraoligotrophy.

cantly correlated with the column variables. The biological variables were negatively correlated (mostly at $p < 0.05$) with the winter air and spring lake temperatures and positively correlated with the mixing depth. Winter temperatures and Z_{SMix} may be considered as the remote causes affecting the trophic characteristics of the lake. These factors act on the ultimate cause, which is represented by phosphorus, and showed a strong positive effect on the whole set of biological

Table 2. Correlation coefficients, *r*, between the descriptors of winter climatic conditions, mixing depth, spring epilimnetic total phosphorus, and the trophic variables in Lake Garda. Column variables report the mean annual values, computed from March to December, of Chl *a* (Chl a_{MD}), Secchi disk depth (SD_{MD}), phytoplankton biovolume ($BiovT_{MD}$), biovolume of cyanbacteria ($BiovCyan_{MD}$), biovolume of conjugatophytes ($BiovConj_{MD}$), and dry weight (DW_{MD}). The correlations refer to the years from 1993 to 2003 (with the exception of the correlations including TP_S and DW_{MD}, 1995–2003). All calculations are based on linearly detrended data. Values are significant at $p < 0.01$ (**), $p < 0.05$ (*), and $p < 0.10$ (+).

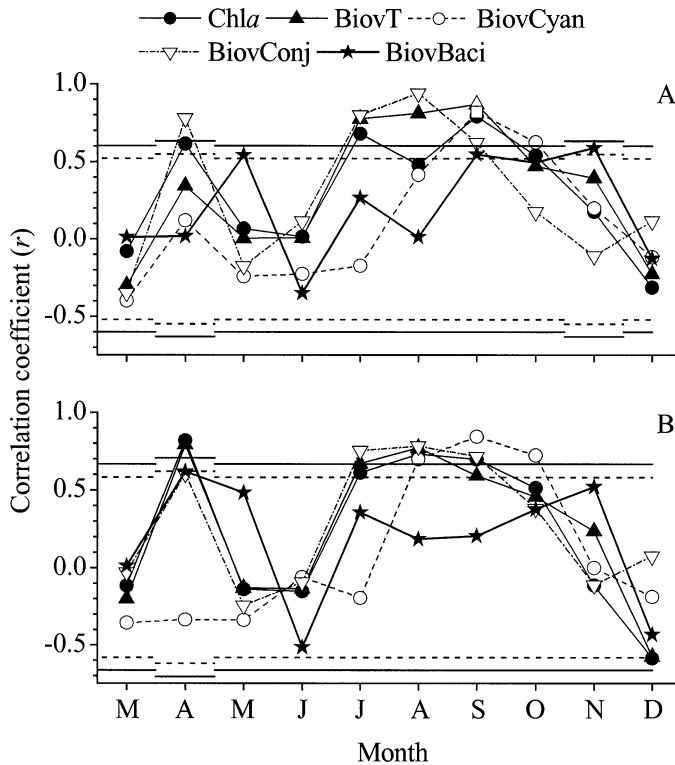|	Chl a_{MD}	SD_{MD}	$BiovT_{MD}$	$BiovCyan_{MD}$	$BiovConj_{MD}$	DW_{MD}
NAO_W	0.42	−0.51	0.27	0.43	0.34	0.37
T_W	−0.66*	0.43	−0.57+	−0.72*	−0.55+	−0.83**
$T_{0–100}$	−0.67*	0.36	−0.65*	−0.76**	−0.65*	−0.71*
Z_{SMix}	0.81**	−0.13	0.64*	0.66*	0.77**	0.68*
TP_S	0.82**	−0.06	0.60+	0.78*	0.67*	0.83**

Fig. 6. Time series of correlation coefficients relating (A) spring mixing depths (Z_{SMix}) and (B) mean spring (February–March) epilimnetic total phosphorus concentrations (TP_S) to monthly values of Chl *a* (Chl*a*), total phytoplankton biovolume (BiovT), and biovolume of cyanobacteria (BiovCyan), Conjugatophyceae (BiovConj), and Bacillariophyceae (BiovBaci); correlations are for the time periods (A) 1993–2003 and (B) 1995–2003. All calculations are based on linearly detrended data. The horizontal solid and dashed lines indicate, for different *n* values, correlation coefficients significant at $p = 0.05$ and 0.10, respectively.

variables. On the contrary, transparency showed no significant association with the climatic fluctuations and mixing regimes. The mean annual (March–December) biovolume values of the Chlorophyceae, Chrysophyceae, Bacillariophyceae, Dinophyceae, and Cryptophyceae did not show any significant ($p > 0.1$) relationship with the NAO_W, T_W, T_{0-100}, Z_{SMix}, and TP_S.

The cyanobacteria were dominated by filaments of *Planktothrix rubescens/agardhii*; other important species were represented by *Planktolyngbya limnetica, Anabaena lemmermannii, Aphanothece* sp., *Aphanocapsa* sp., *Snowella* cf. *aracnoidea,* and *Microcystis aeruginosa.* The conjugatophytes were almost exclusively dominated by *Mougeotia* sp., followed by *Closterium* spp. The ecology of these species has been reviewed by Salmaso (2000, 2002).

To identify the periods most affected by spring fertilization, Fig. 6A,B show the time series of correlation coefficients relating the spring mixing depths (Z_{SMix}) and the spring epilimnetic (depth, 0–20 m) TP concentrations (i.e., TP_S) to the monthly values of phytoplankton abundance (Chl *a* and total biovolume) and to the monthly biovolumes of cyanobacteria and conjugatophytes. In this case, the computations were also carried out for the Bacillariophyceae, which

showed a higher development in April and May, soon after spring TP fertilization. Chlorophyll *a,* phytoplankton biovolumes, and conjugatophytes showed high positive correlations with Z_{SMix} and TP_S in April and from July to September–October, with values either over or near statistical significance after exclusion of the relationship between Z_{SMix} and the total biovolume in April. The diatoms showed high correlations in April and/or May and, in the case of Z_{SMix}, in early autumn. Cyanobacteria were correlated with Z_{SMix} and TP_S only in late summer. Similar results (with correlation coefficients of opposite signs) were also found when considering the influence on the seasonal phytoplankton development of the T_W and minimum lake temperatures (T_{0-100}). On the contrary, no significant correlations and interpretable temporal patterns were found in considering the other algal groups and between the winter NAO index and the seasonal phytoplankton development.

The effects of a major spring availability of epilimnetic nutrients on the phytoplankton community may be evaluated by considering the different temporal evolution of the mean monthly values of Chl *a* and phytoplankton biovolumes in two different conditions exemplified by the years with TP concentrations at spring overturn (TP_S; Fig. 3C) lower or higher than 15 μg L^{-1} (Fig. 7). During the years of greater fertilization, Chl *a,* total phytoplankton biovolumes, and conjugatophytes showed a large, sharp, and significant increase in April (ANOVA, $p < 0.05$) and higher values from July to September–October, whereas cyanobacteria showed a greater development from August to October (Fig. 6B). These differences were significantly different (two-way ANOVA with months and TP lower or higher than 15 μg L^{-1} as categories) for Chl *a* ($p < 0.05$) and total phytoplankton biovolumes ($p = 0.05$) (July–October) and for cyanobacteria ($p < 0.01$; August–October). The differences of the mean values of the conjugatophytes from July to September (Fig. 7D) were not significant ($p = 0.15$) because of a higher variability in the summer development of this group after the spring TP replenishment. Apart from the conjugatophytes, the peak of total phytoplankton biovolume in April was also determined by the development of large diatoms (mainly *Aulacoseira* spp., *Asterionella formosa,* and *Fragilaria crotonensis*), which during the years of greater TP availability showed higher mean biovolumes (931 mm^3 m^{-3}) compared with the other years (327 mm^3 m^{-3}; Fig. 7E). However, these differences were not significant (ANOVA, $p > 0.1$) because of the large interannual variability in the development of this group in April. During the successive months, the diatoms did not show any significant association with TP_S. In general, the remaining algal groups did not show any strong positive effects in response to major TP replenishment (Fig. 7F). The effects of fertilization on phytoplankton development was also confirmed by the higher values of dry weight in April, after major TP replenishment, with mean values of 0.65 and 1.65 mg L^{-1} during the years with TP_S lower or higher than 15 μg L^{-1}, respectively (ANOVA, $p < 0.01$).

Discussion

Lake thermal fluctuations—The temperatures measured in the deep hypolimnion immediately before the cooling epi-
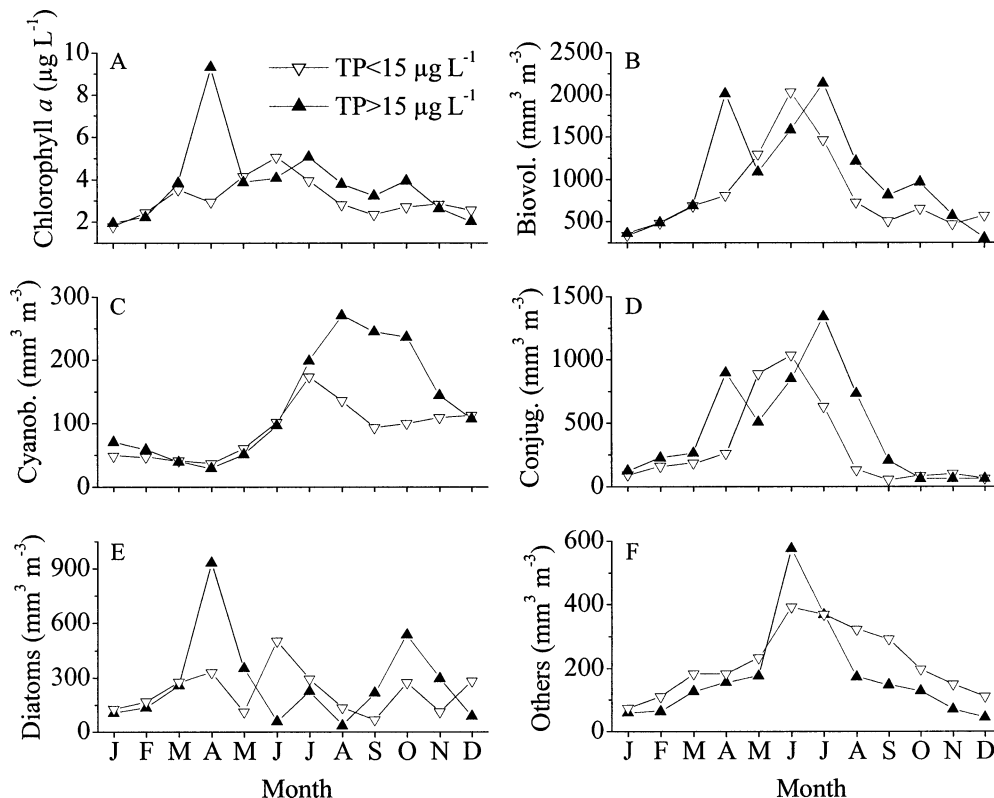
Fig. 7.   Monthly variations of (A) Chl *a,* (B) total phytoplankton biovolume and biovolume of (C) cyanobacteria, (D) Conjugatophyceae, (E) Bacillariophyceae, and (F) other algal groups in the 0–20-m layer. The values represent the monthly averages computed for TP_S concentrations higher (1999–2000 and 2002) or lower (1995–1998, 2001, and 2003) than 15 $\mu g\ L^{-1}$.

sode in 1999 (~8.4°C) represent the highest values ever recorded in the deepest waters of Lake Garda. During the previous two decades, the highest temperatures were observed in the middle of the 1970s (8.20°C at 300 m; Salmaso et al. 1997). At present, these data do not appear to be sufficient for assuming the existence of a warming of the lake. The temporal evolution of hypolimnetic temperatures in deep oligomictic lakes is characterized by periods of several years of gradual warming caused by a downward transport of heat by turbulent diffusion within the hypolimnion during stratification. The hypolimnetic warming thus may occur regardless of whether air temperatures are increasing or not. The warming period is then terminated by sudden cooling during harsh winters (Livingstone 1997). Therefore, time series of deep-water temperatures exhibit both short-term and long-term structures. The long-term series of temperature measured in Lake Zurich from 1947 to 1991 showed the existence of a dominant periodicity of 12–16 yr below 80 m, suggesting that time series shorter than ~50 yr are unlikely to add information relevant to climatic change (Livingstone 1993). However, detailed analyses of the temperatures measured since the 1960s and 1970s in the deep southern subalpine lakes revealed a marked increase in the heat of their water masses (Ambrosetti and Barbanti 1999). A tendency toward an increase in water temperatures was also documented in the deep lakes north of the Alps (lakes Geneva [Ishiguro et al. 2003], Zurich [Livingstone 2003], and Con-

stance [Straile et al. 2003]), in Asia (Lake Issyk-Kul; Peeters et al. 2003), in North America (Experimental Lakes Area; Schindler et al. 1996), and in Africa (lakes Victoria [Hecky et al. 1994] and Tanganika [O'Reilly et al. 2003]). These results are consistent with the positive trend documented in the evolution of atmospheric temperatures, especially during the last decade in northern Italy (0.7 ± 0.1°C per century, during winter; Brunetti et al. 2000), in Europe (Koinig et al. 2002; Luterbacher et al. 2004), and on a worldwide basis (Intergovernmental Panel on Climate Change 2001).

The strong dependence of the thermal structure of the lake on T_W is reflected by a close association between winter climatic fluctuations and mixing processes. The link is particularly evident between the layer that undergoes complete mixing every spring (operationally defined as between 0 m and 100 m) and the T_W computed for the period between December and February. The T_W had a minor impact on the deepest layers, with the fraction of variance explained in the spring (March) lake temperatures measured at 200 m, at 300 m, and at the bottom ranging from 42% to 55% compared with the higher values computed for the upper layers, from 0 m to 100 m (62%). The slight weakening of the winter signal with depth is partly determined by the oligomixis of the lake and by the minor impact of the winter climate on the deep waters during the years of incomplete mixing.

Air temperatures strongly affect the thermal structure of the lake acting on the heat-exchange processes between wa-

ter and atmosphere (Imboden and Wüest 1995). Other factors (like the wind) may influence the mixing processes. However, the wind direction and its speed at ground level are characterized by strong heterogeneities, so it is not always simple to relate the variations in the thermal structure of the lake to the variables expressing this meteorological factor (*see* Straile et al. 2003 and references herein).

Some recent studies have illustrated the existence of a link between the thermal properties of European lakes located in mid and northern latitudes and the NAO. Gerten and Adrian (2000, 2001) showed that the monthly means of air and surface lake temperatures of medium-sized lakes in the lowlands of northern Germany were positively and significantly correlated with the NAO index from December to March. Straile (2000) and Straile et al. (2003) observed that the periods of gradual temperature increase in Lake Constance were associated with high-NAO winters. In Lake Garda, the T_w and the spring lake temperatures showed only slight and nonsignificant negative correlations with the NAO index. Weak correlations and different effects of the NAO on the winter temperatures have been documented recently in the Mediterranean regions (Esteban-Parra et al. 2003; Luterbacher and Xoplaki 2003). This underlines the relative low constancy that such correlations may have in areas on the border of different action centers (*see* fig. 13 in Hurrell et al. 2003). To obtain generalizable results, the study of the effects of NAO on the deep southern subalpine lakes requires longer time series and a large number of measurement stations. However, by extending the measurement period until 1984 (when the first winter measurements were available in the meteorological station of Arco), it was possible to confirm the nonsignificant relationship between NAO_w and T_w ($r = -0.09$, $n = 20$; computations on linearly detrended data).

Trophic trends and interannual trophic variability—The increase in the average content of TP observed from 1996 to 2003 indicates significant nutrient enrichment of the lake in the last decade. This enrichment, as documented by analysis of the data collected during the spring months since 1971 (Mosello et al. 1997), constitutes the last stage of a long-term increase of phosphorus in Lake Garda. Both reactive and TP concentrations measured during spring overturn in the whole lake increased from <10 μg L^{-1} in the first half of the 1970s to 14 μg L^{-1} (reactive concentration) and 17 μg L^{-1} (TP) in 1996 (Salmaso et al. 1997). However, because of the absence of a complete identification and continuous monitoring of the potential pollution sources, the characterization and the relative importance of the causes determining the increase of phosphorus loads and concentrations are not easy to define.

The doubling of phosphorus in the lake since the 1970s was paralleled by considerable changes occurring in the phytoplankton community (Salmaso 2002). During the 1970s, the most important and evident modifications to the pristine oligotrophic conditions were marked by development of the complex *Planktothrix rubescens/agardhii* and by the irregular increase of Conjugatophyceae (*Mougeotia* sp. and *Closterium aciculare*). During the 1980s, the increase of the phosphorus concentrations in the lake and the progress toward more mesotrophic conditions were accompanied by the appearance of new, dense populations of cyanobacteria (*Planktolyngbya limnetica* and *Anabaena lemmermannii*) and by the conspicuous increase of conjugatophytes (particularly *Mougeotia* sp.). In contrast to these signs of alteration, *Fragilaria crotonensis, Asterionella formosa, Ceratium hirundinella,* and *Dinobryon* spp. were among the most abundant taxa from the 1950s to the present.

The analysis of the data recorded in Lake Garda clearly demonstrates the importance of the spring circulation in fertilizing epilimnetic waters in deep lakes. Salmaso et al. (2003*b*) estimated that in 1998, during a limited overturn, the input of TP to the productive layers (depth, 0–20 m) was ~39 × 10³ kg, increasing to ~80 × 10³ kg in 1999, as a consequence of the lake circulation. The importance of this rapid replenishment is clear if we consider that the external load of TP in this lake was estimated at ~170–200 × 10³ kg yr^{-1} and that, during the summer, water flux from rivers is low and mainly limited to the northern shore of the lake. The major fertilization events, occurring after more extended or complete overturns, caused a strong and sudden increase of Chl *a* and total phytoplankton biovolume in April, mainly determined by conjugatophytes (dominated by filaments of *Mougeotia* sp.) and, more irregularly, by large diatoms. The competition between these two groups could have strongly affected the successive growth of *Mougeotia* sp. soon after April. The increase in this conjugatophyte started again after the almost complete disappearance of the large centric diatoms in May and after the reduction of *Fragilaria* sp. in June because of the thermal stabilization of the water column and silica consumption (Salmaso 2003). Laboratory experiments carried out in Lake Constance showed that *Mougeotia* sp. was the most successful competitor for phosphorus at low Si:P ratios among nondiatoms (Sommer 1987). The greater development of phytoplankton biomass from July to October during the years of major spring TP replenishment was caused by cyanobacteria (mainly *Planktothrix* sp.) and an irregular contribution of conjugatophytes that showed a more extended development until August–September. The strong, temporal delimitation of the impact of the overturn on cyanobacteria results from the particular ecological characteristics of the species forming this group. The *Planktothrix* colonies are well adapted to conditions of low irradiance (Reynolds 1984) and show a clear vertical zonation during summer, with metalimnetic maxima around the limit of the euphotic zone and vertical dispersal and homogenization in autumn and winter (Salmaso 2000, 2002). This seasonal evolution is linked to the perennation strategy of *Planktothrix* sp. in the deep lakes, with the autumn populations surviving in the mixing column during the successive coldest months (Walsby et al. 1998). The other subdominant cyanobacteria mainly develop in conditions of high thermal stability; among these, the Chroococcales, in the deep southern subalpine lakes, are present almost exclusively from early summer to mid to late autumn (Salmaso et al. 2003*a*). The higher phytoplankton biomass during the warmest months, after the major TP replenishment episodes, agrees with the findings of Dillon and Rigler (1974), who found a significant relationship between the TP concentrations from spring turnover
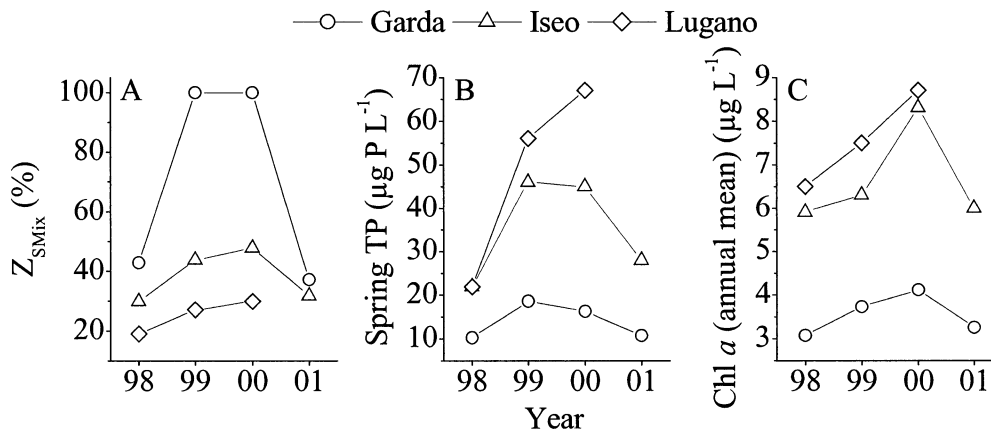
Fig. 8. Extent of the spring lake overturn and trophic variables in the lakes Garda and Iseo from 1998 to 2001 and Lake Lugano from 1998 to 2000. (A) Spring mixing depths (Z_{SMix}). (B) Epilimnetic (depth, 0–20 m) mean spring (February–March) concentrations of total phosphorus (TP_S) in Lake Garda and epilimnetic (depth, 0–20 m) maximum spring concentrations of TP in the lakes Iseo and Lugano. (C) Annual (January–December) concentrations of Chl *a* in the lakes Garda and Lugano (depth, 0–20 m) and Lake Iseo (depth, 0–10 m).

and the mean summer values of Chl *a* in a large number of lakes.

The two groups of phytoplankton most affected by the variable replenishment of nutrients are the same as those that showed their maximum development during the shift of Lake Garda from oligotrophy to oligomesotrophy and mesotrophy. This indicates a substantial consistency between the ecological and historical observations. Moreover, these results have also been confirmed by the synoptic analyses of the phytoplankton communities of the deep southern subalpine lakes, which showed an increasing importance in the more eutrophic lakes of the species identified in the present study for being more susceptible to the spring replenishment of nutrients (Salmaso et al. 2003*a*). In general, apart from the cyanobacteria, which generally are positively linked to gradients of TP concentrations (e.g., Watson et al. 1997), the chlorophytes (including the conjugatophytes) comprise many species that are indicative of mesotrophic and eutrophic conditions (Rott 1984).

The mechanisms mediating the linkage between climate and year-to-year variability in production differ drastically between different typologies of lakes (Goldman et al. 1989; Gerten and Adrian 2001). Weyhenmeyer et al. (1999) found that the snow cover and the timing of ice breakup during winter had a strong influence on timing of the phytoplankton spring peak in Lake Erken in southeastern Sweden. The earlier development of phytoplankton and zooplankton in Lake Müggelsee in northern Germany was explained by similar mechanisms—that is, shortening or lack of periods of ice cover in winter (Gerten and Adrian 2000). Straile (2000) suggested that the positive response of *Daphnia* in some years in Lake Constance probably was a direct effect of altered water temperatures on daphnid growth and was not mediated by changes in phytoplankton concentrations. In all the above cases, the occurrence of milder winters was positively related to fluctuations of the NAO, with the water temperature determining a direct effect on the biological communities. The studies carried out in Lake Garda show

that in large and deep lakes, other and further mechanisms may be involved in the control of phytoplankton by climate. A linked chain of causal factors (i.e., winter climate, T_W, extent of the spring lake overturn, and extent of nutrient enrichment) has measurable effects on total phytoplankton biomass, cyanobacteria, and conjugatophytes. However, because the study of the ecological effects of the NAO is still relatively new, it is not yet possible to have a clear picture regarding the whole range of mechanisms acting on the environment and on the biological communities (cf. Hurrell et al. 2003). The problem is complicated by the absence of a synoptic account of the different impact of the NAO on different ecoregions or, as in the case of the deep southern subalpine lakes, on ecosystems located on the borders of different centers of action.

Temporal coherence in the trophic response of deep lakes to interannual climatic fluctuations—The effects of the temporal fluctuations of T_W, $T_{0–100}$, and Z_{SMix} on the epilimnetic spring concentrations of phosphorus are strongly dependent on the vertical distribution and content of nutrients in the water column. High temporal correlations between the causal factors and TP_S would only be expected when the content and distribution of phosphorus in the lake do not radically change over time. Some of the high TP values recorded recently in the upper layers during conditions of incomplete mixing (e.g., 2002) might have resulted from nonquantified sources; however, taking into account the significant increase of TP observed in the water column during the last decade, an enhanced response of the lake to mixing dynamics could not be excluded.

In lakes with a higher hypolimnetic phosphorus content, the extension of mixing determines a proportionally higher response of the trophic variables. Figure 8 shows the different effects of mixing on the trophic state of Lake Garda compared with the effects on the two more eutrophic deep southern subalpine lakes, Lake Lugano (from 1998 to 2000) and Lake Iseo (from 1998 to 2001), based on the data re-

ported by Salmaso et al. (2003*a,b*) and Simona (2003). In the case of Lake Iseo, the mixing depths were provided by W. Ambrosetti (pers. comm.). From 1998 to 2000, the average TP concentrations in the first 100 m of Lake Lugano were 52–76 μg L^{-1}, as compared to concentrations of 226–294 μg L^{-1} in the layer from 100 m to the bottom (288 m; Simona 2003). In Lake Iseo, during the 1990s, the average TP concentrations in the first 100 m ranged between 36 and 48 μg L^{-1}, as compared to concentrations of $\sim$100–175 μg L^{-1} from 200 m to the bottom (251 m; Salmaso et al. 2003*b*). In the periods taken into consideration in Fig. 8, these two lakes underwent a greater mixing in the biennium 1999–2000, in parallel with the complete overturn observed in Lake Garda. Despite the lower fractions of Z_{SMix}, the consequences of mixing on the epilimnetic TP concentrations were greater in Lake Lugano because of its larger reservoir of nutrients in the deep layers. Lake Iseo experienced intermediate effects, whereas within the considered TP scale, the effects on Lake Garda appeared to be more reduced (Fig. 8B). A similar scaled effect was also found for Chl *a* (Fig. 8C). On the whole, the annual average values of Chl *a* in the three lakes were significantly ($r = 0.91$, $p < 0.01$, $n = 16$) related to the spring concentrations of TP. The parallel response of the three lakes to the larger mixing (lakes Lugano and Iseo) or complete mixing (Lake Garda) in the biennium 1999–2000 was evident in both variables. The trophic descriptors are characterized by a strict temporal correlation that originates from a corresponding synchronism in the interannual variations in the extent of the spring vertical mixing. This synchronicity is determined by the common effects caused by the climatic evolution in the southern subalpine area (cf. Brunetti et al. 2000). In Lake Lugano, Simona (2003) actually found a decrease in the average winter (December–February) air temperatures from 1998 to the biennium 1999–2000, from 5.3°C to 3.9°C and 4.3°C, respectively, with corresponding water temperatures at spring overturn of 6.3°C, 5.6°C, and 5.6°C, respectively. Because of the short period considered in the comparison, the general mechanisms controlling the year-to-year variability in the deep southern subalpine lakes will need to be confirmed or adjusted further by considering additional observations. In general, however, climate has been found to influence significantly the temporal coherence in lakes that are located in defined ecoregions. In the northern perialpine area of Austria, Livingstone and Dokulil (2001) found a high degree of coherence between lakes that reflected much of the temporal structure of the regional air temperature. George et al. (2000, 2004) found a high level of coherence for the water temperatures and some chemical variables in a group of lakes in the English Lake District; the winter temperatures of the lakes studied were strongly and positively related to the NAO.

The effects of the variable extent of the spring lake overturn on the annual productivity only become measurable if certain conditions are met (i.e., the existence of a significant supply of hypolimnetic nutrients and a condition of oligomixis or meromixis). For example, the interannual variations of the algal crop in Lake Maggiore seem to be dependent on meteorological conditions occurring over short time scales rather than on climatic fluctuations (Morabito 2001).

The vertical distribution of TP in this lake is fairly homogeneous, so the impact of a complete or greater overturn triggered by harsh winters is minimized or not easily detectable (Salmaso et al. 2003*a*).

Summary and concluding remarks—Between 1991 and 2003, the deep Lake Garda underwent three complete overturns following three harsh winters (in 1991 and in the biennium 1999–2000). The complete mixing events determined a great fertilization of the trophogenic layers because of the homogenization of the surface waters with the deep hypolimnion, which is richer in nutrients. More generally, a linked chain of causal factors, from winter climate to phytoplankton development, contributed to control the interannual variations in trophic status. The extent of the spring overturn was significantly and negatively associated with the winter air and spring water temperatures. In turn, the epilimnetic concentrations of TP and the annual phytoplankton development were significantly and positively associated with the mixing depths. The T_W and the spring lake temperatures were not significantly or only slightly negatively correlated with the NAO$_W$. This feature contrasts with the positive impact of this climatic pattern on central and northern Europe and may originate from the contrasting actions of the NAO on ecosystems located on the border of different centers of action (the Mediterranean region and central and northern Europe). Further observations, with more extensive datasets and historical analyses, are required to elucidate clearly the mechanisms regulating the impact of the NAO on the lakes of the southern subalpine region and, more generally, on the Mediterranean regions.

The fertilization of the trophogenic layers during spring overturn determined different temporal-scale effects on a limited number of phytoplankton groups. Soon after the major enrichment episodes, the conjugatophytes and the large diatoms peaked high during April, whereas from midsummer to midautumn, the cyanobacteria and, more irregularly, the conjugatophytes provided the larger contribution to the greater phytoplankton development.

The remote cause of the interannual variations of phytoplankton biomass (i.e., climatic fluctuations) determines its effects on a regional scale. The analysis of the available data recorded in the deep southern subalpine lakes revealed the existence of a temporal correspondence in the interannual variations of the extent of the spring vertical mixing and nutrient replenishment in the lakes Garda, Iseo, and Lugano. This temporal synchronism derives from the common effects of the winter evolution of climatic conditions on the subalpine region, which results in a positive association in the temporal evolution of the trophic characteristics of the three lakes. The mechanisms identified in this group of deep lakes indicate that the effects of winter climate on phytoplankton development may last a long time, through an extended and complex chain of factors, with the ultimate cause being the limiting nutrients.

References

AMBROSETTI, W., AND L. BARBANTI. 1992. Physical limnology in Italy: An historical review. Mem. Ist. Ital. Idrobiol. **50:** 37–59.

————, AND ————. 1999. Deep water warming in lakes: an indicator of climatic change. J. Limnol. **58:** 1–9.

AMERICAN PUBLIC HEALTH ASSOCIATION, AMERICAN WATER WORKS ASSOCIATION, AND WATER POLLUTION CONTROL FEDERATION. 1989. Standard methods for the examination of water and wastewater, 17th ed. American Public Health Association, Washington, DC.

BARBIERI, A., AND R. MOSELLO. 1992. Chemistry and trophic evolution of Lake Lugano in relation to nutrient budget. Aquat. Sci. **54:** 219–237.

BRUNETTI, M., M. MAUGERI, AND T. NANNI. 2000. Variations of temperature and precipitation in Italy from 1866 to 1995. Theor. Appl. Climatol. **65:** 165–174.

CHATFIELD, C. 1991. The analysis of time series. An introduction. Chapman and Hall.

DILLON, P. J., AND F. H. RIGLER. 1974. The phosphorus–chlorophyll relationship in lakes. Limnol. Oceanogr. **19:** 767–773.

ESTEBAN-PARRA, M. J., D. POZO-VÁZQUEZ, F. S. RODRIGO, AND Y. CASTRO-DÍEZ. 2003. Temperature and precipitation variability and trends in Northern Spain in the context of the Iberian Peninsula Climate, p. 259–276. *In* H. J. Bolle [ed.], Mediterranean climate—variability and trends. Springer-Verlag.

GARIBALDI, L., V. MEZZANOTTE, M. C. BRIZZIO, M. ROGORA, AND R. MOSELLO. 1999. The trophic evolution of Lake Iseo as related to its holomixis. J. Limnol. **58:** 10–19.

GEORGE, D. G., S. C. MABERLY, AND D. P. HEWITT. 2004. The influence of the North Atlantic Oscillation on the physical, chemical and biological characteristics of four lakes in the English Lake District. Fresh. Biol. **49:** 760–774.

————, J. F. TALLING, AND E. RIGG. 2000. Factors influencing the temporal coherence of five lakes in the English Lake District. Fresh. Biol. **43:** 449–461.

GERTEN, D., AND R. ADRIAN. 2000. Climate-driven changes in spring plankton dynamics and the sensitivity of shallow polymictic lakes to the North Atlantic Oscillation. Limnol. Oceanogr. **45:** 1058–1066.

————, AND ————. 2001. Differences in the persistency of the North Atlantic Oscillation signal among lakes. Limnol. Oceanogr. **46:** 448–455.

GOLDMAN, C. R., AND A. JASSBY. 1990. Spring mixing depth as a determinant of annual primary production in lakes, p. 125–132. *In* M. M. Tilzer and C. Serruya [eds.], Large lakes. Ecological structure and function. Springer-Verlag.

————, ————, AND T. POWELL. 1989. Interannual fluctuations in primary production: Meteorological forcing at two subalpine lakes. Limnol. Oceanogr. **34:** 310–323.

HECKY, R. E., F. W. B. BUGENY, P. OCHUMBA, J. F. TALLING, R. MUGIDDE, M. GOPHEN, AND L. KAUFMAN. 1994. Deoxygenation of the deep water of Lake Victoria, East Africa. Limnol. Oceanogr. **39:** 1476–1481.

HURRELL, J. W. 1995. Decadal trends in the North Atlantic oscillation: Regional temperatures and precipitation. Science **269:** 676–679.

————, Y. KUSHNIR, G. OTTERSEN, AND M. VISBECK. 2003. An overview of the North Atlantic Oscillation, p. 1–35. *In* J. W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck [eds.], The North Atlantic Oscillation. Climatic significance and environmental impact. American Geophysical Union. Geophysical Monograph 134.

IMBODEN, D. M., AND A. WÜEST. 1995. Mixing mechanisms in lakes, p. 83–138. *In* A. Lerman, D. Imboden, and J. Gat [eds.], Physics and chemistry of lakes. Springer-Verlag.

INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE. 2001. Climate Change 2001: The scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge Univ. Press.

ISHIGURO, N., L. TOUCHART, G. BARROIN, G. BALVAY, AND K. MICHIO. 2003. Lake Geneva: Che role of the Rhône and the global warming. International Conference—residence times in lakes: Science, management, education. Bolsena (Viterbo, Italy). September 29th–October 3rd, 2002. Provincia di Viterbo: 187–190.

ISTITUTO DI RICERCA SULLE ACQUE. 1974. Research on Lake Garda. Istituto di Ricerca sulle Acque (IRSA), Quaderni 18. [In Italian.]

KOINIG, K., AND OTHERS. 2002. Environmental changes in an alpine lake (Gossenköllesee, Austria) over the last two centuries—the influence of air temperature on biological parameters. J. Paleolim. **28:** 147–160.

LIVINGSTONE, D. M. 1993. Temporal structure in the deep-water temperature of four Swiss lakes: A short term climatic change indicator? Verh. Int. Verein. Limnol. **25:** 75–81.

————. 1997. An example of simultaneous occurrence of climate-driven ''sawtooth'' deep-water warming/cooling episodes in several Swiss lakes. Verh. Internat. Verein. Limnol. **26:** 822–828.

————. 2003. Impact of secular climate change on the thermal structure of a large temperate central European lake. Climatic Change **57:** 205–225.

————, AND M. T. DOKULIL. 2001. Eighty years of spatially coherent Austrian lake surface temperatures and their relationship to regional air temperature and the North Atlantic Oscillation. Limnol. Oceanogr. **46:** 1220–1227.

LUTERBACHER, J., D. DIETRICH, E. XOPLAKI, M. GROSJEAN, AND H. WANNER. 2004. European seasonal and annual temperature variability, trends, and extremes since 1500. Science **303:** 1499–1503.

————, AND E. XOPLAKI. 2003. 500-Year winter temperature and precipitation variability over the Mediterranean area and its connection to the large-scale atmospheric circulation, p. 133–153. *In* H. J. Bolle [ed.], Mediterranean climate—variability and trends. Springer-Verlag.

MORABITO, G. 2001. Relationships between phytoplankton dynamics in Lake Maggiore and local climate in the period 1978–1998. Atti Ass. Ital. Oceanol. Limnol. **14:** 147–156.

MOSELLO, R., A. CALDERONI, AND R. DE BERNARDI. 1997. Research on the evolution of the deep southern subalpine lakes performed by the CNR Istituto Italiano di Idrobiologia. Documenta Ist. ital. Idrobiol. **61:** 19–32. [In Italian.]

————, AND OTHERS. 1995. AQUACON—MedBas Subproject 6. Acid rain analysis. Intercomparison 1/94. Documenta Ist. ital. Idrobiol. **54:** 1–44.

OECD. 1982. Eutrophication of waters. Monitoring, assessment and control. Organization for Economic Cooperation and Development.

O'REILLY, C. M., S. R. ALIN, P. D. PLISNIER, A. S. COHEN, AND B. A. MCKEE. 2003. Climate change decreases aquatic ecosystem productivity of Lake Tanganika, Africa. Nature **424:** 766–768.

PEETERS, F., D. FINGER, M. HOFER, M. BRENNWALD, D. M. LIVINGSTONE, AND R. KIPFER. 2003. Deep-water renewal in Lake Issyk-Kul driven by differential cooling. Limnol. Oceanogr. **48:** 1419–1431.

PROVINCIA AUTONOMA DI TRENTO. 1991. Lake Garda. Annual report on the hydrobiological investigations. 1991. Ed. Stazione Sperim. Agraria Forestale di S. Michele all'Adige, Trento. [In Italian.]

REYNOLDS, C. S. 1984. The ecology of freshwater phytoplankton. Cambridge Univ. Press.

ROTT, E. 1984. Phytoplankton as biological parameter for the trophic characterization of lakes. Verh. Internat. Verein. Limnol. **22:** 1078–1085.

RYDING S.-O., AND W. RAST. 1989. The control of eutrophication

of lakes and reservoirs. United Nations Educational Scientific and Cultural Organization and Partenon.

SALMASO, N. 2000. Factors affecting the seasonality and distribution of cyanobacteria and chlorophytes: A case study from the large lakes south of the Alps, with special reference to Lake Garda. Hydrobiologia **438:** 43–63.

———. 2002. Ecological patterns of phytoplankton assemblages in Lake Garda: Seasonal, spatial and historical features. J. Limnol. **61:** 95–115.

———. 2003. Life strategies, dominance patterns, and mechanisms promoting species coexistence in phytoplankton communities along complex environmental gradients. Hydrobiologia **502:** 13–36.

———, AND F. DECET. 1998. Interactions of physical, chemical and biological processes affecting the seasonality of mineral composition and nutrient cycling in the water column of a deep subalpine lake (Lake Garda, Northern Italy). Arch. Hydrobiol. **142:** 385–414.

———, ———, AND R. MOSELLO. 1997. Chemical characteristics and trophic evolution of the deep subalpine Lake Garda (Northern Italy). Mem. Ist. ital. Idrobiol. **56:** 51–76.

———, G. MORABITO, R. MOSELLO, L. GARIBALDI, M. SIMONA, F. BUZZI, AND D. RUGGIU. 2003a. A synoptic study of phytoplankton in the deep lakes south of the Alps (lakes Garda, Iseo, Como, Lugano, and Maggiore). J. Limnol. **62:** 207–227.

———, R. MOSELLO, L. GARIBALDI, F. DECET, M.C. BRIZZIO, AND P. CORDELLA. 2003b. 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. (suppl.) **62:** 33–41.

SCHINDLER, D. W., AND OTHERS. 1996. The effects of climatic warming on the properties of boreal lakes and streams at the Experimental Lakes Area, northwestern Ontario. Limnol. Oceanogr. **41:** 1004–1017.

SIMONA, M. 2003. Winter and spring mixing depths affect the trophic status and composition of phytoplankton in the northern meromictic basin of Lake Lugano. J. Limnol. **62:** 190–206.

SOMMER, U. 1987. Factors controlling the seasonal variation in phytoplankton species composition. A case study for a deep, nutrient rich lake. Prog. Phycol. Res. **5:** 123–178.

STRAILE, D. 2000. Meteorological forcing of plankton dynamics in a large and deep continental European lake. Oecologia **122:** 44–50.

———, K. JÖHNK, AND H. ROSSKNECHT. 2003. Complex effects of winter warming on the physicochemical characteristics of a deep lake. Limnol. Oceanogr. **48:** 1432–1438.

TILZER, M. M., AND C. SERRUYA. 1990. Large Lakes. Ecological structure and function. Springer-Verlag.

WALSBY, A. E., A. AVERY, AND F. SCHANZ. 1998. The critical pressures of gas vesicles in Planktothrix rubescens in relation to the depth of winter mixing in Lake Zurich, Switzerland. J. Plankton Res. **20:** 1357–1375.

WATSON, S. B., E. MCCAULEY, AND J. A. DOWNING. 1997. Patterns in phytoplankton taxonomic composition across temperate lakes of differing nutrient status. Limnol. Oceanogr. **42:** 487–495.

WETZEL, R. G. 2001. Limnology. Lake and river ecosystems, 3rd ed. Academic Press.

WEYHENMEYER, G. A., T. BLENCKNER, AND K. PETTERSON. 1999. Changes of the plankton spring outburst related to the North Atlantic Oscillation. Limnol. Oceanogr. **44:** 1788–1792.