Journal of Great Lakes Research 41 (2015) 982–994

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

Multiproxy reconstruction of a large and deep subalpine lake's ecological history since the Middle Ages

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ARTICLE INFO

Article history:
Received 19 March 2015
Accepted 10 August 2015
Available online 11 September 2015

Communicated by Gerald Matisoff

Index words:
Diatoms
Subfossil pigments
Paleolimnology
Subalpine lake
Reference condition
Climate change

ABSTRACT

Two short sediment cores collected at the deepest points of the two sub-basins of Lake Garda (Northern Italy) were radiometrically dated and analyzed for geochemistry, spheroidal carbonaceous particles, photosynthetic pigments and diatoms aimed at reconstructing the lake's ecological evolution over the last ~700 years, and at defining its reference conditions. Both cores showed steady dominance of small *Cyclotella* spp. and oligotrophic diatom-inferred lake TP concentrations from the Middle Ages until the 1960s. During the successive decades, meso- to eutraphentic elongated Fragilariaceae increased at the expense of small centrics, and diatom-inferred TP concentrations increased. Independent records of subfossil pigments revealed higher pytoplankton biomass and abundance of cyanobacteria in both lake basins since the 1990s. Trends of biological proxies and reconstructed lake TP level agree with modern limnological data collected since the 1990s. Multivariate analyses outlined lake nutrient level as the principal driver of long-term trophic and diatom evolution of Lake Garda and suggested that decadal scale climate dynamics (i.e. air temperature, East Atlantic and North Atlantic Oscillation teleconnection indices) may indirectly modulate the nutrient-driven phytoplankton evolution. The comparison of the two cores revealed that only the larger lake basin responded to major hydrological changes in the catchment during the 1940s. The study emphasizes the vulnerability of large and deep subalpine lakes towards the steadily increasing anthropogenic pressures affecting such lakes, under the present context of global warming.

Introduction

The deep lakes south of the Alps (Garda, Iseo, Como, Lugano and Maggiore) contain over 80% of Italy's surface freshwater, making this region the most important lake district in the country. These lakes are part of a dense alpine to subalpine hydrographic network, which accounts for around 40% of the River Po's discharge. In the catchment areas of these lakes and the Po plain, water is used extensively for hydropower generation, in agriculture and industry, and as drinking water. Besides their value as habitats sustaining a rich aquatic biodiversity (Salmaso and Mosello, 2010), these lakes are very important in the tourist economy of the Alpine region.

The natural and economic value of Lake Garda and of the other deep subalpine lakes depends on the maintenance of good water quality. Therefore, an understanding of the lake's current and long-term past ecological trends is essential for the development of effective restoration interventions that will preserve water quality while maintaining ecological integrity, ecosystem services and the lake's economic value. Regular monthly scientific monitoring activities in Lake Garda started in 1996. Though these investigations represent a vital source of short-term data, they cannot provide the temporal perspective necessary to understand lake evolution at secular scale and to identify the lake's ecological characteristics under conditions of low anthropogenic impact (i.e. reference conditions). Such information is necessary for setting and tuning the targets of restoration measures, and its collection is required by the European Union Water Framework Directive (EU WFD) (Bennion et al., 2011a). The timing of the deviation from the reference conditions varies from lake to lake based on local historical events, but for most temperate European lakes it occurred between the middle of the 19th and the early 20th centuries (cit. above).

The extended long-term surveys conducted at lakes Maggiore, Lugano, Zurich, Geneva and Constance showed a common increase in lake nutrient concentrations from the 1960s to the 1980s, followed by partial to complete recovery to oligo-mesotrophic or oligotrophic conditions (Anneville et al., 2005; Berthon et al., 2014; Jochimsen et al., 2013; Marchetto et al., 2004a). These changes in nutrient

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http://dx.doi.org/10.1016/j.jglr.2015.08.008
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availability were followed by pronounced changes in the abundance and structure of phytoplankton communities, including diatoms.

A synoptic examination of historical limnological data collected in Lake Garda since the 1950s highlighted that the lake's status shifted from oligotrophic to oligo-mesotrophic after the 1960s–1970s, with a concomitant modification of its diatom population (Salmaso, 2000). In particular, whereas *Fragilaria crotonensis* and *Asterionella formosa* were among the most abundant taxa throughout the studied period, measurable biomasses of *Aulacoseira granulata* and *Aulacoseira islandica* did not appear until the 1970s (Bonomi, 1974). Since the 1980s, cyanobacteria not previously seen, namely *Planktolyngbya limnetica* and *Dolichospermum lemmermannii*, accompanied the lake's increasing phosphorus concentrations (Salmaso, 2010). While these limnological investigations have provided important insights into the changes in biological communities and water quality of Lake Garda over the last few decades, their time span is not long enough to provide information on the lake's pristine status.

Pioneering studies by Guilizzoni et al. (1983) on sub-fossil algal pigments preserved in non-dated sediment cores provided the first estimate of baseline production levels in the deep subalpine Italian lakes before they were significantly affected by human activity. At the beginning of the last century, annual production in Lake Garda was very low and indicative of oligo- or ultra-oligotrophic conditions (Table 1). The investigations conducted by Marchetto et al. (2004a), though mainly focusing on Lake Maggiore, were the first to provide comparative information on changes in the diatom community of Lake Garda during its transition from the oligotrophic to the meso-oligotrophic regime. Based on the analysis of a non-dated core, this study showed that *Cyclotella* spp. was the dominant genus in the deepest sediment layers. After the increase in the lake's trophic level, small centric diatom taxa were partially replaced by mesotrophic and eutrophic taxa including *Tabellaria flocculosa*, *F. crotonensis*, *A. formosa*, *A. islandica*, and *Stephanodiscus* spp. However, as noted by Marchetto et al. (2004a), this reconstruction of the trophic history of Lake Garda, which was based on sediments collected in 1998, did not capture changes occurring after the improvement in 1998 of the ring trunk sewer that carries waste water away from the lake (Salmaso, 2010). Apparently, the sewer led to the decline in the lake nutrient level and in cyanobacteria since the 2000s (Salmaso and Cerasino, 2012).

Table 1
Major environmental and socio-economical events affecting Lake Garda and its catchment during the study period.

Period	Event
Late Middle Ages–AD 1950s	Oligotrophic conditions[a]; extensive agriculture and handcrafted activities (southern lake shore)[b]
1709, 1864	Documented events of ice cover (complete and partial, respectively)[b]
1930s-1950s	Maximum building activities for the hydroelectric exploitation of the main lake tributary[c]
End of WWII–1970s	Strong increase of building activities around the shoreline[b]
Since 1960s	Booming of tourism industry[d]
Since 1970s	Documented lake nutrient enrichment (mainly from urban sewage and intensive agriculture)[a]
Since 1975	Partial wastewater treatment (south portion of the lake catchment)[b]
2nd half 1980s	Construction of the ring trunk sewer[b]
Since 1990s	Monthly monitoring activities at Brenzone and Bardolino lake basins[a]
1990s–2000s	Improvement of the ring trunk sewer[b]
Middle 2000s	First evidence of lake recovery[a]
2007	Inclusion in the Italian Long Term Ecological Research Network[e]

[a] Collected from literature data.
[b] Sauro et al., 2001.
[c] Lappi, 2008.
[d] Lake Garda community, 2013.
[e] LTER www.lteritalia.it.

Taking into account the information provided by modern limnological studies and by the preliminary paleolimnological investigations, the major objective of this paper is to reconstruct the long-term trophic evolution of Lake Garda from pristine reference conditions to the present day through the study of changes in its algal (especially diatoms) assemblages. The trophic evolution of Lake Garda is analyzed within the context of climate variability recorded since the late 19th century (described by variations of air temperature, and East Atlantic and North Atlantic Oscillation teleconnection indices), in order to test the indirect role of climate change on lake functioning, which has been recently outlined for Italian deep subalpine lakes (Salmaso et al., 2014). To this end, a multiproxy paleoecological study was conducted based on data from two sediment cores, one collected from the larger, deeper NW basin of Lake Garda (Brenzone) and the other from the shallower, smaller SE basin (Bardolino). Though previous limnological investigations showed that nutrient level and temporal development of phytoplankton in the two basins were similar (see study site below), their algal phenology and biomass peaks differed somewhat (Salmaso, 2002). Therefore, a further objective of this work is to evaluate differences in the basins' long-term diatom changes, and in lake phosphorus concentrations, which may be possibly related to differences in their physiography and/or the performance of different inferential approaches.

Study site

Physiographic features

Lake Garda (65 m a.s.l.) has a surface area of 368 km^2, a volume of 49 km^3 (corresponding to 34% of Italy's surface freshwater resources) and a maximum depth of 350 m. Its catchment area has a maximum altitude of 3556 m (Monte Presanella) and a mean altitude of about 1000 m a.s.l. The catchment extends over around 2350 km^2, and the catchment/lake area ratio is small (6:1) compared to other subalpine Italian lakes (Bonomi, 1974). Due to this low ratio and the region's rather low annual precipitation, the theoretical lake water renewal time is about 27 years (Salmaso, 2002). The catchment area is dominated by sedimentary rock (such as limestone, marls, and sandstones), but igneous and metamorphic rocks together with glacial and fluvial deposits prevail in the more mountainous northern portion (Sauro, 1974). The main lake inflow is the River Sarca, which collects waters from the siliceous Adamello–Presanella mountain range. Several other tributaries of minor importance in terms of water discharge are also present (Salmaso, 2010). The lake has two sub-basins separated by an underwater ridge connecting the Sirmione peninsula with Punta San Vigilio (Fig. 1). The western basin (Brenzone) is larger and deeper, and its shores are mainly rocky and steep. The shallower eastern basin (Bardolino) has a maximum depth of 81 m and accounts for 7% of the overall lake volume (Salmaso, 2002). Lake Garda is classified as a warm monomictic lake. Nevertheless, owing to its great depth, complete water mixing occurs only after cold winters.

The temporal milestones of the environmental and socio-economic evolution of Lake Garda and its catchment are reported in Table 1.

Chemical and biological data from previous studies

Monthly data on water chemistry and biology of the Brenzone basin over the entire water column (0-350 m) and the trophogenic layer (0–20 m) have been regularly collected from 1996 to 2012 (Fig. 2a). Prior to 1996 limited data for specific physical variables during the spring overturn (between March and April) are available since 1974 (Salmaso and Mosello, 2010). Chemical and biological data for the Bardolino basin are available only for the period 1996–2008 (Fig. 2b).

Both lake basins exhibit very similar and stable trends in epilimnetic pH, conductivity and oxygen content. The pH ranges from 8 in winter to 8.7 during spring and summer. The conductivity is lowest (195–200

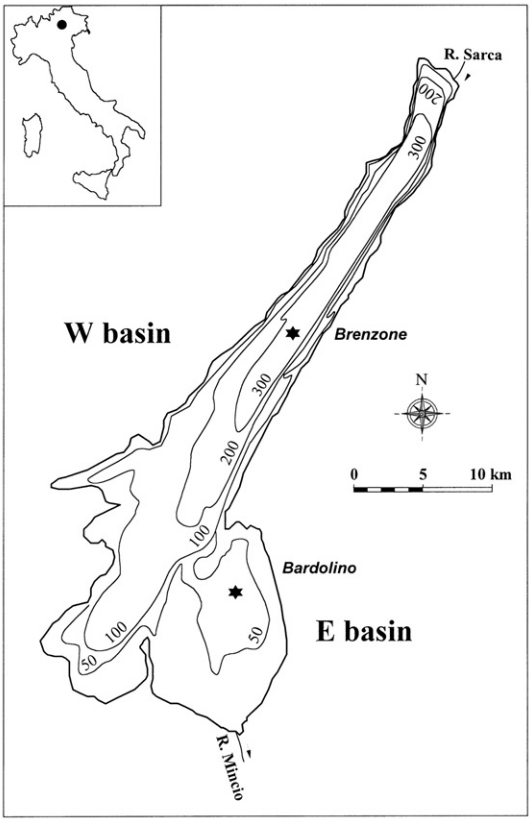

Fig. 1. Bathymetric map of Lake Garda. The stars indicate the coring locations.

μS/cm) in September–October and increases up to 215 μS/cm in June–July. Oxygen saturation also shows higher values in summer (Salmaso, 2002). Although complete re-oxygenation of the deep water layers was recorded only in 1999–2000 and 2004–2005, the lake hypolimnion is not anoxic (Salmaso and Mosello, 2010).

Detailed information on the lake's nutrient levels is available in Salmaso (2010). Prior to 1975 average total phosphorus (TP) was below 10 μg/L (Salmaso, 2002). Monthly averages of major nutrients in the whole water column and in the epilimnion (0–20 m) of both lake basins since 1996 are plotted in Fig. 2. TP concentrations in both lake basins gradually increased till 2004–2005 and irregularly decreased thereafter to the present oligo-mesotrophic level (Salmaso, 2010). DIN and Si concentrations did not show major changes since 1996, excluding the increase observed since 2011. The nutrient concentrations in Bardolino are comparable to those measured in the epilimnion of Brenzone.

The mean annual phytoplankton biovolume increased steadily during the monitoring period, peaking at ~1500 mm^3/m^3 in 2008 and in 2012 in the Brenzone basin (Fig. 2a). In general, Brenzone exhibited the highest concentrations in years involving deeper overturn in late winter and consequent replenishment of epilimnetic phosphorus, such as in 1999–2000 and 2005. The most abundant algal groups in Lake Garda are typically chlorophytes (with *Mougeotia* sp. as the dominant taxon until 2003), diatoms and cyanobacteria. Within the latter groups Oscillatoriales became the most abundant algal group after the decrease of *Mougeotia* sp. (Salmaso, 2010). The two lake basins exhibited very similar annual averages of chlorophyll *a* concentrations (2.3–4 μg/L) and temporal trends comparable to those of total biovolume.

Methods

Sediment coring

Two sediment cores were collected with a gravity Kajak corer (UWITEC, Austria) from the deepest parts of Brenzone (45°41′51″N, 10°43′15″E; water depth 350 m; core length 56 cm) in October 2009 and Bardolino (45°32′58"N, 10°40′34″E; water depth 81 m; core length 65 cm) in January 2011. Both cores were extruded vertically and sliced in the laboratory at 0.5 cm intervals from 0 to 30 cm and at 1 cm intervals from 31 cm down to the core bottom. Subsamples of individual sections were analyzed for radionuclides, spheroidal carbonaceous particles (SCPs), water and organic content, algal and bacterial photosynthetic pigments, and sub-fossil diatoms.

Radiometric dating and SCPs

Sediment samples were analyzed for ^{210}Pb, ^{226}Ra, ^{137}Cs and ^{241}Am by direct gamma assay at ENSIS Ltd (University College London, UK), using an ORTEC HPGe GWL series well-type coaxial low background intrinsic germanium detector. As the use of the CIC (constant initial concentration) model was precluded due to the non-monotonic variations in unsupported ^{210}Pb activity, core chronologies were calculated using the CRS (constant rate of ^{210}Pb supply) dating model (Appleby, 2001).

Spheroidal carbonaceous particles (SCPs), used as a proxy for atmospheric deposition of particulate pollutants originating from fossil fuel combustion (Renberg and Wik, 1985), were carried out by ENSIS Ltd (University College London, UK), following the method outlined by Rose (1994). Two vegetal remains (a twig and a leaf fragment) found at depths of 19.5 and 48.5 cm, respectively, in the Brenzone core were dated based on ^{14}C at the Poznan Radiocarbon Laboratory, Poland (http://radiocarbon.pl/index.php?lang=en), using the age calibration curve r:5, atmospheric data from Reimer et al. (2009) and the software OxCal v.4.1.5 (Bronk Ramsey, 2010).

Geochemistry and subfossil pigments

Water content was determined after drying ~2 g of wet sediment at 105 °C for 24 h, while organic matter (estimated as loss-on-ignition, LOI) was determined after heating at 550 °C for 2–3 h.

Concentrations of total carotenoids (TCar) relative to the content of organic matter were determined spectrophotometrically in subsamples from the two sediment cores according to the methods described by Züllig (1982) and Guilizzoni et al. (2011, 1983). The fresh subsamples (3 g) were sonicated in an ice bath for 3 min before and 2 min after overnight extraction in 4 ml acetone/water (90/10) at 4 °C. The 430:410 spectrophotometric absorbance ratios of the acetone extracts were calculated to assess the extent of chlorophyll degradation to phaeopigments (Guilizzoni et al., 1992). The TCar concentrations were used to infer past total phosphorus concentrations (Car-TP) according to Guilizzoni et al. (2011).

After determination of their absorbance ratios, the acetone extracts were analyzed for the quantitative carotenoid by HPLC (Agilent 1200, Agilent Technologies, USA). Carotenoid concentrations were expressed as nmol/g organic matter (LOI) and determined by using an autosampler to inject 10 μL of acetone extract onto an RP-8 column (Agilent ZORBAX Eclipse XDB-C8) and then detecting the eluted analytes with a photodiode array detector (Agilent 1220 Series, Agilent Technologies, Santa Clara, USA). A solution (final concentration 1.0 mg/L) of β-apo-8-carotenal (internal standard) was used as a marker, and individual carotenoid pigments were identified on the basis of their retention times and by comparing their absorbance spectra to those of reference standards obtained from DHI Water & Environment (Denmark). Pigment assignments were further supported by analyses conducted with a Bruker Esquire-LC QIT mass spectrometer (Bruker Daltonics, Bremen, Germany). Analytical separation was achieved using a gradient program (constant flow 0.8 mL/min) starting with a 65:35 ratio of mobile phases A (70:30 CH_3OH/H_2O containing 12 mM ammonium acetate) and B (CH_3OH with12 mM ammonium acetate) that was gradually increased to 100% B over 40 min.

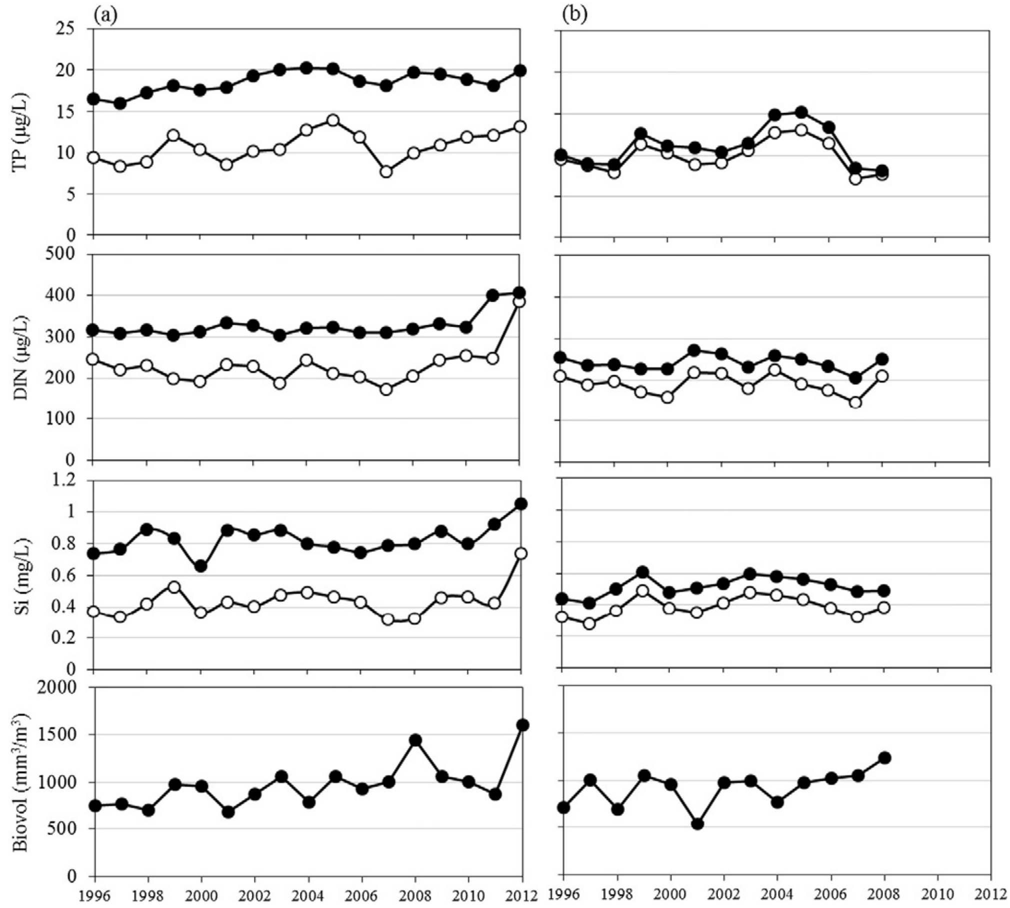

Fig. 2. Annual averages of major nutrients for the whole water column (filled circle) and the trophogenic layers (empty circles) of Brenzone (a) and Bardolino (b) basins. Annual average phytoplankton biovolume for the water layer 0–60 m at Brenzone (a) and Bardolino (b).

Diatom analyses

Around 1 g of wet sediment from every sediment layer was treated with H_2O_2 (30%) and HCl (10%) according to standard procedures (Battarbee et al., 2001) in order to clean sub-fossil diatom frustules. The cleaned samples were then permanently mounted using Naphrax® resin (refraction index = 1.7). For each permanent slide at least 500 valves were counted at 1000× magnification under a light microscope (LEICA DM2500) equipped with Nomarski differential interference contrast (DIC) optics. Diatoms were identified at the lowest possible taxonomic level, on the basis of standard literature (Krammer, 2002; Krammer and Lange-Bertalot, 1986–1991; Lange-Bertalot, 2001) and recent literature on singular taxa (Houk et al., 2010).

Selection of variables and data analysis

The diversity of the sub-fossil diatom assemblages in the sediment samples was assessed by the log2-based Shannon Index (Shannon and Weaver, 1949). The classification of the identified taxa according to their ecological preferences followed Van Dam et al. (1994). The results of these analyses are presented as stratigraphic plots created with the C2 version 1.7.2 (Juggins, 2007). Homogeneous diatom zones were identified within the cores using the CONISS method as implemented in Tilia version 1.7.16 (Grimm, 1992).

Diatom-inferred total phosphorus concentrations (DI-TP) were reconstructed using a weighted-average regression model with inverse deshrinking that was calibrated against the Northwest European training set (NWEu-TP), which includes data from 152 lakes in the United Kingdom, Northern Ireland, Denmark and Sweden (Bennion et al., 1996). This training set was selected after comparison with models calibrated against other European lake datasets including the Central Europe training set (Wunsam and Schmidt, 1995) and the Combined European training set (Battarbee et al., 2001). The NWEu-TP training set was selected on the basis of: i) the good agreement between its inferred TP concentrations and TP values measured in the lake water since the beginning of regular lake monitoring in 1996; ii) its superior statistical performance, as it achieved higher regression coefficients than competing models, with low apparent and prediction errors; and iii) higher cumulative relative abundance of fossil diatoms represented in the modern training set samples.

Only data for diatom taxa with relative abundance values of ≥0.5% in each sample were used for the DI-TP reconstruction, which was performed using transfer functions implemented in C2 version 1.7.2 (Juggins, 2007). Some taxa that were recently re-named or re-stated (e.g. *Cyclotella comensis, Cyclotella pseudocomensis*) were merged prior to reconstruction to ensure compatibility with the nomenclature used in the EDDI database.

Homogenized monthly mean air temperatures obtained from the HISTALP data set (Auer et al., 2007) were used as proxy for climate variability. Temperatures recorded at the weather stations of Torbole–Riva del Garda (ca. 20 km away from the deepest point of the Brenzone basin, data available from AD 1760 to 2004) and Villafranca (ca. 24 km away from the deepest point of the Bardolino basin, data available from AD 1788 to 2006) were used as proxies for the air temperature over the two lake basins, respectively. Annual, summer (June–August) and winter (December–February) average air temperatures were computed and used in this work.

The values of two teleconnection indices, i.e. the North Atlantic Oscillation (NAO) and East Atlantic pattern (EA), both computed by the National Oceanic and Atmospheric Administration-Climate Prediction Centre (NOAA-CPC, www.cpc.ncep.noaa.gov), were tested to outline possible relations between ecological dynamics in Lake Garda and global atmospheric circulation patterns at decadal scale. Positive and negative status of EA, which is structurally similar to the NAO and is defined as a north–south dipole of anomaly centers spanning from east to west over the North Atlantic, has been shown to drive climate pattern over the Mediterranean basin (Josey et al., 2011). Recent findings (Salmaso et al., 2014; Salmaso and Cerasino, 2012) indicated that the EA as an important driver of the ecological dynamics in the Italian subalpine lakes, including Lake Garda. In particular, it exerts a strong indirect control on the spring phytoplankton growth of these lakes through a cascading process involving deep water overturn and phosphorus recycling.

A non-metric multidimensional scaling (NMDS, Kruskal and Wish, 1978) was used to identify patterns in the temporal evolution of sub-fossil diatom assemblages. NMDS was applied to a Bray & Curtis dissimilarity matrix (Legendre and Legendre, 1998) based on the relative abundance of the diatom taxa used for the TP reconstruction, and computed with SYSTAT 10.2 (Wilkinson, 1990). The NMDS solution with the lowest 'stress', which is a measure of stable configuration (Legendre and Legendre, 1998), was selected after 100 trials. The definitive number of NMDS dimensions was determined by the analysis of the scree plot, i.e. of the stress values plotted against the number of NMDS dimensions (Legendre and Legendre, loc. cit.). Sample scores on the first two NMDS dimensions were correlated with i) data from independent sediment analyses (i.e. geochemistry, pigments), and ii) data from decadal lake and climate monitoring, aimed at better understanding the lake's ecological evolution at secular scale, and at identifying major drivers of long-term diatom changes. A LOWESS interpolation of radiometrically-determined dates for non-contiguous sediment layers was performed using R 3.1.1 (R Core Team, 2014) in order to assign an age to each sediment layer, thereby increasing the number of sediment and limnological data points that could be used in correlation analyses. The latter was performed with the software SigmaStat version 3.5. Because a Kolmogorov–Smirnov test revealed that both the sediment and limnological data were non-normally distributed, non-parametric Spearman rank order correlation analysis without data transformation was applied.

Results

Radiometric dating and SCPs

Total ^{210}Pb activity reached equilibrium with the supporting ^{226}Ra at a depth of ca. 30 cm in the Brenzone core. Low ^{210}Pb activities between 15 and 11.5 cm depth suggested high sedimentation rates in this core section. The ^{137}Cs activity showed two well-resolved peaks at 16.25 and 5.75 cm, corresponding to the Chernobyl accident in 1986 and the atmospheric testing of nuclear weapons in 1963, respectively. The raw chronology provided by the CRS model was recalculated using the ^{137}Cs and ^{241}Am records as reference layers. The sedimentation rates provided by the core dating showed a base-line value of ~0.04 g/cm^{2-} year until 1930, with the highest values occurring in the 1940s (up to 0.29 g/cm^2 year) and 1970s (~1.6 g/cm^2 year). The vegetal remains found in the Brenzone core at depths of 48.5 and 19.5 cm were dated to 1388–1448 AD and 1939–1955 AD, respectively, by radiocarbon dating. The ^{14}C-calibrated age of the vegetal material found at 19.5 cm is consistent with the correspondent ^{210}Pb age.

In the Bardolino core, the total ^{210}Pb activity reached equilibrium with the supporting ^{226}Ra at a depth of 32 cm. The mean ^{210}Pb flux to the coring location (613 Bq/m^2 year) was higher than the atmospheric ^{210}Pb deposition flux for the region, suggesting a degree of sediment focusing. Two well-resolved peaks in the ^{137}Cs activity identified the Chernobyl accident in 1986 and the nuclear tests in 1963. The CRS dating model placed 1963 and 1986 at ~18.3 and 10 cm depth, respectively, in agreement with the ^{137}Cs and ^{241}Am records. Sediment accumulation rate remained around 0.05 g/cm^2 year until the 1950s, when it started to gradually increase to the present-day value (0.12 g/cm^2 year).

The deepest SCP record in the Brenzone core dated back to the beginning of the 20th century (Fig. 3a). The SCP concentration increased rapidly after the 1950s, and peaked at over 30,000 /g dw in the middle 1980s before decreasing rapidly and steadily towards the core top. In the Bardolino core, SCPs appeared 50 years earlier than the Brenzone core, i.e. in the late 19th century (Fig. 3b). However, SCP concentrations, temporal patterns, and accumulation rates are broadly similar to those recorded in the Brenzone core.

Geochemistry and sub-fossil pigments

The water content of the deepest sediment layers of the Brenzone core (Fig. 3a) was quite low (~40% of the fresh weight), but rapidly increased to 90% in the upper 20 cm, which were deposited during the last 64 ± 15 years. Organic material accounted for <15% of the dry weight from the core bottom up to a depth of 16 cm (corresponding to a deposition date of 1969 ± 5), but represented 20–30% of the dry weight in the core topmost 15 cm. The wet density remained above 1.50 g/cm^3 before the 1940s but fell to ~1.3 g/cm^3 during the last 50 years. In the Bardolino core, the water content increased from 60% in the lower section up to 93% in the top section (Fig. 3b). The organic content varied cyclically from 10% to 30% and peaked in the layers deposited during the early 1990s. The cycle period decreased from centuries to a few decades on moving from the bottom up to the core top. The wet density remained around 1.2 g/cm^3 over the core's entire length.

The average ratio of the pigment extracts' absorbances at 430 and 410 nm was 0.77 for the Brenzone core and 0.82 for the Bardolino core. Chlorophyll *a* (Chl *a*) concentrations were very low (~0.14 nmol/g LOI) along the whole Brenzone core until the early 1970s, when the concentration started increasing progressively to a maximum of 4.3 nmol/g LOI at the end of the 1980s (Fig. 3a). In the Bardolino core, Chl *a* was recorded only at the bottom (~0.2 nmol/g LOI) and in the layers deposited after the 1960s (0.3–19.8 nmol/g LOI, Fig. 3b).

In the Brenzone core, the abundance of zeaxanthin (a proxy for colony-forming cyanobacteria) started increasing rapidly in the 1970s, and reached a maximum in the early 1990s (Fig. 3a). Similar trends were observed for the proxies of other dominant algal groups, i.e. diatoms (diatoxanthin) and chlorophytes (lutein), as well as for echinenone (cyanobacteria), and astaxanthin (a proxy for invertebrates). The profiles of the latter two pigments are not shown in Fig. 3 due to their low concentrations. The algal pigments in the Bardolino core exhibited the same trends observed for the deeper basin, but their concentrations were higher (Fig. 3b).

The total carotenoid (TCar) concentrations in the Brenzone core remained below 0.005 mg/g LOI until the middle 1940s, when they briefly increased up to 0.007 mg/g LOI. TCar values increased again in the early 1970s, reaching a maximum of 0.039 mg/g LOI in the early 1990s. Concentrations of total carotenoids were higher in the Bardolino core and showed a different temporal trend. The values were relatively high at the core bottom (up to 0.097 mg/g LOI) but rapidly decrease to 0.013–0.039 mg/g LOI at depths of 44.5–19.5 cm. The TCar concentrations then increased to a maximum of 1.976 mg/g LOI during the mid-1990s before decreasing slightly as observed in the Brenzone core.

The lake TP concentrations inferred from the total carotenoid levels (CarTP, Fig. 3a) in the Brenzone core remained around 7 μg/L along the entire core. A slight increase was observed after the mid-1970s, with a peak in the early 1990s (7.2 μg/L), which was followed by a decrease down to levels comparable to those at the core bottom over the last two decades. The CarTP levels estimated for the Bardolino core (Fig. 3b) were also around 7 μg/L in the deeper core sections, but increased since the early 1980s, rising to around 10 μg/L. After peaking

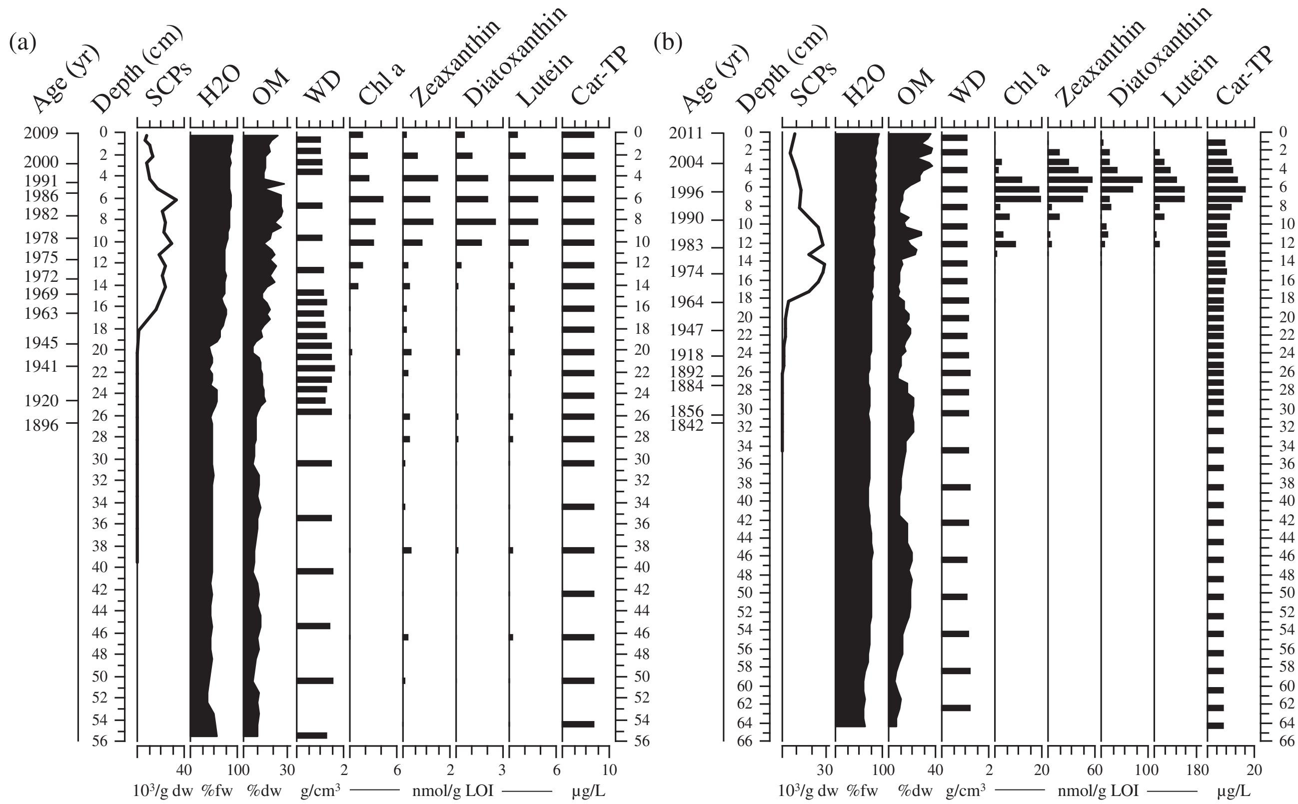

Fig. 3. Geochemical and sub-fossil pigment concentrations (nmol/g LOI) in the (a) Brenzone and (b) Bardolino cores. SCPs: spheroidal carbonaceous particles; water content (H_2O) and organic matter content (OM); WD: wet density; Chl *a*: chlorophyll *a*; Car-TP: TP concentration reconstructed from total carotenoid levels.

at 16 µg/L during the mid-1990s, the concentrations decreased to ~8 µg/L in recent years.

Sub-fossil diatoms

As shown in Fig. 4, the Brenzone core was divided into two major zones (BR-D1 and BR-D2) based on diatom relative abundances, while four distinct diatom zones were identified in the Bardolino core (BA-D1 to BA-D4). In Brenzone, BR-D1 extended from the core bottom to the section deposited in 1960, BR-D2 from 1960 to the present (Fig. 4a). Planktonic taxa dominated the diatom assemblages throughout the whole core. *C. comensis* and *C. pseudocomensis* were the most abundant taxa in BR-D1, accounting together for >90% of the total diatom abundance. *Cyclotella atomus* and *Stephanodiscus* spp. (i.e. *Stephanodiscus neoastraea* and *Stephanodiscus hantzschii*) showed low relative abundances in BR-D1, but their abundance increased up to ~12% in the BR-D2 zone (1960s to present day). During the same period, colony-forming planktonic Fragilariaceae, such as *F. crotonensis*, *T. flocculosa*, and to a lesser extent *A. formosa*, increased rapidly at the expense of *C. comensis* and *C. pseudocomensis*, whose abundance did not exceed ~50% (Fig. 4a). After the 1970s, *A. granulata*, and *A. islandica* appeared for the first time, while *Stephanodiscus* spp. further increased, reaching a maximum at the beginning of the 21st century. Benthic taxa were present throughout the Brenzone sediment core, especially in BR-D1, but their cumulative relative abundance never exceeded 8%. The most common benthic taxa were *Pseudostaurosira brevistriata* and *Amphora* spp., which were present throughout the entire core and become slightly more abundant after 1960. *Achnanthidium* spp. sensu lato was the most frequent benthic taxon in the deepest core section.

In the diatom stratigraphy of Bardolino (Fig. 4b), BA-D1 extended over the deepest 22 cm of the core and was characterized by a strong dominance of *C. comensis* and *C. pseudocomensis*, which together accounted for up to 95% of the total diatom abundance. Benthic taxa (in particular *Achnanthidium* spp., *Amphora* spp. and *Gomphonema* spp.) accounted for at most 1%. The next zone (BA-D2) extended from 43 to 27 cm and was separated on the basis of an even lower proportion of benthic taxa. Zone BA-D3 covered the section deposited between 1884 ± 16 and 1968 ± 3 (Fig. 4b) and was characterized by a gradual increase in the relative abundance of *S. hantzschii*, *Amphora inariensis*, *C. atomus*, *F. crotonensis*, *T. flocculosa*, and *Staurosirella pinnata* at the expense of *C. comensis*, and, to a lesser extent, of *C. pseudocomensis*. The progressive change in these taxa during the 1960s resulted in the establishment of the final diatom zone (BA-D4, Fig. 4b), which covered the core's uppermost 15 cm. BA-D4 is characterized by a further decline in *C. comensis*, abundances of *C. pseudocomensis* around 40%, and by the dominance of planktonic Fragilariaceae, *Stephanodiscus* spp. and *Aulacoseira* spp.

The diatom changes recorded after 1960 in both the Brenzone and Bardolino cores were paralleled by increases in the Shannon index from 1.6 to 2.6 bits and 1.4 to 2.7 bits, respectively (Fig. 4). The diatom ecological classification by Van Dam et al. (1994) indicated a rapid increase in the abundance of mesotraphentic species since the 1950s in Brenzone and since the 1960s in Bardolino, and a successive increase in the abundances of meso-eutraphentic and eutraphentic species since the 1970s in both cores (Fig. 4).

Diatom-based total phosphorus reconstruction

Out of the 33 diatom taxa with a relative abundance of ≥0.5% in the Brenzone samples, 24 could be used to reconstruct the lake's DI-TP values. However, as these 24 taxa accounted for 95-99% (average = 98%) of the total diatom content, they still provide a good representation of the sub-fossil diatom assemblages in the modern training set (Table 2, Smol and Stoermer, 2010). The taxa excluded from the Brenzone reconstruction were mainly benthic and quite sporadic. The

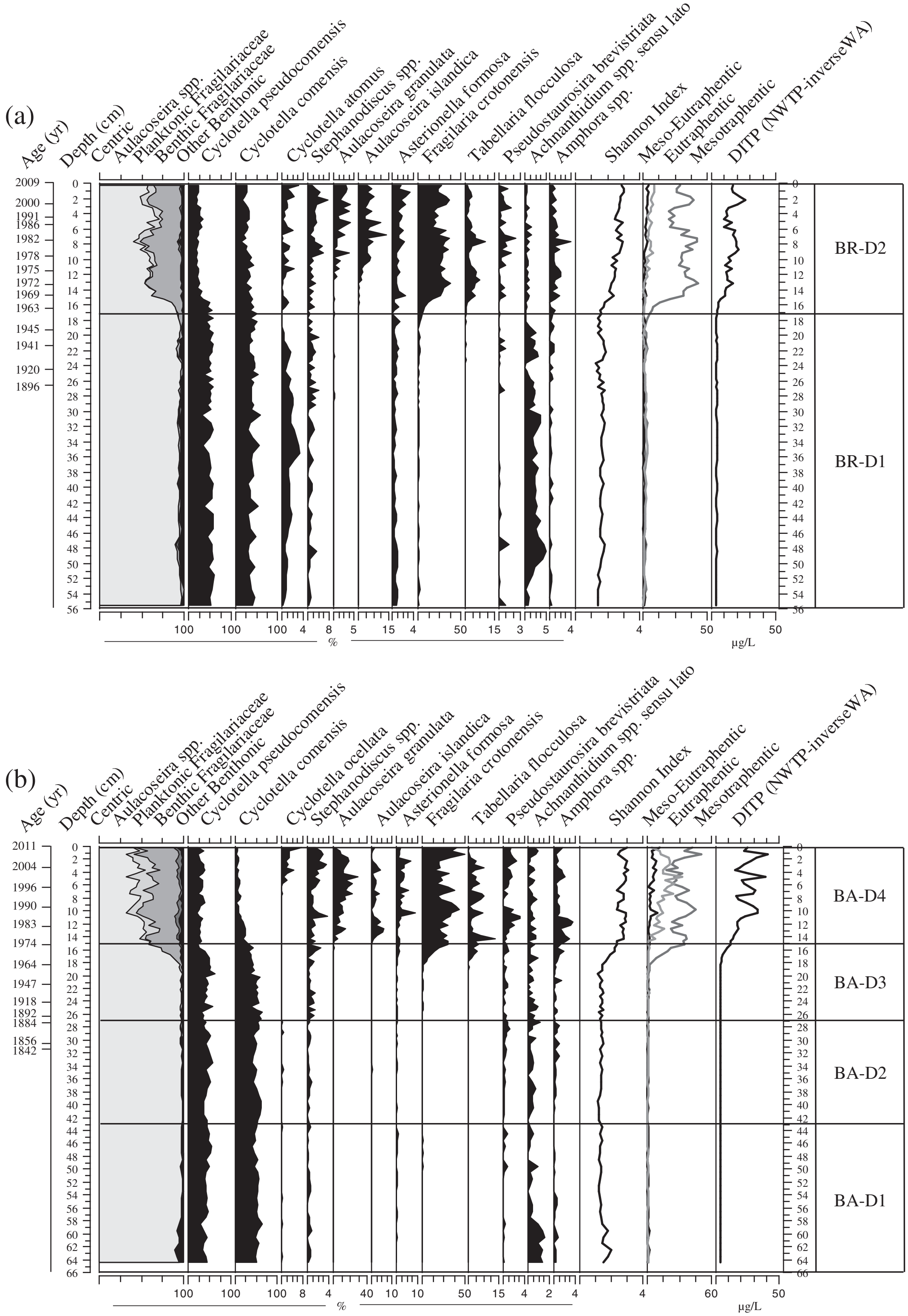

Fig. 4. Results of diatom analyses. Relative abundances of key diatom taxa, Shannon Index values, ecological classification of diatoms according to Van Dam et al. (1994), and TP concentrations reconstructed from sediment diatom abundance data (DI-TP) using an inverted weighted averaging procedure developed based on the North West Europe training set (standard error of reconstructed DI-TP: min 2 µg L^{-1}, max 2.7 µg L^{-1}) (Bennion et al, 1996). (a) Brenzone core and (b) Bardolino core.

diatom-based lake TP reconstruction for the Bardolino basin was performed using data for 28 taxa that collectively accounted for 92–99% (average = 98%) of the samples' total diatom abundance.

The best performing DI-TP reconstruction (see statistical performance reported in Table 2) was obtained using the Northwest European dataset and applying a weighted-average regression (WA) model with inverse deshrinking. The same training set and model were used to reconstruct past TP from the Bardolino core data, in order to facilitate the comparisons between the two lake basins and considering their very similar diatom patterns. The DI-TP values for

Table 2
Errors of estimation (apparent) and prediction (jack-knife) relative to the TP concentration reconstructed from sediment diatom (DI-TP) levels using the inverted weighted averaging procedure applied to the NW-Europe training set (Bennion et al, 1996) for both cores.

	Apparent statistics	Jack-knifed statistics
r^2	0.79	0.72
RMSE	0.23	0.27
Average bias	0.00	0.01
Max bias	0.57	0.78

Brenzone were very low (3–5 μg/L) between the core bottom and the layers deposited in the 1960s, and increased up to 26.0 μg/L in the early 2000s (Fig. 4a). The long-term TP pattern obtained for the Bardolino basin mirrored that for Brenzone (Fig. 4b), with very stable DI-TP concentrations (3–5 μg/L) prior to the early 1960s followed by a rapid and more irregular increase up to ~40 μg/L in the late 2000s.

Sub-fossil diatom drivers

Air temperature over Lake Garda has increased stepwise by almost 2.0 °C during the 20th century, with a first warming in the 1940s and a steady increase since the 1960–70s. Mean summer air temperatures at Torbole–Riva del Garda ($T_{(summer)}$, Fig. 5a) showed a first gradual increase during the period 1896–1952, and secondly from the early 1980s to 2004 (up to 23.4 °C). Mean winter air temperatures, $T_{(winter)}$, slightly decreased down to ~2 °C from 1896 to 1970 (reaching a minimum of 1.9 °C in 1955), and then rapidly increased up to 6.4 °C in the early 1970s. Decreasing values (down to 2.5 °C in 1984) were observed again till the 1980s, and were followed by a new increase in the 1990s. Mean summer and winter air temperatures measured at Villafranca show more gradual decadal changes with respect to those of Torbole–Riva del Garda (Fig. 5b), while short term oscillations are more pronounced.

The EA index calculated for the period December–March ($EA_{(Dec–Mar)}$, Fig. 5a) maintained negative values until the 1970s and oscillated between negative and positive ranges from the late 1970s to the present day. The mean annual EA index ($EA_{(annual)}$, Fig. 5b) behaved similarly but with a more prolonged positive stage after the late 1970s. Both the NAO index relative to the periods February–May ($NAO_{(Feb–May)}$, Fig. 5a) and December–March ($NAO_{(Dec–Mar)}$, Fig. 5b) were characterized by stable negative values from 1950 till the early 1970s, and by alternate negative and positive stages since then. The annual $NAO_{(annual)}$ index also showed a negative stage from the 1950s to the late 1970s, followed by 15 years of positive values, and by stable negative stage from the middle 1990s to present day. $NAO_{(annual)}$ is not shown in Fig. 5 and not further discussed due to its scarce correlations with air temperature over both basins of Lake Garda.

The scree plot analysis indicated the two-dimension NMDS analyses of subfossil diatoms of the two studied cores as the better performing. NMDS for the Brenzone core provided a quite stable configuration, as indicated by the very low stress value (0.048). The sample scores on the first NMDS dimension (DIM1, Fig. 5a) were much less variable between the core bottom and the layer deposited in the 1960s than during the last 50 years. After a rapid increase between the 1960s and the 1980s, the sample scores initially shifted towards their pre-1960 values but then increased again, peaking at the beginning of the 21st century. As the sample scores on the second dimension (DIM2) oscillated between −1.3 and 0.7 without showing any clear trend over the studied period, the corresponding data are not shown in Fig. 5a.

The correlation coefficient between sample scores on NMDS DIM1 and DIM2, respectively, and sediment proxies from the Brenzone core are reported in Table 3. Several significant correlations were found also among sediment proxies (reported only in the text). DI-TP was strongly correlated with Car-TP ($r = 0.841$, $p < 0.001$), organic content

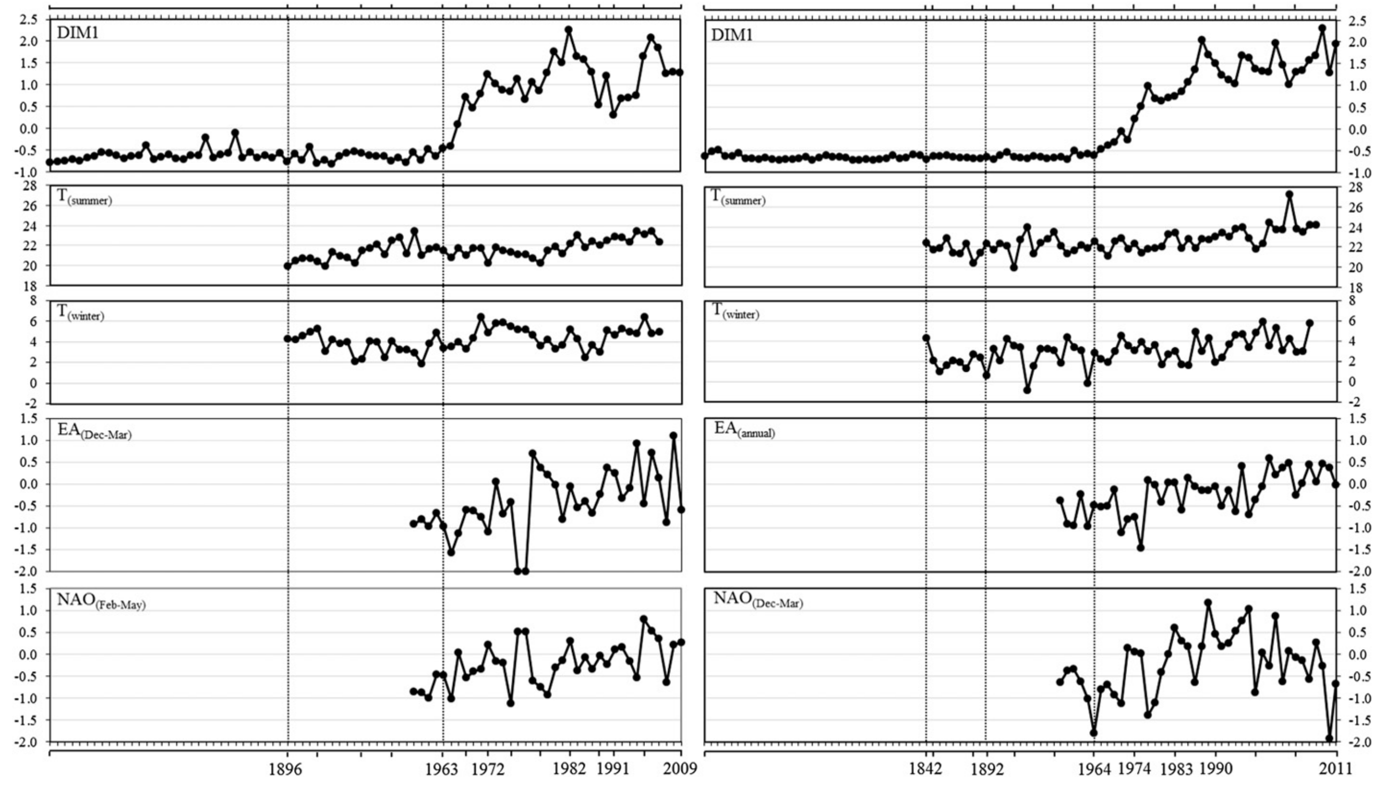

Fig. 5. Diatom sample scores on NMDS DIM1 versus climatic variability. (a) Brenzone basin. $T_{(summer)}$ and $T_{(winter)}$: mean summer (June–July–August) and winter (December–January–February) recorded at Torbole–Riva del Garda; $EA_{(Dec–Mar)}$: average EA index computed for the period December to March; $NAO_{(Feb–May)}$: average NAO index from February to May. (b) Bardolino basin. $T_{(summer)}$ and $T_{(winter)}$: mean summer and winter recorded at Villafranca; $EA_{(annual)}$: annual average EA index; $NAO_{(Dec–Mar)}$: average NAO index from December to March. Positioning of teleconnection indices according to the strength of their correlation with sample scores on NMDS DIM1 of Brenzone or Bardolino, respectively.

Table 3
Spearman rank-order correlations (*r*) of selected variables with the first (DIM1) and second (DIM2) dimensions of the non-metric multidimensional scaling (NMDS) configuration for both cores. Variables considered are: organic matter (OM) concentration, subfossil pigment concentrations (Chl *a*: chlorophyll *a*; Zea: zeaxanthin), total phosphorus concentrations reconstructed from total carotenoid levels and diatom distributions (Car-TP and DI-TP respectively), mean annual air temperature $T_{(annual)}$, and four teleconnection indices — $EA_{(Dec–Mar)}$ (East Atlantic index from December to March), $EA_{(annual)}$ (annual EA index), $NAO_{(Feb–May)}$ (North Atlantic Oscillation index from February to May), and $NAO_{(Dec–Mar)}$ (NAO index from December to March). Correlations shown in bold are significant at the $p < 0.001$ level; n.s. = not significant. N: number of cases.

	Brenzone			Bardolino		
	N	DIM 1	DIM 2	N	DIM 1	DIM 2
OM	86	**0.687**	n.s.	95	0.259*	0.208*
Chl *a*	22	**0.707**	−0.597**	35	**0.814**	n.s.
Zea	22	0.456*	−0.602**	35	**0.798**	n.s.
Lutein	22	**0.669**	−0.561**	35	**0.838**	n.s.
Car-TP	22	**0.743**	−0.517*	47	**0.802**	n.s.
DI-TP	86	**0.925**	n.s.	95	**0.888**	n.s.
$T_{(annual)}$	51	**0.461**	n.s.	59	**0.674**	n.s.
$EA_{(Dec–Mar)}$	37	0.415*	n.s.	42	0.334*	n.s.
$EA_{(annual)}$	37	0.413*	−0.344*	42	**0.587**	n.s.
$NAO_{(Feb–May)}$	37	0.463**	n.s.	42	0.385*	n.s.
$NAO_{(Dec–Mar)}$	37	n.s.	n.s.	42	0.453**	n.s.

** $p < 0.01$.
* $p < 0.05$.

($r = 0.670$, $p < 0.001$), sub-fossil pigments concentrations ($0.6 < r < 0.8$, $p < 0.001$), $T_{(annual)}$ ($r = 0.468$, $p < 0.001$), $NAO_{(Feb–May)}$ ($r = 0.447$, $p < 0.01$) and the $EA_{(annual)}$ index ($r = 0.447$, $p < 0.001$). Car-TP was correlated negatively with the relative abundances of *Cyclotella* spp. ($r = -0.864$, $p < 0.001$), and positively with the abundances of all other diatom taxa used for TP reconstruction ($0.600 < r < 0.831$, $p < 0.01$). Moreover, Car-TP was positively correlated with the $T_{(annual)}$ ($r = 0.694$, $p < 0.01$) as well as the mean spring and summer air temperatures ($r = 0.666$, $p < 0.05$, $r = 0.556$, $p < 0.05$), the $NAO_{(Feb–May)}$, and the $NAO_{(annual)}$ ($r = 0.648$, $p < 0.05$, and $r = 0.685$, $p < 0.05$, respectively). The abundance of all the most abundant diatom taxa (Table 4) was significantly correlated with the $T_{(annual)}$. *A. formosa, S. pinnata*, *A. islandica* and *T. flocculosa* showed the strongest correlation with measured lake TP, DIN/Si, $DIN/TP_{(Lake)}$, and $DIN/Si_{(0–20)}$ concentrations (Table 4). *Stephanodiscus neoastraea* was the sole species significantly correlated with $DIN_{(0–20)}$ concentrations, while no significant correlation was found between any diatom taxon and $Si_{(0–20)}$ or $Si/TP_{(0–20)}$.

The 2-dimension NMDS analysis performed on the Bardolino diatom data provided a configuration with a low stress value (0.048). The temporal variations of the sample scores on NMDS DIM1 were very similar to those obtained for the Brenzone core (Fig. 5b), and scores on DIM2 oscillate as well without any temporal trend (not shown in Fig. 5b). Correlations between sample scores on the two NMDS dimensions and sediment proxies from the Bardolino core were very similar to those for Brenzone (Table 3). Bardolino DI-TP values were positively correlated with concentration of subfossil pigments ($r = 0.844$, $p < 0.001$), chlorophyll a ($r = 0.822$, $p < 0.001$) and Car-TP ($r = 0.787$, $p < 0.001$), beside with $T_{(annual)}$ ($r = 0.621$, $p < 0.001$), $NAO_{(Dec–Mar)}$ ($r = 0.499$, $p < 0.001$), $EA_{(annual)}$ index ($r = 0.561$, $p < 0.001$). Although Car-TP values of Bardolino presented equivalent correlations with diatom abundances and annual and seasonal air temperature ($r = 0.704$, $p < 0.001$, $r = 0.550$, $p < 0.01$, respectively) with respect to those seen for the Brenzone core, they correlated only with $EA_{(annual)}$ and $EA_{(Dec–Feb)}$ ($r = 0.529$, $p < 0.05$, $r = 0.525$, $p < 0.05$, respectively). All the most abundant diatom species but *Cyclotella* spp. were positively correlated with the $T_{(annual)}$ (Table 4). *C. comensis* showed the strongest negative correlation with water $TP_{(0–20)}$ and $DIN/TP_{(Lake)}$ ratio, while *C. pseudocomensis* and *A. granulata* showed the strongest correlation with the $DIN_{(0–20)}$ concentration ($r = 0.842$, $p < 0.001$, $r = -0.842$, $p < 0.001$, respectively). No diatom taxon showed significant relation to either $Si_{(0–20)}$ or $Si/TP_{(0–20)}$.

Discussion

The study of the deep sediments of Lake Garda provided an overview of the long-term ecological changes that occurred in the lake during the last ~700 years and identified anthropogenic driven nutrient enrichment as the main driver for secular changes in the lake's trophic status. Multiple dating methods (^{137}Cs, ^{210}Pb, SCPs) yielded concordant sediment chronologies for the two cores collected at Brenzone and Bardolino. The ^{210}Pb chronology provided information on the last ~150 years, while the ^{14}C-based age of the Brenzone core bottom indicated a time span extending from the late Middle Ages to the present

Table 4
Spearman rank-order correlations (*r*) between the abundances of key algal species and the first NMDS dimension (DIM1), mean annual air temperature ($T_{(annual)}$), total phosphorus ($TP_{(0–20)}$) and dissolved inorganic nitrogen ($DIN_{(0–20)}$) concentrations in the trophogenic layers, and DIN/TP concentration in the water column ($DIN/TP_{(Lake)}$). BR = Brenzone; BA = Bardolino. Correlations shown in bold are significant at the $p < 0.001$ level; n.s. = not significant. N: number of cases.

		N	DIM 1	N	$T_{(annual)}$	N	$TP_{(0–20)}$	$DIN_{(0–20)}$	$DIN/TP_{(Lake)}$
Cyclotella spp.	BR	86	−0.924	51	**−0.506**	7	n.s.	n.s.	n.s.
	BA	95	−0.920	59	**−0.644**	10	n.s.	n.s.	n.s.
Achanthidium minutissimum sensu lato	BR	86	−0.416	51	n.s.	7	n.s.	n.s.	n.s.
	BA	95	n.s.	59	n.s.	10	n.s.	n.s.	0.650*
Asterionella formosa	BR	86	**0.579**	51	**0.478**	7	**0.893**	n.s.	n.s.
	BA	95	**0.708**	59	**0.580**	10	n.s.	n.s.	n.s.
Aulacoseira granulata	BR	86	**0.663**	51	**0.548**	7	n.s.	n.s.	n.s.
	BA	95	**0.796**	59	**0.657**	10	n.s.	**−0.842**	n.s.
Aulacoseira islandica	BR	86	**0.812**	51	**0.551**	7	n.s.	n.s.	−0.750*
	BA	95	**0.701**	59	**0.474**	10	n.s.	n.s.	n.s.
Cyclotella comensis	BR	86	**−0.590**	51	**−0.469**	7	n.s.	n.s.	n.s.
	BA	95	**−0.901**	59	**−0.692**	10	−0.709*	n.s.	0.745*
Cyclotella pseudocomensis	BR	86	**−0.840**	51	−0.418**	7	n.s.	n.s.	n.s.
	BA	95	**−0.513**	59	−0.368**	10	n.s.	**0.842**	n.s.
Fragilaria crotonensis	BR	86	**0.768**	51	**0.480**	7	n.s.	n.s.	n.s.
	BA	95	**0.782**	59	**0.533**	10	n.s.	n.s.	n.s.
Staurosirella pinnata	BR	86	**0.402**	51	0.313*	7	−0.768*	n.s.	0.867**
	BA	95	**0.552**	59	n.s.	10	n.s.	n.s.	n.s.
Stephanodiscus neoastraea	BR	86	**0.650**	51	**0.510**	7	n.s.	−0.821*	n.s.
	BA	95	**0.683**	59	**0.631**	10	n.s.	n.s.	n.s.
Tabellaria flocculosa	BR	86	**0.804**	51	**0.473**	7	n.s.	n.s.	n.s.
	BA	95	**0.782**	59	**0.557**	10	n.s.	n.s.	n.s.

** $p < 0.01$.
* $p < 0.05$.

day. The SCP trend observed in both the cores is comparable to that observed in other lakes in the Eastern Alps (Rose et al., 1999). However, the absolute SCP concentrations in both cores were appreciably higher than those reported for other Alpine lakes, and among the highest in Europe (Rose, pers. comm.), likely because of Lake Garda's location at the border of the Po Plain, which is one of Italy's most densely populated and industrialized regions (Marchetto et al., 2004b).

The peak sedimentation rate, recorded around 20 cm depth in the Brenzone core, corresponds to a period of high sediment deposition that does not seem to be related to any sediment slumping because it is accompanied by a sharp increase in water content and a clear decrease in the organic proportion. The enhanced sedimentation may be related to the important hydrological perturbations that have occurred in the catchment of Lake Garda since the inter-war period. As was the case for most Alpine rivers (Tödter, 1998), the basin of the main tributary of Lake Garda (the River Sarca) has been intensively exploited for hydropower production since the first decades of the 20th century, but especially just after the Second World War. Lakes within the Sarca catchment were dammed and several reservoirs and impoundments were built (Lappi, 2008), generating a decanting effect that explains the low mineral content of the sediments deposited in Lake Garda's main basin after the early 1940s. Comparable changes in sedimentation rates have been observed in other large deep, lowland lakes in Northern Ireland, North Italy and Estonia, which exhibited a baseline sedimentation rate of 0.04 ± 0.02 g/cm^2 year before major increases since the 1950s related to hydroelectric changes in their catchments (Rose et al., 2011). As no major changes in the biological proxies were recorded during this period, the lake's general ecological conditions were apparently insensitive to the observed changes in sediment transport by the main tributary. Moreover, no correspondent changes in sedimentation rates were recorded in the core from the Bardolino basin during the 1940s–1950s, probably because of its distance from the major lake inlet and the presence of an underwater ridge separating the smaller from the deeper lake basin.

The moderate sediment organic content throughout both cores indicates that Lake Garda's productivity was consistently low over the last seven centuries. However, the organic content approximately doubled in both the lake basins over the last ~50 years, thus suggesting an increase in lake productivity. The significant correlation between the organic content and concentrations of sub-fossil pigments is consistent with such an increase in lake productivity. The organic content varied cyclically, with secular to decadal periodicity, particularly at Bardolino. Similar cyclical trends in biology-related variables have been observed in other large lakes (e.g. Padisák and Dokulil, 1994), where they were linked to a cyclical development of phytoplankton biomass. The more pronounced cyclic trend observed in Bardolino suggests that the shallower basin is more dynamic than the deeper Brenzone basin, where long-term changes of bio-geochemical proxies were generally less pronounced and smoother.

The 430:410 spectrophotometric absorbance ratios indicated pronounced pigment degradation (Guilizzoni et al., 1992) in both lake basins, probably in relation to the oxygenated conditions at the bottom of Lake Garda. The great depth of the Brenzone basin (i.e. 350 m) likely enhances the pigment degradation rate (Leavitt, 1993), thus explaining the very low concentrations found in the corresponding core. The poor pigment preservation hampers the evaluation of possible differences in long-term primary productivity of the two lake basins. However, recent surveys of lake surface chlorophyll concentrations based on remote sensing (Bresciani et al., 2011) suggested minor differences in the annual productivity of the two lake basins and more pronounced seasonal variations at Bardolino. The same survey also confirmed that Lake Garda is the least productive of the large subalpine lakes both south and north of the Alps. The increased concentrations of chlorophyll *a*, phaeopigments, and β-carotene observed in the 1980s layers of the Brenzone core confirmed the results of a preliminary study by Guilizzoni et al. (1983). In general, the depth profiles of the sub-fossil pigments were broadly consistent with the gradual increase in phytoplankton biovolume indicated by the first phytoplankton surveys in the early 1990s (Salmaso, 2010). In particular, the zeaxanthin pattern indicated a moderate presence of cyanobacteria before the 1970s, while the peak in the early 1990s was validated by limnological data (Salmaso, 2000), which showed a progressive development of *Planktothrix rubescens* and irregular blooms of *Dolichospermum lemmermannii* since the 1990s. Limnological data show unusually higher phytoplankton biovolume at Bardolino in 1997 in comparison to Brenzone (Salmaso, 2002), mainly due to increased abundance of cyanobacteria. This finding is consistent with the zeaxanthin profile in the Bardolino core.

The long-term evolution of the carotenoid-inferred lake TP agreed with the trend of diatom-inferred TP in both basins. In general, compared to the DI-TP concentration, the Car-TP values exhibited lower and smoothed TP peaks, as typical for scarcely productive lakes with high pigment degradation rates (Guilizzoni et al., 2011).

The geochemical and biological proxies, as well as the TP profiles inferred from sub-fossil pigments and diatoms, clearly indicated that Lake Garda remained in ultra-oligotrophic conditions from the late Middle Ages until the 1960s. This agrees with the scattered limnological information on Lake Garda available prior to the 1970s. Garbini (1898) considered the lake productivity as extremely poor, while Marchesoni (1952) found only very small phytoplankton densities. During this whole period, diatom species composition and abundances remained very stable in both the studied cores, and small unicellular oligotraphentic *Cyclotella* species were dominant. Even large scale climate variations such as the cold period of the Little Ice Age (LIA) were not reflected by variations in any of the biological proxies considered in this work. This suggests a considerable inertia of Lake Garda towards climatic changes, which is provided by its large size and water volume (Gerletti, 1974).

As previously mentioned, the first changes observed in the early 1940s affected exclusively the geochemical proxies of the Brenzone core, and have been related to the hydroelectric exploitation of the main lake tributary. The first clear biological response of Lake Garda to environmental perturbations occurred in the early 1960s and consisted of a pronounced increase in the abundance of mesotraphentic colony-forming taxa such as *A. formosa*, *F. crotonensis* and *T. flocculosa* at the expense of small *Cyclotella* species in both the analyzed cores. The rare limnological information prior to the 1970s refers to very small densities of elongated planktonic Fragilariaceae (e.g. 2–4 colony/ml for *F. crotonensis*, Marchesoni, 1952). Multivariate statistical analyses of sediment data combined with correlation analyses allowed for the linking of these major diatom changes to nutrient enrichment from uncontrolled discharge of urban sewage water into the lake since the beginning of the economic boom in the 1950s. The increase in planktonic Fragilariaceae was very rapid, and the enhanced abundance of eutrophic taxa, such as *Aulacoseira* spp. and *Stephanodiscus* spp. (Bennion et al., 2004; Van Dam et al., 1994), recorded after the early 1970s in both cores coincided with a major change in the concentrations of sub-fossil pigments. Especially the increase of *A. granulata*, which was found to characterize eutrophic stages of several subalpine large lakes (e.g. Berthon et al., 2014; Marchetto et al., 2004a; Wessels et al., 1999), suggested a further increase in nutrient availability in Lake Garda during this period. Recent *Cyclotella*–*Aulacoseira*–*Fragilaria* shifts have been reported in numerous lake sediment records across the Northern Hemisphere (Rühland et al., 2015). In particular, the increase in colony-forming and mesoeutraphentic Fragilariaceae over previously dominant oligotrophic *Cyclotella* species represents a highly coherent phytoplankton response to moderate nutrient enrichment in small and large Alpine lakes (Bennion et al., 1995; Bigler et al., 2007; Jochimsen et al., 2013; Marchetto et al., 2004a; Thies et al., 2012).

Not only phosphorus, but also nitrogen, might have been involved in controlling the increase in elongated planktonic Fragilariaceae in Lake Garda since the 1960s. In fact, results from alpine regions affected by large scale industrial and agricultural activities in the USA principally attributed the increase in Fragilariaceae to enhanced atmospheric nitrogen deposition (Saros et al., 2005; Wolfe et al., 2003). Information on nitrogen in Lake Garda are available only after 1996, which may contribute to the poor correlation observed in the present study between abundance of elongated Fragilariaceae and nitrogen. It is however plausible that nitrogen load to Lake Garda increased in the second half of the 20th century in relation to the post-war agriculture and industrial development in the Po Plain. Long-term monitoring indicated a general increase in atmospheric NO_x deposition over the Alps in the last few decades (Rogora et al., 2006), and the hypothesis of an intense industrial atmospheric contamination over Lake Garda is supported by the SCP record in both the studied cores, which shows concentrations among the highest in Europe (Rose pers. comm.).

As shown by previous investigations (Salmaso, 2010), silica does not play a major role in controlling diatom growth in Lake Garda. Annual average concentrations <0.5 mg/L since 1996 indicate the possibility of seasonal silica limitation. However, the absence of a temporal Si trend during the monitoring period indicates a constant effect of silica on diatoms in recent times.

Increasing abundance of elongated Fragilariaceae has been reported in Alpine and non-alpine lakes also without major changes in nutrients, but in concomitance with increases in regional temperature (Rühland et al, 2015). In fact, elongated Fragilariaceae are known to have competitive advantage in warm and stratified water, in relation to a set of ecophysiological characteristics related to the elongated shape and the colony formation, which slow the sinking velocity, increase the surface area to volume ratio, increase the light harvesting capability, and decrease the grazing vulnerability (Padisák et al., 2003). Such competitive advantages may have helped the increasing nutrients in supporting the increase in Fragilariaceae in Lake Garda during the major climate warming registered since the 1960s.

Timing and magnitude of diatom changes were highly comparable in the two studied cores. The sole relevant difference consisted of an earlier increase in meso- to eutraphentic *Stephanodiscus* species at the expense of the oligotraphentic *C. comensis* in the Bardolino core since the last decade of the 19th century, i.e. before the beginning of nutrient enrichment. Similar pre-enrichment increases in eutraphentic diatoms were recorded in several other lakes of the Alpine region, where they have been often attributed to climate-related factors (Berthon et al., 2013; Catalan et al., 2013; Marchetto et al., 2004a; Thies et al., 2012). However, the information available is not sufficient to verify this hypothesis for Lake Garda. The fact that such early changes have been observed only in the Bardolino core suggests a lower resistance to environmental changes of the smaller basin with respect to the larger basin of Lake Garda.

While the overall temporal evolution of the reconstructed TP in the two basins of Lake Garda were highly comparable, the diatom-inferred TP concentrations at Bardolino for the period 1996–2008 were higher than those in Brenzone and overestimated the corresponding monitoring values. This is due to the different abundances in the Bardolino core of some diatoms characterized by high TP-optimum in the training set used in the present study. In particular, the nutrient tolerant *A. islandica* (TP-optimum = 76.7 μg/L) is more abundant in the Brenzone core (1.55 vs 0.64%), while the eutraphentic *A. granulata* (TP-optimum = 153.5 μg/L) showed higher abundances in the Bardolino core (average = 3.72 vs. 0.56%). Diatom-inferred TP levels exceeding values measured in the water column have been found in other large and deep lakes, such as Maggiore and Mjoesa (Bennion et al., 2011b), and have been interpreted as related to the under-representation of large and deep lakes in most of the currently used training sets, which were calibrated on smaller and shallower lakes.

The comprehensive secular evolution of geochemical and biological proxies in the two studied cores made it possible to identify the reference conditions for Lake Garda as those characterizing the period between the late 19th and early 20th centuries, when the lake was still clearly oligotrophic. The nutrient enrichment of Lake Garda during the second half of the 20th century is highly coherent with the trophic evolution of several other large deep Alpine lakes (Alefs and Müller, 1999; Berthon et al., 2013; Marchetto et al., 2004a; Wessels et al., 1999), which was characterized by very low and stable TP level till ~1900 and by a rapid increase during the post-war economic growth. The intensive restoration measures launched at these lakes in the 1970s–1980s produced their recovery down to pre-impact oligotrophic level. In contrast, at Lake Garda the waste water treatment started only in the second half of the 1980s (Boscaini, 2009), while both resident and tourist population steadily increased over time (Lake Garda Community, 2013). As a consequence, present TP level of Lake Garda is still oscillating around the mesotrophic level (Salmaso, 2010).

Because most of the reported sediment studies of subalpine deep lakes were based on cores collected before the late 1990s (Alefs and Müller, 1999; Bennion et al., 1995; Marchetto et al., 2004a), they do not provide information on the possible effects on lake ecological evolution by the more pronounced climate changes that occurred since the 2000s (Chimani et al., 2013). On the contrary, the sediment profiles of Lake Garda were useful to interpret the potential role of recent climate events in modulating the response of planktonic diatoms to nutrients. Simultaneous correlations between sediment proxies and trophic and climatic variables make it difficult to analyze diatom responses to climate variability in temperate lakes, as significant relations may be merely due to the confounding concomitance of independent events, such as nutrient enrichment and global warming occurred since the 1960s. Nevertheless, the timing and phenology of the changes observed in sediment diatoms of Lake Garda allowed the application of a weight-of-evidence approach based on the comparison of the literature information (Rühland et al., 2015). This provided a plausible interpretation of ecological tipping points in Lake Garda during the last few decades and allowed some conclusions on possible effects of both current climate warming and rare extreme cold events on the diatom communities of this lake.

Diatom responses driven by increasing air temperatures are particularly evident and pronounced in remote high latitude or high altitude lakes (Catalan et al., 2013), as well as in temperate lakes with pronounced seasonality (e.g. Adrian et al., 2009; Bigler et al, 2007; Thies et al., 2012), where phenology of ice cover affects numerous physical, chemical and habitat properties able to control the algal growth. Moreover, the negligible direct human impact usually characterizing remote lakes allows disentangling the cascading interactions between climate, lake properties and biological response (Catalan et al., 2013). Conversely, climate-driven ecological perturbations are typically smoothed in large temperate lakes, which do not freeze in winter and have a large thermal inertia. Effects of increasing temperature can also produce unexpected effects in lakes not freezing in winter, as recently observed by Michelutti et al. (2015) in high altitude tropical lakes, where warm summers combined with mild winters prevents deep circulation. This causes a persistent nutrient depletion in the epilimnion, which can mimic a re-oligotrophication stage, and at the same time trigger oxygen depletion and nutrient sequestration in the hypolimnion. As climate and weather conditions ultimately affect lake nutrient dynamics and the phytoplankton capacity to exploit these resources, effects of climate change in temperate large and deep lakes are particularly smoothed when not associated with increasing nutrient load (Rühland et al., 2015). This can explain why the deep sediments of Lake Garda recorded first biological changes only after the beginning of nutrient enrichment in the 1960s, while no response could be found during the previous centuries. This is consistent with results provided by limnological investigation of Lake Garda (Salmaso, 2010), as well as with data from other deep subalpine lakes, such as Maggiore, Constance, Mondsee, Ammersee and Starnbergsee, Geneva, Bourget and Annecy (see citations above).

Both the studied cores indicated a spike in pigment and diatom inferred TP concentrations during the first half of the 2000s, which was accompanied by a short term increase in sediment eutraphentic centrics (*C. atomus*, *Stephanodiscus* spp., *Aulacoseira* spp.). This agreed with the limnological data, which showed high epilimnetic TP concentrations accompanied by a spring pulse in the biovolume of centric diatoms and total phytoplankton in 2005 (Salmaso, 2010). As equivalent changes were found in the same period in several temperate lakes within the Alpine region without evident changes in the lakes' nutrient level and regardless of the lakes' trophic conditions (Berthon et al., 2014; Tolotti et al., 2012; Tolotti pers. comm.), it seems reasonable to consider recent climate events as being involved in the observed nutrient pulse. Salmaso and Cerasino (2012) demonstrated the crucial role of the EA pattern in controlling the winter air temperature in the region of Lake Garda. In turn, the winter air temperature controls nutrient availability and spring diatom growth through cascading processes involving deep water mixing in late winter. The diatom changes observed in the 2000s have been interpreted as the response to a nutrient pulse induced by sporadic cold winter events over the Alpine region (Salmaso, 2010). Lake Garda surely experienced several cold-winter events during the period covered by the chronology of the studied sediment cores, e.g during the Little Ice Age, and in the particularly negative EA years 1939 and 1955. Historical documents even report some lake winter freezing, e.g. in 1709 and 1864 (Sauro et al., 2001), but no change in the biological sediment proxies could be associated with these cold events. In contrast, the complete mixing events which occurred since the 1970s (reported in Salmaso, 2010) after cold winters in the SE Alpine region (Auer et al., 2007) were associated with episodes of increased lake productivity. This suggests that cold winters that occurred in the last few decades contributed to reinforce the response of Lake Garda to the nutrient enrichment started in the 1960s. These observations suggest the possibility to sort out particular ecological responses to climate dynamics even in large temperate lakes.

The sediment records from the two sub-basins of Lake Garda underline the potential offered by multi-core paleolimnological studies of deep and large lakes for outlining particular ecological responses in different basins, which are possibly related to complex lake morphologies (e.g. Edlund et al., 1995). The sediments deposited in the deepest lake basin appear more suitable for inferring the lake trophic evolution at secular scale, while the cores from smaller and shallower lake basins can be affected by local ecological dynamics and ecotone disturbances.

Conclusions

Paleolimnological investigations are essential for defining the lake reference conditions, and to place limnological investigations within a secular temporal perspective. This is of paramount importance given that even decadal limnological surveys usually provide information on lakes' ecological evolution since the maximum nutrient enrichment, or in the successive recovery stage. Information on earlier lake perturbation since the early 20th century is rare.

The paleolimnological study of Lake Garda contributed to evolving models of ecosystem functioning for large and deep lakes, which still remain poorly investigated in Europe and worldwide with respect to other lake categories. The study confirmed a moderate nutrient-enrichment of Lake Garda since the early 1960s, which is highly comparable with what happened in other deep subalpine lakes south and north of the Alps. Conversely, this study showed that the lake recovery following the restoration measures established in the late 1990s is still incomplete for Lake Garda.

In contrast to most paleolimnological investigations on subalpine lakes, the sediment records from Lake Garda provided supplementary information on the lake's evolution over the last 10–15 years. The study confirmed the findings of recent limnological research in indicating climate variability as a possible modulating factor for the ecological responses of large deep lakes to nutrient changes. Apparently, the strength of this modulating effect largely depends on the lake's nutrient status.

Temperature variability has a strong, though indirect, control over the thermal dynamics of deep lakes, especially on thermal stability and a set of related factors, such as the interannual winter deep circulation patterns, which in turn can affect nutrient availability and nutrient uptake by phytoplankton. These complex and interlaced relations appear to be particularly important for large and deep subalpine lakes within the present context of global warming and increasingly extreme climate events, as they can produce unexpected effects and possible misinterpretation. Warm summers combined with mild winters can prevent water deep circulation, thus producing opposite changes in nutrient levels of the epilimnion and hypolimnion, respectively. Conversely, cold winter events allow for the nutrient replenishment of the lake epilimnion, thus promoting pulses in lake productivity possibly accompanied by algal blooms.

These findings suggest that climatic factors should be considered as equally important as nutrient availability in controlling the temporal development of plankton communities at seasonal and decadal scales on large and deep lakes. The interconnection between trophic status and climate also emphasizes the importance of maintaining and improving measures aimed at controlling nutrient inputs in both recovering and re-oligotrophicated lakes, especially given the increasing human utilization of large lake water resources at global level.

Acknowledgments

This research was partly funded by the EULAKES Project (Reg. Nr. 2CE243P3). The authors thank Adriano Boscaini and Nicola Merlo for their support in the field and laboratory. Andrea Lami is acknowledged for helpful suggestions concerning pigment analysis. Neil Rose and Handong Yang (ENSIS Ltd.—University College of London-UK) are thanked for assistance with radiometric and SCP analyses. Finally we thank Vincent Berthon and an anonymous reviewer for their critical and constructive comments.

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