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Diatom community response to extreme water-level fluctuations in two Alpine lakes: a core case study

M. Leira · M. L. Filippi · M. Cantonati

Abstract Water-level fluctuations (WLF) often represent one of the greatest impacts on the development of lake ecosystems. In the year 1931, the Trentino Hydroelectric Company (SIT) requested the hydroelectric use of water bodies in the Upper and Middle Sarca basin. The largest and deepest lakes were dammed to increase lake volume and exploited since mid 1950s. This research uses the sediment record of two small lakes in close proximity to each other (Garzonè and Serodoli) in northern Italy, used for hydroelectric power generation to determine the dependence of diatom-assemblage dynamics on WLF that have taken place over the last 60 years. Historical WLF are clearly reflected in the lithological composition and grain-size variations of the sediment cores. During the regression and transgression phases, the boundaries between the erosion, transport and accumulation zones fluctuated, causing redistribution of previously accumulated sediments, and their return into the lake's cycling of biogeochemical matter. The water-level changes not only caused distinct taxonomic shifts in the diatom communities, which were dominated by different species in the core sections of each lake, but also significant shifts in the composition of the diatoms' ecological, morphofunctional and life-form groups. Diatoms with a low- and high-profile attachment type were the dominant morphological forms in the upper core levels, where the most extreme fluctuations in water level had occurred. Increased turbulent mixing caused by WLF favours the presence of large, heavily silicified centric diatoms, while more stable levels would select for smaller centric diatoms through thermal stratification.

Keywords Water-level fluctuations · WLF · Resedimentation · Alpine lakes · Diatoms · Physiognomic groups

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Introduction

Water-level fluctuations (WLF) often represent one of the greatest impacts on the development of lake ecosystems, particularly on the trophic state, underwater light climate, plankton dynamics and littoral

development (Moos et al. 2005; Laird and Cumming 2008; Shuman et al. 2009; Wolin and Stone 2010). WLF alter lake morphometry and directly affect sedimentation, resuspension, and biogeochemical dynamics (Håkanson 1977). Sediment properties as mineral matter content and grain-size provide additional insight into lake basin processes (Digerfeldt 1986; Boyle 2001) and water-level changes indicative of the hydrological balance of lakes that can be altered in case of changes in this balance (Shteinman and Parparov 1997; Punning et al. 2004a). Even small fluctuations in water level may result in large changes in assemblages of aquatic vegetation and macrophyte zones (Tarras-Wahlberg et al. 2002; Coops et al. 2003; Punning et al. 2004b). Water movement in freshwater environments have an important effect on sediment composition, particle size and sediment dynamics in and around submerged macrophyte beds (Madsen et al. 2001). Therefore, sediment content—above all organic matter—can reflect a number of factors, including aquatic productivity, input of detritus from terrestrial vegetation and the flow of mineral matter into lakes.

Alpine lakes are a highly valuable resource. Focal points for tourism, they attract visitors who appreciate their natural beauty. These lakes have also been put to work—for hydroelectricity generation and water storage. Eleven lakes in the western, siliceous part of the Adamello-Brenta Nature Park were exploited for hydropower generation between the 1950s and 1991. One lake (L. Scuro al Mandrone) continues to be partially used to produce electricity for a mountain hut, and a second one (L. Serodoli) is still being used to provide drinking water.

Exploiting lakes in these ways has altered lake ecosystems, and their littoral zones are often the first to suffer the effects of WLF. This zone is particularly important in such high altitude oligotrophic lakes, where the euphotic zone can reach a substantial part of the water column (O'Sullivan and Reynolds 2005). The littoral zone is a very dynamic region with high biodiversity and productivity, where important physical processes take place. Any significant change to a lake's level, whether spatial or temporal, will affect not only the lake's physical environment, but could also either affect individual plants and animals directly or populations and communities through ecological processes (Leira and Cantonati 2008). Direct effects on the biological communities include slumping, which can impact on terrestrial and aquatic vegetation, and displacement of the shoreline, thus changing the zones affected by wave activity. Indirect effects include the reworking of substrates and alteration of the type and vertical zonation of vegetation around the edge of a lake, as this vegetation is dependent on the type of substrate as well as exposure to waves and water-level range. Moreover, in clear-water lakes, which have potentially large areas suitable for the growth of benthic algae, a substantial part of the photosynthesis occurs in benthic algal communities. It follows that any activity that affects the littoral zone can have a significant ecological effect.

The composition and structure of lake sediments enable us to reconstruct the influence of extreme changes in water levels on lake ecosystems, and to provide a prognosis for lake evolution under changing environmental conditions. Given the scope of the study, we targeted the high mountain lakes of the Adamello-Brenta, as many of them have been involved in a huge hydroelectric project (Betti 2003). Lakes Garzonè and Serodoli were selected for this study (Fig. 1). Both were dammed to increase lake volume for hydroelectric power generation, although only the latter is still exploited for drinking water supply. The objective of our study was threefold: (1) Define the pre-impact ecological reference conditions for those lakes that have been subjected to alteration; (2) Assess how current and past water level fluctuations have influenced the diatom community for selected lakes; and (3) Compare diatom life forms and morphofunctional groups.

Environmental reconstructions based on a single-core study are often inadequate because changing bathymetry and WLF result in highly variable sedimentation. Digerfeldt (1986) advocated transects of coring sites from shallow to deep water. We applied the transect method to examine at least two sediment cores from each lake, one from the deepest part and the other from a shallow area close to the shore.

Site description

The Adamello-Brenta Nature Park is a protected area of about 600 km^2 in NE Italy (Fig. 1). It comprises two mountain ranges with contrasting geology: the Adamello Massif formed by crystalline rocks, such as granites and tonalites, and the Brenta Massif, made up of sedimentary rocks (Cantonati et al. 2002). In the

Fig. 1 Map of Italy (**a**) showing the location of the Adamello-Brenta (**b**) Park boundaries (**c**), and bathymetries of the Serodoli (**d**) and Garzoné (**e**) lakes, with location of the gravity cores
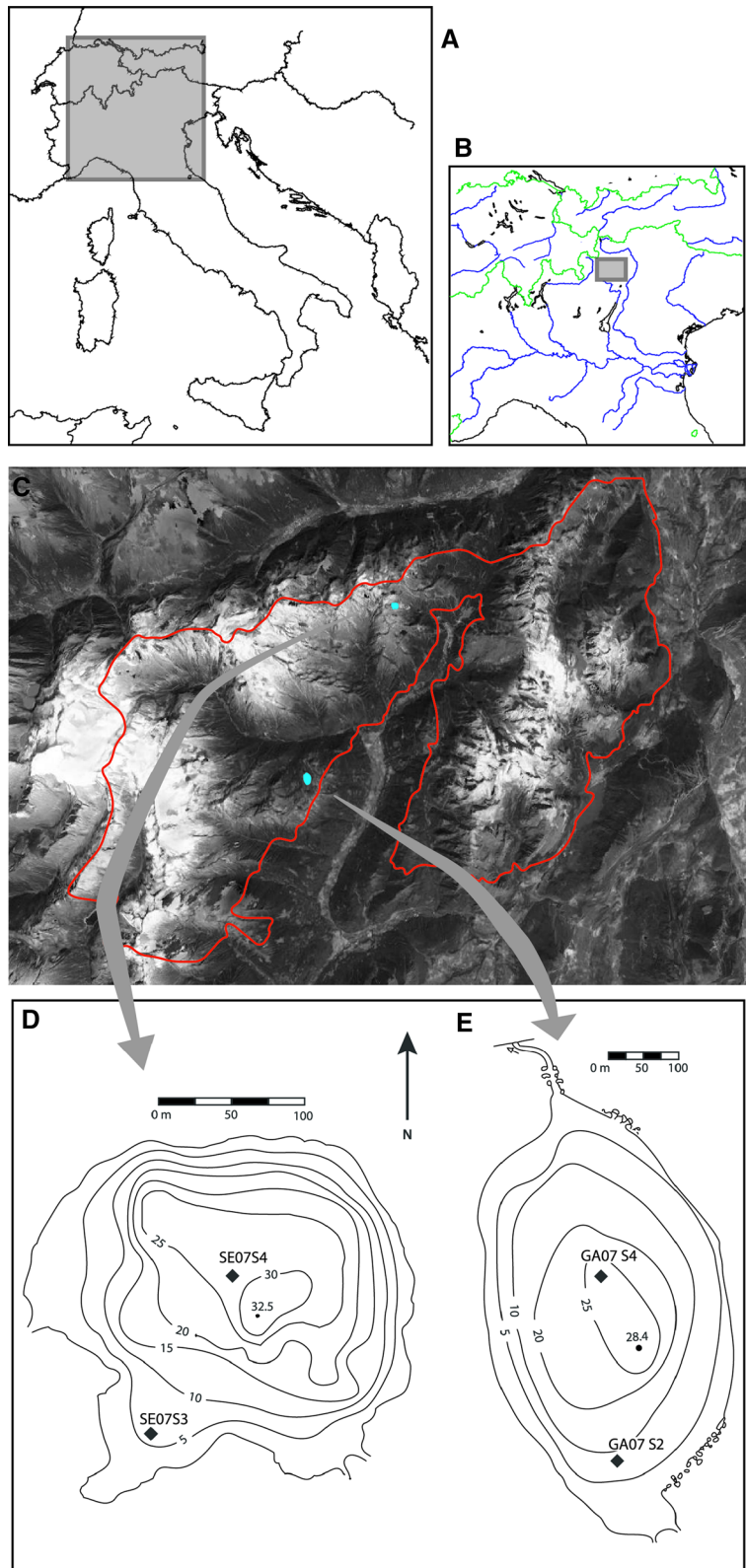
Adamello-Presanella mountain range high mountain lakes are only found in the western part of the park. Few specifically limnological studies of lakes have been undertaken in this district (Baldi 1932; Zucchelli 1952; Cantonati et al. 2002; Corradini et al. 2005; Tardio et al. 2005). Most of the lake surveys have been carried out as part of general limnological investigations devoted to broader areas within the Italian Alps (Tonolli and Tonolli 1951; Tomasi 1962; Giussani et al. 1986). For this reason the primary objective of our research project was to select two high mountain lakes for a paleolimnological study, based on a first screening and morphological assessment of lakes in the park that were exploited for hydroelectricity generation.

The two lakes are located above the tree line (1,940–2,371 m a.s.l., Table 1) in landscapes dominated by rocky outcrops, slope debris, grassland and shrub patches, in various proportions depending on altitude and substratum. The lakes are of glacial origin and have a median catchment area of 1.6 km^2. Lake area ranges from 6.5 to 10.7 ha and lake depth varies between 27 and 33.2 m (Cantonati et al. 2002).

The hydroelectric plant of S. Massenza, now the ENEL (Ente Nazionale per l'energia Elettrica), was built after the end of the Second World War, mainly between 1948 and 1957, under the initiative of the hydroelectricity company Sarca Molveno (SISM) (Betti 2003), following a project on the Sarca river basin. Lakes Toblino and S. Massenza are the centre of

Table 1 Limnological and geomorphological features of lakes Garzonè and Serodoli (Cantonati et al. 2002)

Limnological and geomorphological parameters	Garzonè	Serodoli
Latitude (N)	46°08′34″	46°14′54″
Longitude (E)	10°42′20″	10°46′48″
Altitude (m a.s.l.)	1,940	2,371
Length (m)	575	352
Width (m)	265	305
Maximum depth (m)	27	33.2
Mean. depth (m)	12.1	15.0
Lake area (ha)	10.7	6.5
Lake volume (m^3)	1,400,000	9,65,000
Catchment surface (ha)	172	145
Lithology	Granite	Granite and tonalite
Secchi depth (m)	15	12.5
Tempeature (°C)	9.5	5.8
Oxygen (%)	74	96
pH (20 °C)	6.2	6.0
Conductivity (µS cm^{-1})	20	11
Alkalinity (µeq l^{-1})	93	42
Ca^{2+} (mg l^{-1})	2.3	1.2
Mg^{2+} (mg l^{-1})	0.2	0.1
Na$^+$ (mg l^{-1})	0.5	0.2
K$^+$ (mg l^{-1})	0.3	0.2
SO$_4^{2-}$ (mg l^{-1})	2.5	1.3
Cl$^-$ (mg l^{-1})	0.3	0.5
SiO$_2$ (mg l^{-1})	3.0	1.6
N–NO$_3^-$ (µg l^{-1})	187.2	178.9
N–NH$_4^+$ (µg l^{-1})	23.2	<20
P–PO$_4^{3-}$ (µg l^{-1})	2.0	1.6
TP (µg l^{-1})	8	4
TDS (mg l^{-1})	12.7	7.2

Limnological variables were measured once a month for water chemistry during the open-water season between 1996 and 1999 (March–October). In the winter of 2006–2007 the lakes were sampled once approximately from the same location

this massive hydropower system, which diverts waters at a high altitude (in the headwaters of the Sarca basin) and collects them in Lake Molveno, which was transformed in its turn into a hydropower reservoir. These waters, along with the residual flow coming from the middle course of the Sarca (Dam Bridge Pià) are whirled at the hydroelectric plant of S. Massenza and discharged into the lake of the same name, after which they flow into Lake Toblino. Next, they arrive at Lake Cavedine through the Rimone canal, feeding the resorts of Fies and, further downstream, Dro, and finally arriving at the resort of Torbole sul Garda.

High altitude lakes were modified by artificially increasing either their volume, with damming, or their watershed, by means of water diversion. This complex of lakes between the Val di Genova, Val Nambrone and Val Nambino (located at altitudes between 1,900 and 2,700 m a.s.l.), has been affected by water being piped out during the winter, so as to increase the water volume discharged into the major bypass at the Val di Genova basin.

The environmental impact of these operations has been, at times, very intense (Table 2). The effects were particularly great during construction work in the mid-1950s, owing to the misuse of bypasses (between 1955 and 1995), and continue to this day because the dams and pipes that were put in place still exist. During construction of the tunnel for the water-diversion pipe under Lake Serodoli in 1954, the lake floor collapsed and 700,000 m^3 of water poured out of the lake, reaching the tourist area of Madonna di Campiglio, where several hotels were damaged (luckily the accident didn't cause victims). The project therefore made enormous changes to the ecosystem—particularly in the high-altitude lakes—which led to the disruption of their naturally highly stable physical and ecological setting, changes to plankton cycles and

to the entire food web, and the reduction or extinction of fish populations that were of great interest from the natural history standpoint.

Materials and methods

Sediment coring

Field observations and sediment coring in Lakes Garzonè and Serodoli were performed through winter ice in winter 2007. Coring was performed using a gravity corer (Aquatic Research Instruments; http://www.aquaticresearch.com/universal_core_head.htm).

Sediment description was based on sedimentological features visible to the naked eye, using terminology proposed by Schnurrenberger et al. (2003) and plates of Munsell colours (1954), with the preparation of some smear slides to increase detail.

A total of two sediment cores were extracted from each lake, one core from the centre of the lake and a second one from a more littoral position (Table 3). Water depth was measured at each sampling location. Cores were split in the lab for sedimentological description. One half was archived while the other was used for sediment subsampling. Subsampling was done in the laboratory prior to the analysis, in 1 cm sections. All samples remained refrigerated in the dark until they could be analysed.

Dating

Chronological control in the current research is based on radiometrically determined sediment accumulation rates (Robbins et al. 1978) of the deep water cores. Relative concentrations of ^{210}Pb (a naturally occurring isotope) and ^{137}Cs in 10–14 sediment samples per core

Hydrological features	Garzonè	Serodoli
Dam heigth (m)	1	3
Altitude after artificial damming (m a.s.l.)	1,941.5	2,370.0
Volume after artificial damming (m^3)	1,400,000	965,000
Piped volume (m^3)	1,280,000	890,000
Altitude after maximum piped (m a.s.l.)	1,920.5	2,347.0
Maximum piped volume/total volume (%)	91.43	92.23
Pipe diameter (cm)	200	200
Year of construction	1954	1954

Table 2 Principal characteristics of the hydrological management of lakes Grazonè and Serodoli (Betti 2003)

Table 3 List of cores taken at lakes Garzonè and Serodoli

Core ID	Longitude	Latitude	Water depth (m)	Core length (cm)
GA07 S2	46°08′26.19″	10°42′16.09″	8.4	8
GA07 S4	46°08′31.89″	10°42′15.85″	26.6	25
SE07 S3	46°14′52.08″'	10°46′38.00″'	7.6	10
SE07 S4	46°14′55.12″'	10°46′41.90″'	28.4	26

were determined by high-resolution gamma spectrometry (Appleby 2001). Sediment chronologies and accumulation rates were used to calculate age using the constant rate of supply (CRS) of ^{210}Pb model, and were verified using anthropogenic ^{137}Cs activity profiles. The supported ^{210}Pb was determined from concentrations of ^{214}Pb and ^{214}Bi in each sample. Levels of unsupported ^{210}Pb (^{210}Pb$_{excess}$) were then calculated as the difference between the total and the supported ^{210}Pb concentrations. Limited resources meant that only one core per lake could be dated in this way, so ^{210}Pb activities were only measured in the deep water cores. Chronological control was extended to other cores from the same lake by stratigraphic correlation using smear slide descriptions, visual assessment, and integration of mineralogical and grain size data, and bulk density properties. Samples for chronological control were dated in the Institute of Physics at University College Dublin (Ireland).

Sediment analysis

Wet sediment density and percentage water (as dry weight density) were determined from the weight of known volumes of fresh sediment samples after drying the samples in the oven at 50 °C for 72 h. Organic content (loss on ignition, LOI, measured at 1 cm intervals) was determined using standard procedures (Heiri et al. 2001). The porosity of the sediment was calculated through the relationship between its wet bulk density and the wet-volume.

Samples from sediment cores were prepared for diatom analysis and treated using standard procedures (Battarbee et al. 2001). Samples were heated with 30 % H_2O_2 in a water-bath at 90 °C until all organic material was oxidised, then some drops of 10 % HCl were added to remove carbonates. The suspensions were mounted on glass slides using Naphrax (r.i. 1.74). At least 400–500 diatom valves per sample were counted along random transects under oil immersion using a ZEISS microscope at 1,000× magnification.

Diatom taxonomy follows Krammer and Lange-Bertalot (1988–1991). Nomenclature was updated using Round et al. (1990) and Hofmann et al. (2011). Diatom abundance was expressed as a relative percentage. Diatoms were classified according to two habitat groups: planktic and periphytic. Periphytic taxa in this study include all epilithic, epipelic, epiphytic, and shallow-water benthic life forms. Diatom growth morphologies were grouped into three ecological guilds, i.e. low profile, high profile and motile species, according to Passy (2007). The low profile guild comprises species of short stature, including prostrate (adhering to the substrate with the entire valve surface), adnate (apically attached but parallel to the substrate), erect (apically attached but perpendicular to the substrate), solitary centrics and slow moving species. The high profile guild encompasses species of tall stature, including erect, filamentous, branched, chain-forming, tube-forming, stalked, and colonial centrics. The motile guild includes comparatively fast-moving species from the genera *Navicula*, *Nitzschia*, *Sellaphora*, and *Surirella*. Diagrams were compiled using the C2 program (Juggins 2003).

Statistical analysis

Principal correspondence analysis (PCA) was used to identify the main patterns of variation in the diatom data, and to establish the direction and magnitude of changes in biological conditions at each coring location. Version 4.5 of CANOCO was employed (ter Braak and Ŝmilauer 2002). Prior to all analyses, diatom abundances were square-root transformed in order to stabilise variance, and rare species were down-weighted.

Finally, we tested the significance of the null hypothesis that there was no difference in the composition of the diatom assemblages between upper and deeper core sections, using a Monte Carlo randomisation procedure with 10,000 permutations.

Results

Lithological setting

Three sections can be identified in SE07S4 (Fig. 2a). The upper layers of sediment in Lake Serodoli, from 0 to 2 cm sediment depth, are regularly laminated light brown to dark brown topped by a thin layer of sandy silt. The basal section of the core (4 to 27 cm sediment depth) consists of homogeneous dark brownish silt. A relatively thick structureless sandy layer occurred between the two sections (2–4 cm sediment depth) consisting of a distinctive lighter layer with a transition to dark brown and graded similarly to turbidite layers. The SE07S3 littoral core is characterised by a uniform dark brown silt (0–3 cm sediment depth) (Fig. 2a). The mid-section (3–9 cm sediment depth) consists of sediment richer in organic matter and vegetation macroremains. The bottom of the core (9–10 cm sediment depth) is formed by a mineral greyish sediment with larger grain size.

The core stratigraphy at GA07S4 has been divided into two sections (Fig. 2b). The upper (0–7 cm sediment depth) is regularly laminated with thin layers of grey to greenish-grey, with vegetation remains and sand grains intercalated throughout. A thin layer of organic brown silt, very rich in diatoms, capped this section (0–0.3 cm sediment depth). The second section, from 9 cm to at least 25 cm, consists primarily of diatom ooze and vegetation macroremains (9–10 cm sediment depth) with sand grains scattered throughout. A small layer (7–8 cm sediment depth) of organogenic micaceous sand topped the second section. The upper layers of the littoral core taken at Garzonè (GA07S6) consist of a homogeneous dark brown silt (0–1 cm sediment depth) (Fig. 2b), with intercalated layers of irregularly stratified sand with subangular feldspar grains (1–4.5 cm sediment depth) and plant fragments (a 4.5 cm piece of bark, a pine needle at 5 cm sediment depth). Below, from 5 to 7 cm sediment depth the core consists of a greyish brown silt.

Chronology

^{210}Pb chronology for SE07S4 core (Serodoli)

The unsupported ^{210}Pb (^{210}Pb$_{excess}$) activity versus depth profile shows a clear irregularity at about 3.5 cm (1.49 g cm^{-2}), characterised by a virtual absence of $^{210}Pb_{excess}$ (Table 4). This type of irregularity in the ^{210}Pb$_{excess}$ profile has been reported in other European mountain lakes by Appleby (2000), and can be interpreted as evidence of an episodic event, possibly associated with slumping from the catchment or from the margins of the lake. Application of the CRS model to the profile measured suggests that the topmost 3 cm of the core (corresponding to a cumulative mass of 1.18 g cm^{-2}) contain sediments deposited over 60 ± 10 years prior to sampling. Considering that the date of sampling was 2007, this dates the 3 cm horizon to ~1,947, and suggests a date for the episodic event at around this time. Below ~4 cm, ^{210}Pb decreases monotonically, reaching supported levels at a depth of ~8 cm. This represents the ^{210}Pb dating horizon, corresponding to ~1,865. Apart from the episodic event, sediment accumulation rates for each of the layers, based on the application of the CRS model, are low and relatively uniform, with values ranging between 0.006–0.032 g cm^{-2} year^{-1} (0.05–0.12 cm year^{-1}). These values are in good agreement with those reported for other European mountain lakes (Appleby 2000).

Independent validation of the ^{210}Pb$_{excess}$ chronology is provided by the ^{137}Cs profile. The bulk (99 %) of the inventory for this nuclide is contained in the top 3 cm. This is consistent with the derived CRS chronology, which suggests that all ^{137}Cs fallout from atmospheric weapons testing and from Chernobyl should be contained within this depth range. Potassium-40 concentrations are quite variable throughout the profile, suggesting sediments of varying composition (^{40}K can be taken as an indicator of clay content).

The ^{210}Pb$_{excess}$ inventory in the core, at 2360 ± 130 Bq m^{-2}, implies a ^{210}Pb supply rate of 74 ± 4 Bq m^{-2} year^{-1}, which is in excellent agreement with measured direct deposition values at mid-latitude sites. The ^{137}Cs inventory, at ~7100 Bq m^{-2}, is within the range of values reported for other European mountain lakes (Appleby 2000).

^{210}Pb chronology for GA07S4 core (Garzonè)

The unsupported ^{210}Pb (^{210}Pb$_{excess}$) activity versus depth shows a steady decline in concentrations with depth. Supported ^{210}Pb (^{226}Ra) concentrations are reached at a cumulative mass of ~3.3 g cm^{-2} (12.5 cm) (Table 4). The ^{210}Pb$_{excess}$ inventory, at 7,900 ± 300 Bq m^{-2}, implies a ^{210}Pb supply rate of 250 ± 10 Bq m^{-2} year^{-1}. This is well in excess of the estimated atmospheric flux,
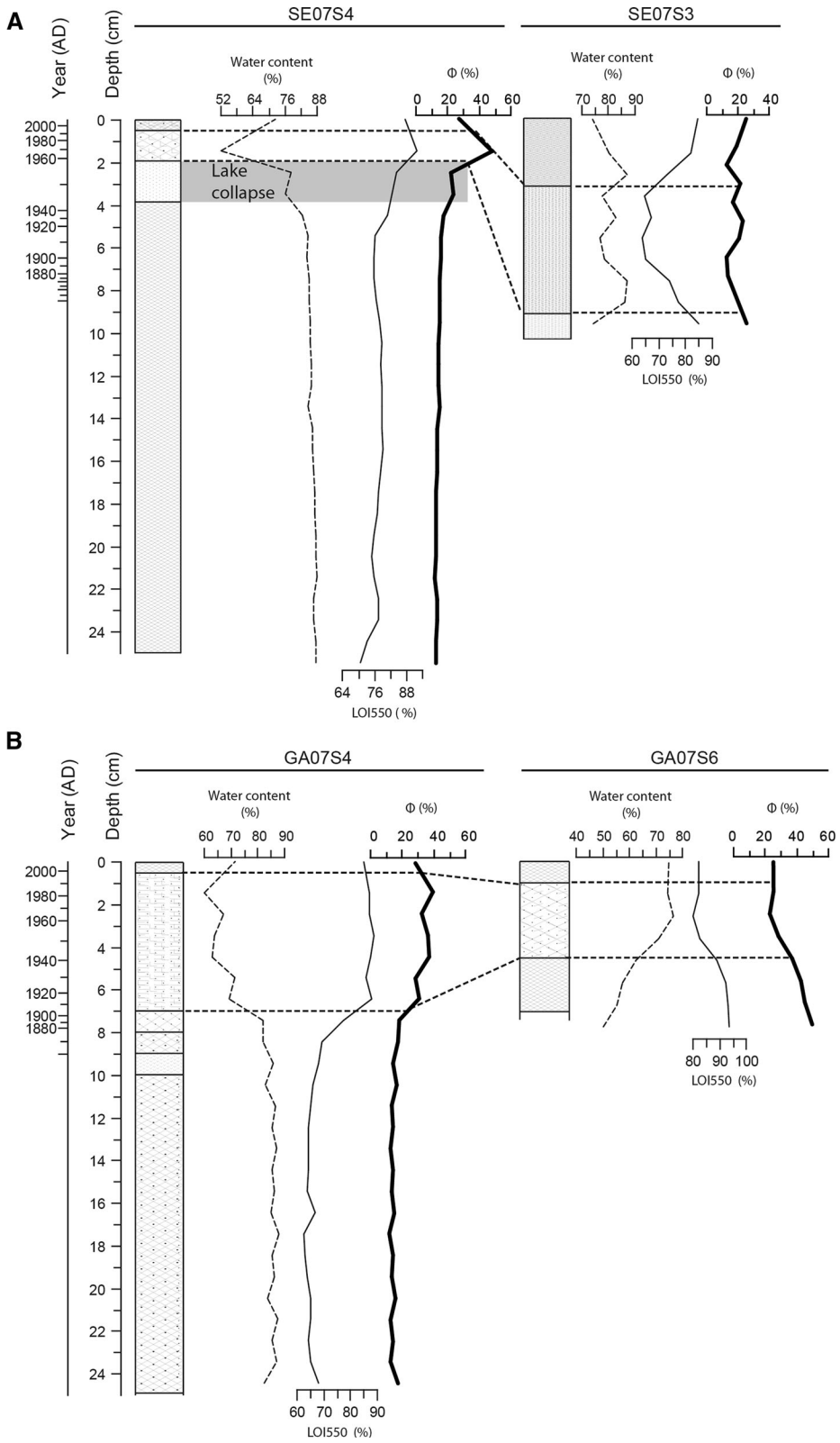
and implies either sediment focusing or significant inputs from the catchment. This is also reflected in the ^{137}Cs inventory which, at ~20,500 Bq m^{-2}, is much higher than that for the SE core. These values, however, are within the range obtained for other European mountain lakes (Appleby 2000).

Application of the CRS model to the measured ^{210}Pb$_{excess}$ profile yields an average sedimentation rate of 0.023 ± 0.010 g cm^{-2} year^{-1}, with values ranging between 0.016 – 0.049 g cm^{-2} year^{-1} (0.05–0.14 cm year^{-1}).

Independent validation of the ^{210}Pb$_{excess}$ chronology is again provided by the ^{137}Cs profile. The bulk (96 %) of the inventory for this nuclide is contained within the top 3 cm (0.93 g cm^{-2}), which is dated to 1956 by the CRS model. No distinctive peaks (weapons and Chernobyl) are apparent, with the highest ^{137}Cs concentration taking place within the topmost layer.

Water content and organic matter in sediment cores

The water content of the surface layers is 65–75 % in all cores, and increases with depth to near constant values of 75–90 %, except in GA07S6 where values are highest in the topmost layers and decrease downwards to values of 50 % (Fig. 2).

The LOI550 contents for cores SE07S3, SE07S4, and GA07S4 vary from 80 to 90 % in the top layers and from 60 to 70 % in the deeper parts of the cores, although at SE07S3 there is an increase below 7 cm (to a maximum of 85 %) (Fig. 2). The general trend of LOI550 in all the cores is rather similar: low organic matter concentration in basal layers, which is followed by generally constant values and an increase in LOI (80–90 %) in the surface sediment. The variation of LOI550 in core SE07S3 is different than in the other cores. The most obvious features are the high concentration in the bottom layers (90–100 %) and the gradual decline, attaining values of 80–90 % in surface layers.

Table 4 ^{210}Pbtotal, ^{210}Pbexcess, ^{137}Cs and ^{40}K concentrations in SE07S4 and GA07S4 core

Core	Depth (cm)	Activity concentration (Bq kg^{-1}, dry wt)				CRS date
		^{210}Pb$_{total}$	^{210}Pb$_{excess}$	^{137}Cs	^{40}K	
SE07S4	0.5	404 ± 18	372 ± 19	1279 ± 51	36 ± 6	1978
	1.5	140 ± 14	90 ± 15	366 ± 17	75 ± 10	1955
	2.5	80 ± 13	39 ± 14	86 ± 6	72 ± 11	1947
	3.5	31 ± 12	1 ± 13	19 ± 7	20 ± 13	1947
	4.5	119 ± 10	91 ± 12	12 ± 3	25 ± 7	1919
	5.5	61 ± 16	25 ± 17	ND	41 ± 13	1909
	6.5	59 ± 11	32 ± 13	ND	ND	1890
	8.5	44 ± 13	6 ± 15	ND	37 ± 14	1836
	12.5	49 ± 17	3 ± 18	ND	ND	1802
GA07S4	0.5	1386 ± 62	1201 ± 62	4950 ± 198	ND	1990
	1.5	744 ± 36	508 ± 37	1310 ± 53	ND	1973
	2.5	690 ± 35	400 ± 37	443 ± 22	ND	1956
	3.5	343 ± 18	90 ± 20	124 ± 6	ND	1947
	4.5	305 ± 17	94 ± 19	64 ± 6	ND	1935
	5.5	289 ± 16	110 ± 19	5 ± 1	ND	1922
	6.5	279 ± 20	70 ± 25	ND	ND	1906
	10.5	163 ± 12	32 ± 14	ND	ND	1873
	12.5	154 ± 17	12 ± 20	ND	ND	1860

Diatom analysis

Diatom assemblages in core GA07S4

Core GA07 S4 was taken from the deepest part of the lake and represents at least the last 200 years. Over 200 diatom taxa were identified in 22 subsamples from this core. Diatoms were present throughout the sediment core; on the basis of their distribution and composition two zones can be identified (Fig. 3a). The bottom diatom assemblages (7–22 cm) are represented mainly by planktic taxa (over 80 %) such as *Aulacoseira alpigena* (Grunow) Krammer, *A. valida* (Grunow) Krammer, *A.lirata* (Ehrenberg) Ross, *A. distans* (Ehrenberg) Simonsen and *A. ambigua* (Grunow) Simonsen.

The species composition changed markedly at a depth of 7 cm. Planktic diatoms decrease their dominance in the upper zone (0–7 cm), whereas benthic taxa become dominant, mainly as a result of the occurrence of *Pseudostaurosira brevistriata* (Grunow) Williams and Round, *Staurosira venter* (Ehrenberg) Cleve and Moeller, and small *Staurosirella pinnata* (Ehrenberg) Williams and Round. The percentage of benthic taxa rises to 80 %, and the species richness of periphytic taxa is higher. A variety of *Achnanthidium*, *Pseudostaurosira*, *Psammothidium*, *Staurosirella*, and *Stauroforma* taxa occur. Often, these species are found in shallow littoral areas. However, despite the decrease of the planktic component, several *Aulacoseira* species still occur and even increase slightly: *A. ambigua*, *A. lirata*, and *A. valida*.

Diatom assemblages in core GA07 S6

From core GA07S6, taken from the shallow littoral area (Fig. 3b), eight subsamples were analysed for diatom content. *Pseudostaurosira brevistriata* dominates the lower part of the diatom record but its percentage decreases. The proportion of other periphytic taxa such as *Karayevia suchlandtii* (Hustedt) Buktiyarova, *Naviculadicta schmassmanii* (Hustedt) Werum and Lange- Bertalot, and *Staurosirella pinnata* is also relatively high but decreases as well. Planktic *A. valida* also decreases in abundance towards the top of the core.

The number of planktic diatoms increases slightly in the uppermost part of the core (0–4.5 cm), although this part is also characterised by the dominance of periphytic diatoms. The percentage of *S. construens* Ehrenberg, *A. minutissimum* (Kützing) Czarnecki, and *S. pinnata* starts to rise and the planktic species *A. ambigua* and *A. lirata*, which prefer nutrient-rich waters, reach a peak.

Diatom assemblages in core SE07S4

From core SE07S4, taken from the central deeper area of the lakes, 25 subsamples were analysed for diatom content. Again, in the diatom diagram of the core, two diatom zones can be identified (Fig. 4a). The lowest part of the core (3–25 cm) is characterised by the individual dominance of the *Aulacoseira* planktic species. Benthic *Nitzschia perminuta* (Grunow) Peragallo and *Pinnularia isselana* Krammer were also found.

In the top of the core (0–3 cm) periphytic diatom taxa are more diverse. Major species are *Pseudostaurosira pseudoconstruens* (Marciniak) Williams and Round, *P. brevistriata*, and *Psammothidium marginulatum* (Grunow) Bukhtiyarova and Round. Above 3 cm, *A. alpigena* declines but other *Aulacoseria* species (*A. lirata* and *A. valida*) still occur and reach a peak.

Diatom assemblages in core SE07S3

Core SE07S3 was taken from the littoral part of the lake (Fig. 4b). *P. pseudoconstruens* dominates the lower part of the diatom record but its percentage decreases. Above 5.5 cm, however, it begins to decline in relative terms, and in the upper part of the core (0–5.5 cm) planktic diatoms such as *Aulacoseira lirata* and *A. valida* are dominant. The proportions of other periphytic taxa such as *A. minutissimum*, *Eolimna minima* (Grunow) Lange-Bertalot and Schiller, *N. schmassmanii*, and *Psammothidium* species are also relatively high, although they, too, decrease.

Samples from the deep cores in each lake were combined on the same PCA ordination plot to evaluate the main down-core differences in diatom assemblages (Fig. 5).

The PCA results revealed a clear axis of variation for both lakes, with 41.3 and 19.1 % of the variance explained by axes 1 and 2, respectively. PCA (Fig. 5) enabled us to identify the diatom taxa mainly responsible for the differences between the two lakes. Upper sediment samples (i.e. during hydroelectric exploitation) from Serodoli and Garzonè concentrated on the
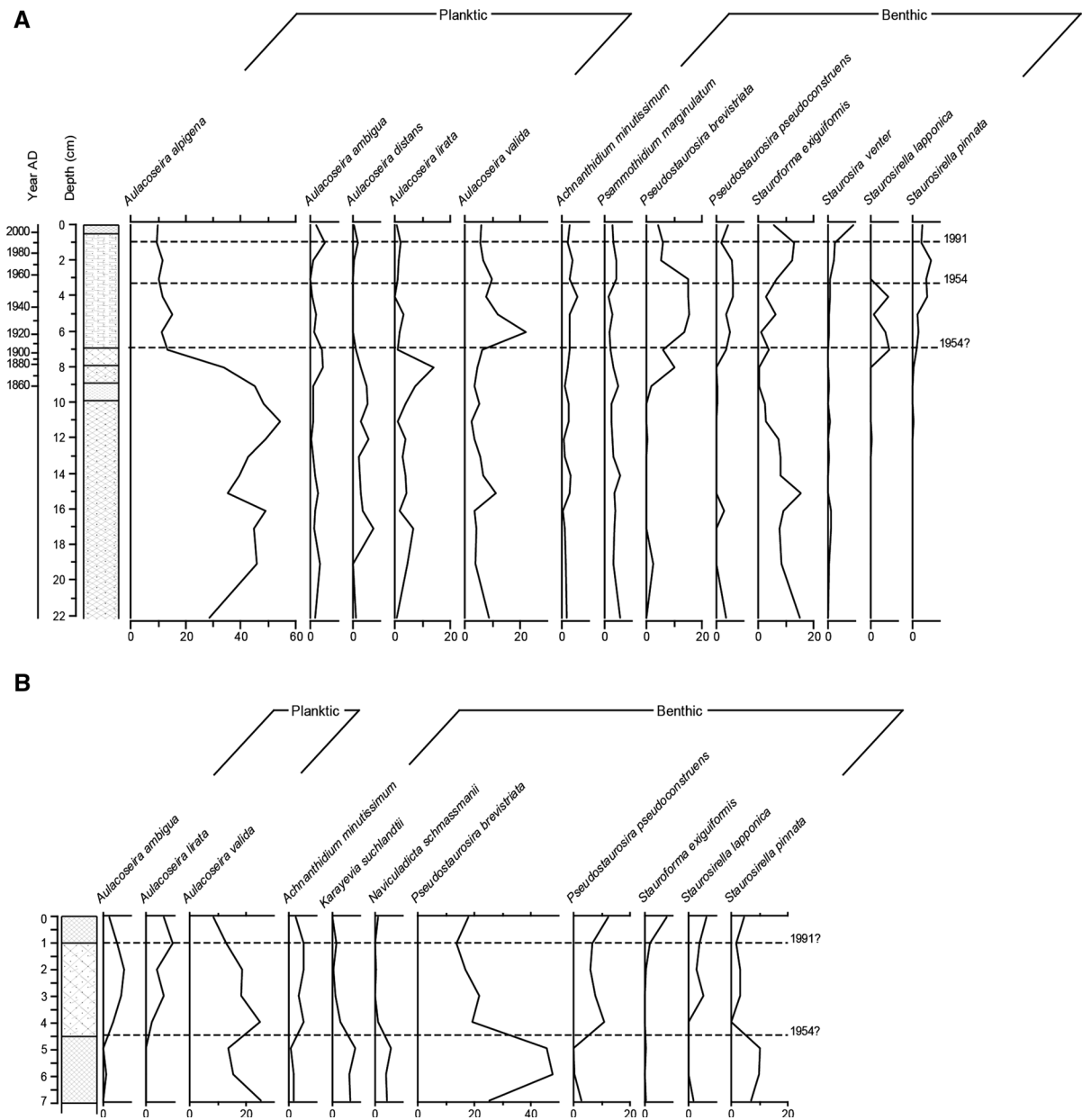
Fig. 3 Diagram of Garzonè deep (**a**) and littoral (**b**) cores and diatom zones. Relative abundances of major taxa are shown

upper left and right quadrants respectively. The changes followed similar trajectories from a planktic assemblage characterized by the presence of *Aulacoseira alpigena* to a periphytic assemblage (e.g. *Pseudostaurosira pseudoconstruens*, *P. brevistriata*), as is indicated by the upward-direction of the trajectory lines. The lakes had experienced important biological changes at a unique point in their recent history, indicating a clear change in ecological status when compared with the reference benchmark. In addition, in both cores, the close proximity of samples at the core top and bottom on the two axes reflects very similar diatom composition, thus providing support for the abrupt ecological change in both lakes in response to the increased WLF. The Monte Carlo permutation test indicated significant differences
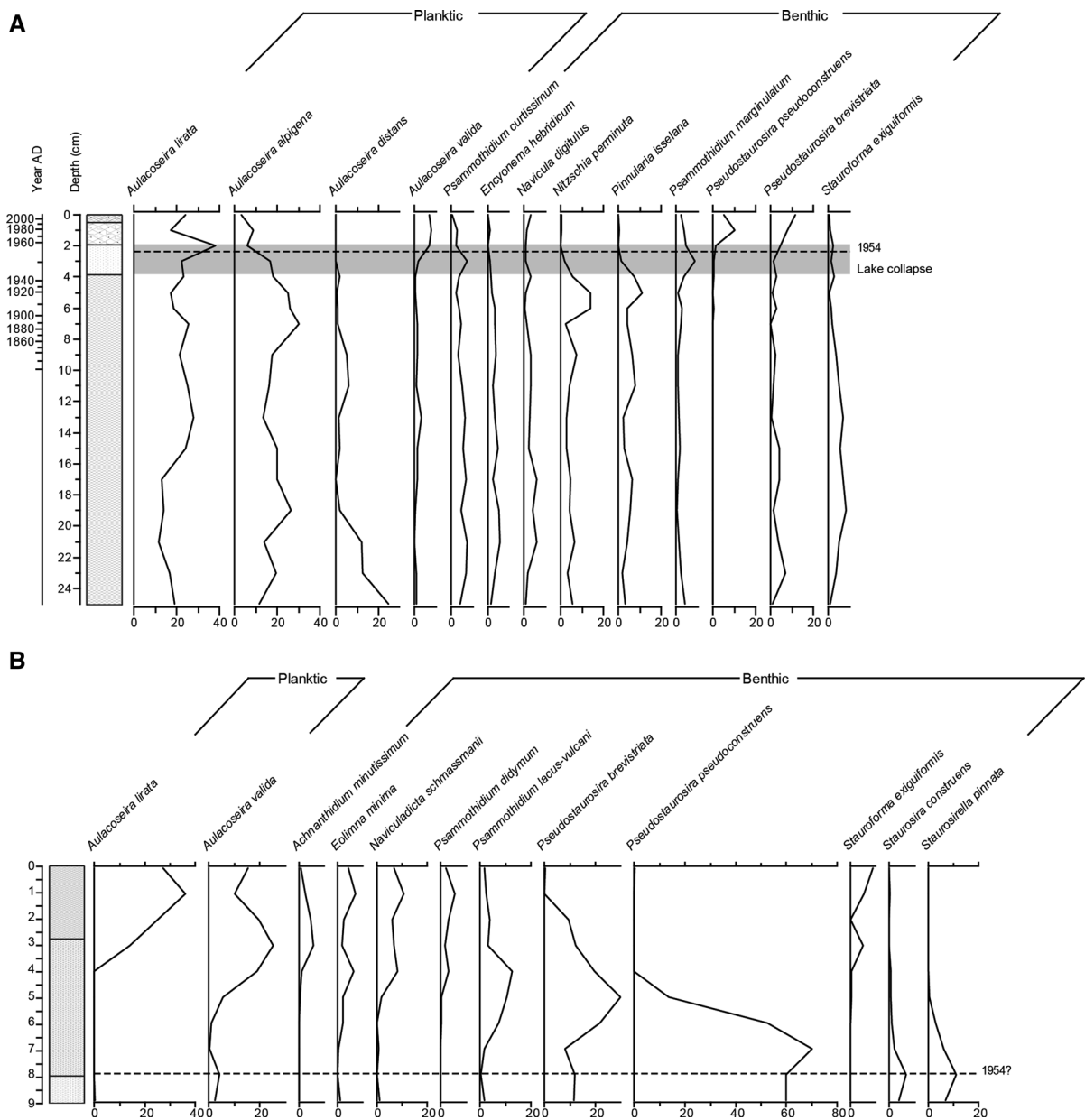
Fig. 4 Diatom diagram of Serodoli deep (**a**) and littoral (**b**) cores and diatom zones. Relative abundances of major taxa are shown

between the groups identified in the PCA ($p = 0.0028$).

This pattern was also determined by the variations of diatom morphofunctional groups and life forms. Planktic and benthic diatoms correlated with the first PCA axis (Fig. 6). Low- and high-profile benthic diatoms correlated positively with the first PCA axis and showed higher abundance in surface sediment samples. Small centric planktic and motile diatoms were, however, negatively correlated with the first axis, thus contributing to the complete separation between top and bottom samples from the two lakes. Large centric diatoms and motile diatoms are both correlated with the second PCA axis and appeared to be responsible for the complete separation of samples from the two lakes.
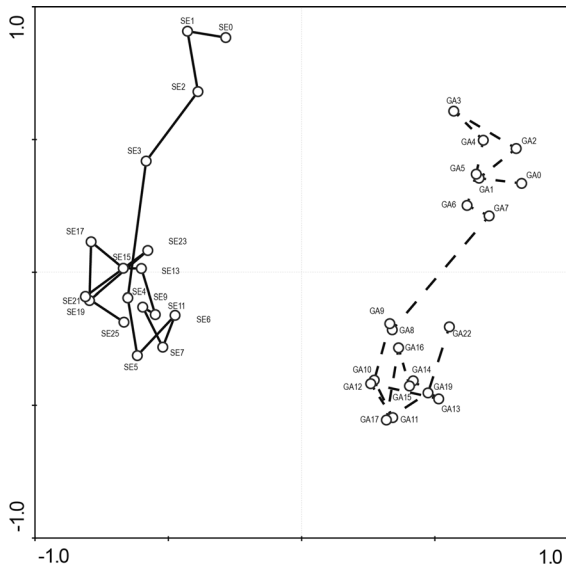
Fig. 5 Principal component analyses *PCA* sample plots for lakes Garzonè and Serodoli based on variability of diatom abundance and species composition in the study of sediment cores. Code SE refers to Serodoli and GA to Garzonè. The number indicates the depth of the sample analysed
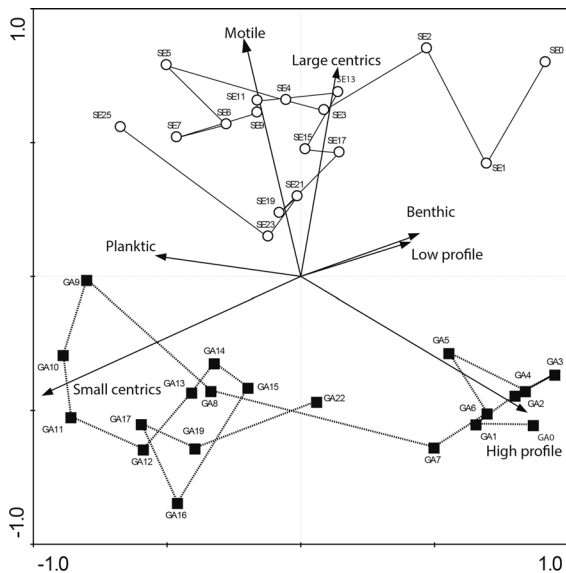

Fig. 6 Biplot of Principal components analyses *PCA* of the diatom life forms and morpho functional groups in the sediment cores of lakes Serodoli and Garzoné identified on the first two PCA axes. Sample codes as in Fig. 5

Discussion

Essential fluctuations in the lakes' levels took place immediately during the hydroelectric system's

construction and exploitation. These were characterised by intensive erosion and changes in the sedimentation regime. The LOI values and water content in the samples from the studied profiles showed clear shifts that may be related to changes in the distribution and composition of sediment as a response to water fluctuations. In fact, ^{210}Pb profiles reflect these changes in the lakes, so at least the tipping point of 1954 can be placed precisely. Application of the CRS model to the measured profile at Serodoli suggests that the topmost 3 cm of the core (corresponding to a cumulative mass 1.18 g cm^{-2}) contain sediments deposited over 60 ± 10 years prior to sampling. This dates the 3 cm horizon to ~1947, and suggest a date for the episodic event at around this time, corresponding to the 1956 lake collapse when they spike by several orders of magnitude. The ^{210}Pb chronology of the sediment record at Garzonè is in contradiction with the sediment records. Changes in sediment dynamics resulting from lake-level fluctuation strongly impact the apparent ^{210}Pb flux, leading to a mismatch between CRS ^{210}Pb chronologies and independently dated marker horizons, which suggests that changes in ^{210}Pb flux and the focusing of sediments caused by lake-level change have invalidated the dating model for this lake. The profiles for both ^{210}Pb (excess) and ^{137}Cs decrease rather quickly, indicative of a relatively low sedimentation rate, and relatively uniform throughout the core (around 0.02 g cm^{-2} year^{-1}), except for a significant increase (to 0.05 g cm^{-2} year^{-1}) at around 4 cm. Dating uncertainty increases substantially for dates older than ca. 1960, largely because of the high and somewhat variable values for supported ^{210}Pb. The date for the 6 cm layer, within the uncertainties, would match possible sedimentation increases in the 1950s as a result of hydrology changes, which we relate to the beginning of the exploitation period.

According to the descriptive and textural classification of the sediment records, three phases could be distinguished in the sedimentation process: (1) regression phase; (2) minimum lake level; (3) transgression phase. The regression of the lake has resulted in extensive erosion and redeposition of sediments, changes in the distance to the shore and displacement of the boundaries between the erosion, transport and accumulation zones. When water levels are low, wave action and precipitation runoff remove sediments from the upper part of the lake profile. During low-water periods, accumulated sediments originate from two

main sources: in-lake concurrently accumulated sediments (mainly from atmospheric input, influx from the catchment and autochthonous organic matter) and matter eroded from the near shore area, from which water has retreated in the course of regression. The eroded matter consists of fine-grain sands as well as previously accumulated lacustrine sediments. At the beginning of transgression, the flooding of the shores caused increasing shore erosion. Later, after the initial rise in water-level, the sedimentation regime stabilised and sediments became better sorted and finer in the direction of sediment transport. Thus, WLF were responsible for essential changes in the composition and structure of sediments and consequently in the biogeochemical matter cycling in the lake. In addition, the unstable LOI values in all cores (Fig. 2) suggested heterogeneity of the source material and depositional environment.

The comparative study of diatom patterns in these two lakes, at periods of different hydrology, enabled us to outline common ecological traits and differences between present day and reference conditions. The fact that these lakes were seriously modified as a result of hydroelectric exploitation contributes to a further understanding of the potential effects of hydrology-related factors on lake functionality. Changes to the lake level can have a dramatic effect on the distribution of organisms, and in extreme cases, where water depth and/or water clarity start to limit growth, certain species may be eliminated altogether. Norwegian studies have shown that lakes with WLF from 3.5 to 6 m suffered the complete eradication of all the main aquatic plant communities (Rørslett 1991). Moreover, the effects of large lake-level fluctuations on benthic communities can be passed on through the food web, and may thus trigger a cascade effect (James et al. 1998).

Long-term changes to lake-level fluctuations, and even some short-term changes (i.e. extreme highs or lows), are likely to lead to changes in habitats. Extensive water-level fluctuations, along with direct physical forcing, can constrain the size of the niche available to a particular biological community. Periphyton communities are generally very resistant and resilient to changes in lake level, particularly the taxa found in the upper littoral zone. The periphyton community most likely to be affected by low lake levels is the epiphytic. Three zones along the depth-distribution gradient have been defined for both

diatoms and total epilithic phytobenthos, using physiological, functional and community organisation parameters (Cantonati et al. 2009). The upper depth limit is set by disturbance, water level and wave action. The lower depth limit is generally a function of light availability (Schwarz et al. 1996, 2000). The mid-depth zone is characterised by high stability with favourable conditions for growth. The depth-distributions of these benthic diatoms may be used to explain the association of these taxa with the different core zones. Taxa occurring in the deep zone (e.g. *Staurosirella pinnata*, *Pseudostaurosira brevistriata*) have a preference for slightly higher trophic conditions, and are relatively tolerant of the poor light. This is reflected in their occurrence mainly in the upper part of the cores retrieved from the deepest part of the lakes, while they decrease in the littoral cores. *Achnanthidium minutissimum* is distributed throughout the depth gradient; this is reflected in their stability throughout the sediment record. *A. minutissimum* is also reported as a primary coloniser in disturbed environments (Peterson and Stevenson 1992; Hodgson et al. 1997). Being pioneer species, *Pseudostaurosira* are indicative of shallow waters, and tend to colonise the bottom sediment of open, shallow waters with unstable conditions of fluctuating physical or chemical characteristics. They are also commonly found growing around the stems of emergent plants (Griffiths et al. 2002).

Succession of *Aulacoseira* species can also be related to the water level changes experienced. The bottom sediment layers were dominated by *Aulacoseira alpigena*, a cosmopolitan species preferring oligotrophic lakes with low conductivity, while upper layers were dominated by the large *A. valida* and *A. ambigua*. Heavily silificated *Aulacoseira* spp. are common under conditions of increase turbulent mixing and silica content as well as low light conditions (Reynolds 2006; Kilhan et al. 1996), but since they are often associated with lake turnover, it is more likely the change in nutrient availability that's the more consistent control. Nutrients that remain in the hypolimnion are not available to the primary producers in the illuminated upper layers. Various processes related to WLF may lead to changes in diapycnal and boundary mixing and, thus, affect the upward flux of hypolimnetic nutrients and their supply into overlying water layers. These include boundary mixing (Imberger 1994; MacIntyre et al. 1999) and, at extreme water

level drawdown, also full mixing events (Naselli-Flores [2003](2003); Baldwin et al. [2008](2008)); or uplifting and mixing of the hypolimnion by large cold inflows that plunge under an existing hypolimnion (Vilhena et al. [2010](2010)). The presence of large diatom species with well-silicified valves during extreme water fluctuations may also reflect the potential influence of increasing nutrient levels with decreasing depth (Jonsson [1992](1992); Hawes and Smith [1994](1994)). *Aulacoseira ambigua* is common and widespread in shallow, moderately nutrient-rich lakes during periods of mixing and lower light levels. According to Houk ([2003](2003)), *A. valida* is a Nordic-alpine cosmopolitan species, relatively infrequent, occurring in dystrophic and oligotrophic lakes and pools. Mixed conditions are essential for the growth of large centric diatoms, while stable thermal stratification would select for smaller centric diatoms (Reynolds [1988](1988)), as the latter are able to perform better in lakes and reservoirs characterised by strong physical and chemical gradients (Reynolds [2006](2006); Clegg et al. [2007](2007)).

Water-level changes have not only brought about distinct taxonomic shifts in diatom communities, different species of which dominated in each lake's core sections, but have also generated significant shifts in the composition of the diatoms' ecological, morphofunctional and life-form groups (Fig. [7](7)). The low- and high-profile diatoms were the dominant morphological forms in the upper core levels, which suffered the most extreme fluctuations in water level. Water depth is a major factor that controls the processes of resuspension and redistribution of sediment. Compared to the motile diatoms, the low and high profiles displayed the strongest response to disturbance. Motile taxa increased in the lower levels of the core with water level stability. Birraphid motile diatoms are useful indicators of sediment since their shape and motility makes them able to exploit silted habitats. Differences in growth forms can lead to different assemblages, depending on the type of substratum. For example, stable rock surfaces favour attached (i.e. low profile) species such as *Achnanthidium* and *Gomphonema,* while less stable surfaces lead to different assemblages. Fine sediments favour motile species such as *Nitzschia* while sand grains bear a distinctive flora of attached diatoms such as *Staurosira*. The effects of drawdown rates (the speed at which the level of a lake is lowered) or ramping (the speed of rising water levels) on lake communities are likely to be very

important. Rapid drawdown rates (leading to rapid changes in water level) resulted in a poor water-column light regime and a substantial reduction in colonisable substrate. Pioneer species (low profile) that are able to colonise highly disturbed environments increase in quantity over time. These pioneers are subject to competition from other species until a disturbance removes most of the latter, allowing pioneer species to re-establish. Shifts in the proportions of benthic and planktic diatoms over time also indicate fluctuations in water level and retention (Søballe and Kimmel [1987](1987)). Low-profile ecological guilds (dominated by prostrate taxa) became more abundant in accordance with their expected resistance to increased scouring forces during drawdown. In these periods the communities are often dominated by low-profile diatoms like *Cocconeis* or *Cymbella* (Poff et al. [1990](1990)). The scouring stress of rapid drawdown rates may have also restricted the proportion of the high-profile guild (Biggs and Thomsen [1995](1995); Yangm et al. [2009](2009)). However, these forms may have the advantage of being able to survive and maintain themselves under the low light conditions caused by sediment resuspension and siltation while water levels are dropping. Increased turbidity and the dominance of a high-profile guild may indicate lower irradiances and increased shading, which would restrict the development of the low-profile guild.

The most important strength of the low-profile guild is its resistance to high scour. Under high erosion conditions, species in this guild were able to use irradiance more effectively than others. However, the direct access of the high-profile guild to irradiance enabled this guild to thrive better in a turbid environment than the other guilds despite its sensitivity to scouring. In contrast, the motile guild was positively associated with more stable water levels, which indicated finer sediments covering the lake bottom, as these would favour a higher relative abundance of this guild. The low resource availability, light conditions, and high disturbance prevented the establishment of a complex three-dimensional biofilm. This was beneficial for the high-profile forms, whose access to light from the water column was unimpeded. By contrast, although favoured by the high levels of disturbance, the low-profile guild underwent a significant decline in relative abundance, most likely as a result of shading within the biofilm. Shifts from generally low-profile species, i.e. single-celled,
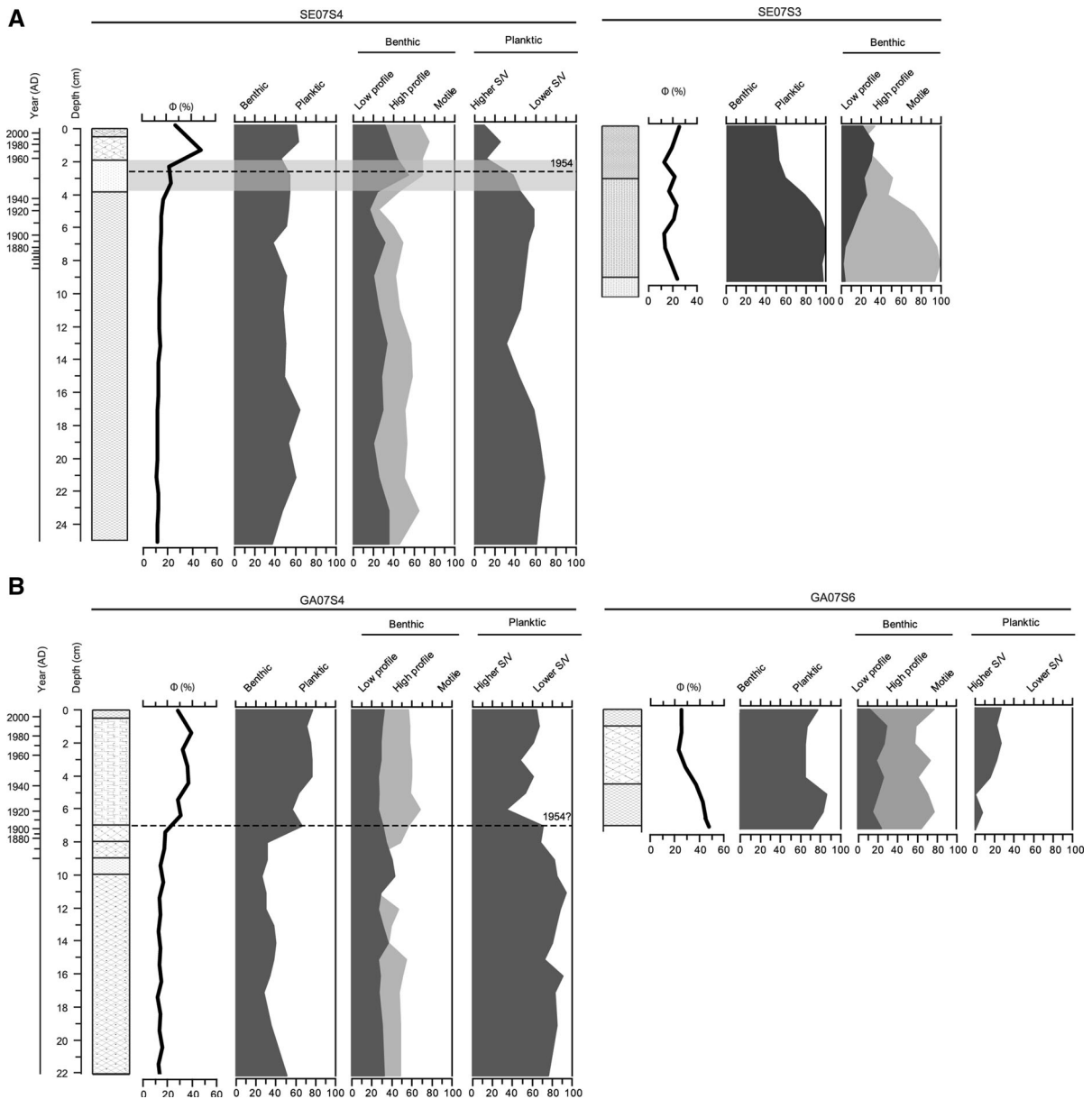
Fig. 7 Composite diagram plots against age showing sedimentary (sedimentary facies and grain size) and diatom (planktic/benthic ratio and diatom guilds) data for the Serodoli (**a**) and Grazoné (**b**) cores analysed in this study

prostrate, and erect to generally high-profile species, i.e. filamentous, chain-forming or large diatoms, were documented with the increase in light (Steinman et al. 1987; Steinman et al. 1989; Bourassa and Cattaneo 1998). However, this guild still showed high numbers. This is possibly a result of the complex nature of high-profile growth, as many representatives are colonial forms and, depending on local conditions, they may comprise multiple cells, thus possessing the tall stature

characteristic of this guild, or just a few cells, in which case they should be classified as low-profile species.

The variation among the three guilds across substrate grain size is also pronounced; e.g. the low-profile guild dominates the epipsammon, where it is significantly more numerous than in the other three habitats. The epipsammon is an inhospitable habitat where diatoms, mostly with short stature and a firm attachment, can withstand the abrasion

and physical damage from moving sand grains (Krejci and Lowe 1987; Round and Bukhtiyarova 1996). The high-profile guild is significantly more abundant in the epilithon and epiphyton, i.e. in habitats that are comparatively stable, less prone to dislodgement than the soft sediments and/or provide shelter from the drag (among the macrophyte leaves). The motile guild is significantly more numerous in the epipelon than in the other three habitats. Algae frequently get buried in the unstable epipelic substrates, so selection favours motile species (Bahls 1993). The instability and movement of the soft substrates can create enough disturbance to keep the motile guild in check and allow species from the other two guilds to establish viable populations. Disturbance is more severe in the epipelon, which is generally found in deep-water conditions. This can explain why motile guild diversity was significantly lower in the top of the cores, where the greatest range of water-level fluctuation took place. At the same time, the high-profile guild is favoured by macrophytes because they provide shelter from the damaging impact of water drawdown. This could explain the greater presence of high-profile diatoms in Lake Garzonè, which is at a lower altitude than Lake Serodoli and presents a better developed community of aquatic plants.

Conclusions

Lake-level fluctuations are responsible for essential changes in the composition and structure of sediments, and consequently in the cycling of biogeochemical matter in the lake, as well as for changes in diatom composition and ecological, morphofunctional and life-form groups. Diatom assemblages in the lower section of the cores were dominated by typical birraphid motile species and small centrics. The relative contribution of low- and high-profile and large centric diatoms, morphologically and physiologically adapted to growth in well-flushed and turbid environments, increased in the upper layers of the sediment record when the lakes were subjected to abrupt water-level changes. In summary, the response of the diatom assemblages to WLF can be used in interpretations of water-level changes in the past.

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