Assessing the ecological vulnerability of the shallow steppe Lake Neusiedl (Austria-Hungary) to climate-driven hydrological changes using a palaeolimnological approach

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ABSTRACT

Lake Neusiedl, the largest steppe lake in Europe, is particularly sensitive to climate variations due to its extreme shallowness (z_{max} = 1.8 m) and low ratio of catchment to lake area (3.5 : 1). Changes in water budget, salinity and turbidity have key implications for the lake's ecology and management. Here, we present a multi-proxy palaeolimnological reconstruction of the evolution of Lake Neusiedl since the end of its last complete desiccation (1865–1868), based on an undisturbed radiometrically dated core taken from the open water portion of the lake. Geochemical and biological (algal) proxies outline the succession of three major ecological stages since 1873 ± 16 yrs, with the first major changes appearing already in the 1930s as driven by climate related hydrological variability. Subfossil diatoms proved to be reliable for tracking long-term changes in the trophic conditions of Lake Neusiedl while diatom-inferred lake conductivity revealed to be unreliable due to a combination of lake environmental settings and the absence of a site-specific training set. Nonetheless, multivariate statistical analyses and comparisons with limnological data confirm a great potential of subfossil diatoms for revealing past ecological changes and tipping points of shallow lakes, as long as studies rely on a multi-proxy approach. In agreement with limnological surveys, the sediment record corroborates the high vulnerability of Lake Neusiedl, both in present and past times, towards climate-driven changes in water level and salinity, and allows the prediction, by analogy with the past, of future ecological changes in a context of global warming and increasing nutrient inputs from non-point sources.

Introduction

Lake Neusiedl, the westernmost shallow steppe lake of the Euro-Asiatic continent, is located on the Austria and Hungary border between the eastern Alpine margin and the Pannonian lowlands (Fig. 1). Due to its unique environmental settings, including high water salinity, turbidity, and extreme shallowness, Lake Neusiedl is crucial for both the nature conservation and the local economy, as it is valued for nature tourism and aquatic sports. Its shallowness and location in the semi-arid Pannonian plain make the lake particularly vulnerable to hydrological and anthropogenic disturbances. Lake Neusiedl is subject to various protection measures (Soja et al., 2013) and has been studied since the 1950s (Löffler, 1979). However, regular limnological surveys started only in the early-1980s after the deterioration of lake water quality originating from intensive agriculture, settlements and recreational activities during the post-war economic boom (Herzig, 2014; Herzig and Dokulil, 2001).
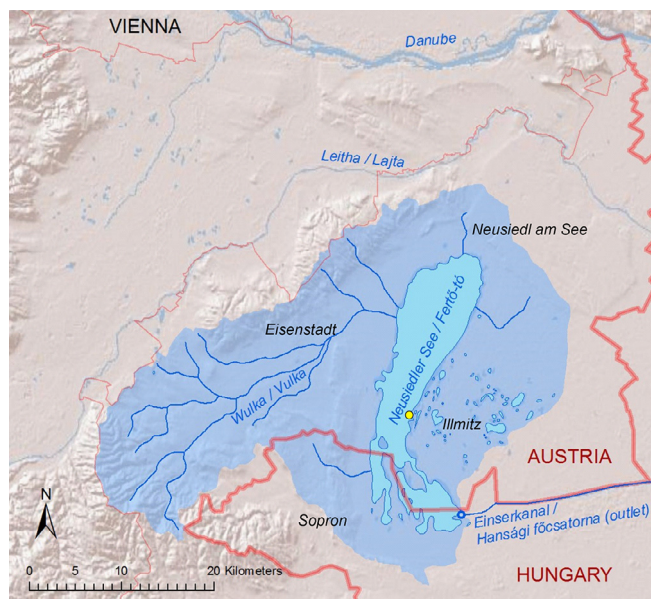

Fig. 1. Lake Neusiedl and its catchment (blue area). Blue lines: rivers and channels; red lines: regional (thin) and national (thick) borders; yellow bullet: coring site. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Data originating from decadal-scale monitoring, though crucial for short-term lake quality control and management, are hardly sufficient to provide the temporal perspective necessary to reconstruct lake evolution at a long-term scale, to define pre-disturbance lake reference conditions, and to predict lake ecological response to future human driven impacts (Battarbee et al., 2012; Jackson, 2007). Long term records are particularly important when considering effects of climate change on lake ecology, which are often complex, difficult to disentangle from other influences, and hard to generalize (Livingstone et al., 2010). Palaeolimnological investigations of deep lake sediments represent a powerful tool, in combination with limnological surveys, to close the knowledge gap between past and present lake conditions within the context of global change (Batterbee et al., 2005). In addition, the sediment-based definition of lake reference conditions preceding the beginning of major human impacts can sustain the setting of realistic lake quality targets within conservation or restoration actions. Sub-fossil diatoms represent one of the most reliable biological proxies to reconstruct past lake pH and trophic status (Battarbee et al., 2010; Hall and Smol, 2010). Moreover, their sensitivity to ionic concentration and composition makes them useful indicators to reconstruct past lake salinity and water level in relation to climate and hydrological conditions in a variety of freshwater to saline ecosystems on all continents (Fritz et al., 2010; Wolin and Stone, 2010).

The few existing sediment studies at Lake Neusiedl have been conducted in the undisturbed portions of its reed belt, or in the Hansag marsh area (e.g. Bobek et al., 1978; Gunatilaka, 1990; Löffler, 1991), where remnants of the old Pleistocene lake sediments still exist. An orderly sediment stratification in the open water area was considered not possible due to continuous wind-driven sediment resuspension (Löffler, 1979; 1991). However, sediment deposits within the reed belt are not representative of the open water lake, as the reed stands strongly affect local hydrological, chemical and biological dynamics (Dokulil and Herzig, 2009; Kogelbauer and Loiskandl, 2015).

Whilst a range of factors (such as wind-induced sediment resuspension, sediment–water interface mixing, bioturbation)

may complicate the use of sediment records from shallow lakes, the palaeolimnological approach can be successfully applied to such waters if coring location is carefully chosen, even with some analytical advantages (Smol, 2008). For instance, shallow, productive lakes typically have high sedimentation rates, which allow high resolution studies. Additionally, sediments of shallow lakes typically include abundant remains from littoral epilithic and epipelic assemblages that are commonly underrepresented in sediments of deep lakes (Bennion et al., 2010). These aspects may strengthen the interpretation of long-term lake ecological evolution.

Limnological research conducted during the last two decades provides increasing evidence that current global warming tends to exacerbate the responses of lakes to cultural eutrophication that include increasing hypolimnetic anoxia and nutrient release from lake sediments, accelerated nutrient recycling, and increased algal productivity (Salmaso and Tolotti, 2021). Though the overall lake response is difficult to predict due to complex interactions and the confounding effects of multiple stressors (Dokulil et al., 2010; Moos, 2012), it is now clear that climate change has the potential to adversely affect the objectives of good water quality defined by the international directives on water quality (Bennion et al., 2011), such as the European Water Framework Directive (2000). The effects of climate warming on lake ecological dynamics are stronger for extreme ecosystems, such as alpine lakes (IPCC, 2019; Psenner, 2003) and shallow lakes located in arid regions, where the combination of climate and hydrological regime exerts a strong control on the concentration of water solutes (Barone et al., 2010; Jeppesen et al., 2015; Ludovisi and Gaino, 2010; Padisák et al., 2006; Teubner et al., 2018a, 2020; Weyhenmeyer et al., 2019).

The study presented here aims at the palaeolimnological reconstruction of the ecological responses of Lake Neusiedl to environmental changes and anthropogenic disturbances since its last complete desiccation, in the late-19th century, based on open water sediment records. The responses of planktic and benthic microalgae to human-related changes in lake nutrient concentrations and water salinity are studied, and the potential and actual biases of open-water sediment studies in shallow lakes are discussed. A further objective is to look for evidence of interactions between chemical and trophic evolution and climate-related hydrological variability of Lake Neusiedl. Understanding the lake's response toward past natural and anthropogenic stressors can help in predicting its future vulnerability toward climate driven changes, and can point out critical aspects of the management of shallow lakes in semi-arid regions within the context of increasing human impact and changing climate scenarios.

Materials and methods

Study site

Lake Neusiedl, the largest Austrian lake, is an alkaline steppe lake situated at 115.5 m a.s.l. in an endorheic basin originated by a tectonic subsidence in the late Pleistocene, ~13000 years B.P. (Löffler, 1979). The lake catchment (1120 km^2) is only ~ 3.5 times larger than the open water lake area, and the lake water balance largely depends on local precipitation and evapotranspiration (Soja et al., 2013). Originally without a natural outlet, the lake experienced numerous desiccations and high-water events affecting an area almost twice as large as the present lake size. The last complete lake desiccation occurred in the period 1865–1868 (Herzig, 2014; Herzig and Dokulil, 2001). Since the construction of an artificial outlet and sluice (Einser Kanal) in 1965, and an agreement between Austria and Hungary, the annual lake level

variations over the last 50 years were limited to ± 50 cm only (Herzig, 2014; Löffler, 1979).

The lake is very shallow (z_{max} = 1.8 m), polymictic, and includes two different habitat types: a larger open water zone (~320 km²), which is turbid due to high amounts of wind-mixed suspended solids, and the reed belt (~180 km²), where the water is calm and humic. The open lake is characterized by low transparency (20–100 cm), large annual variations in water temperature (from 0 °C just under the ice cover to 30 °C in recent summers), high alkalinity (7.5 – 14.6 meq L⁻¹) and conductivity (1.3 – 3.2 mS cm⁻¹, Fig. 2a) values. Conductivity is mainly due to carbonates and bicarbonates combined with Ca and Na, the latter responsible for the definition of Lake Neusiedl as a soda lake (Weyhenmeyer et al.,

Fig. 2. Decadal key limnological data measured in Lake Neusiedl in the period 1983–2010 (1987–2010 for chlorophyll *a*). White circles: annual averages of lake water variables with standard deviations; black circles: values inferred from subfossil sediment diatoms. Average standard errors for DI-EC and DI-TP: 14.2% (13.1 – 14.5) and 22.8% (17.2 – 29.8) of the inferred values, respectively (Table 1). DI-EC and DI-TP values are discontinuous since not all years are represented in the studied sediment core due to sedimentation rates < 1 cm yr⁻¹ before 1991.

2019), and in minor proportion by sulphates (Herzig, 2014; Löffler, 1979). Changes in water turbulence and salinity modulate seasonal and inter-annual phytoplankton dynamics and periodic changes of species composition, while the high water turbidity is considered as responsible for frequent light limitation on phytoplankton growth (Padisák and Dokulil, 1994). Nevertheless, Lake Neusiedl suffered from cultural eutrophication from the late-1960s to the late 1970s due to nutrient load from sewage and agriculture (Dokulil and Herzig, 2009; Löffler, 1979). Annual average total phosphorus concentrations (TP) increased up to 180 μg L⁻¹ (hypertrophic level according to the Austrian legislation ÖNORM M6231 (2001)) and phytoplankton biomass doubled during this period (Fig. 2b, e). Restoration measures started in the early-1980s led to the reduction of the lake TP level down to 50 μg L⁻¹ (highly eutrophic status according to ÖNORM., loc cit.) in the late-1990s (Herzig and Dokulil, 2001). After a short-term increase in TP concentrations up to ~ 100 μg L⁻¹ in the mid-2000s, TP values decreased toward moderately eutrophic levels (ÖNORM, loc. cit.) around 2010 (Fig. 2b). Lake NO₃-N concentrations progressively increased up to ~ 270 μg L⁻¹ from the mid-1980s to the late-1990s (Fig. 2c), while the subsequent decrease was attributed to up-graded wastewater treatment practices since the early-2000s (Herzig, 2014; Fig. 2c, d). Recent investigations outlined a progressive increase in the annual nitrogen load from atmospheric deposition and intensive agriculture within the lake catchment (Soja et al., 2014; Spangl and Nagl, 2011), that is reflected by the slight increase in lake NO₃-N since the early-2000s.

Sediment coring and chronology

A 68 cm core was collected with a gravity corer (UWITEC, Austria) in August 2010 from the northern margin of the Bay of Illmitz (Electronic Supplementary Material (ESM) Fig. S1). This area of open water is protected from the NW wind by a narrow reed tongue that also reduces the sediment resuspension. The core was vertically extruded and sliced at contiguous 1 cm intervals while annotating the sediment visual aspect and texture. Subsamples were preserved in the dark at 4 °C until further analyses.

Sediment samples were analysed for ²¹⁰Pb, ²²⁶Ra, ¹³⁷Cs and ²⁴¹Am by direct-assay in the Environmental Radiometric Facility at University College London (UK), using an ORTEC HPGe GWL series well-type coaxial low background intrinsic germanium detector (Appleby et al., 1986). ²¹⁰Pb was determined via its gamma emissions at 46.5 keV, and ²²⁶Ra by the 295 and 352 keV gamma rays emitted by its daughter isotope ²¹⁴Pb following 3 weeks storage in sealed containers to allow radioactive equilibration. ¹³⁷Cs and ²⁴¹Am were measured by their emissions at 662 and 59.5 keV (Appleby, 2001). The absolute efficiencies of the detector were determined using calibrated sources and sediment samples of known activity. Corrections were made for the effect of self-absorption of low-energy gamma rays within the sample. Chronological data were calculated using the constant rate of supply (CRS) dating model (Appleby, 2001).

Lithology and geochemistry

Spheroidal carbonaceous particles (SCPs), a component of fly-ash that originate from the combustion of fossil fuels and have no natural sources, were investigated as an unambiguous proxy for industrial contamination. SCPs isolation and microscopic identification in the core from Lake Neusiedl followed the method by Rose (1994) that includes a sediment reference standard and an analytical blank in each digestion (Rose, 2008).

Sediment wet density (WD), water and organic content (OM, calculated from loss on ignition, LOI, at 550 °C) were determined at 1 cm intervals according to standardized methods (Dean,
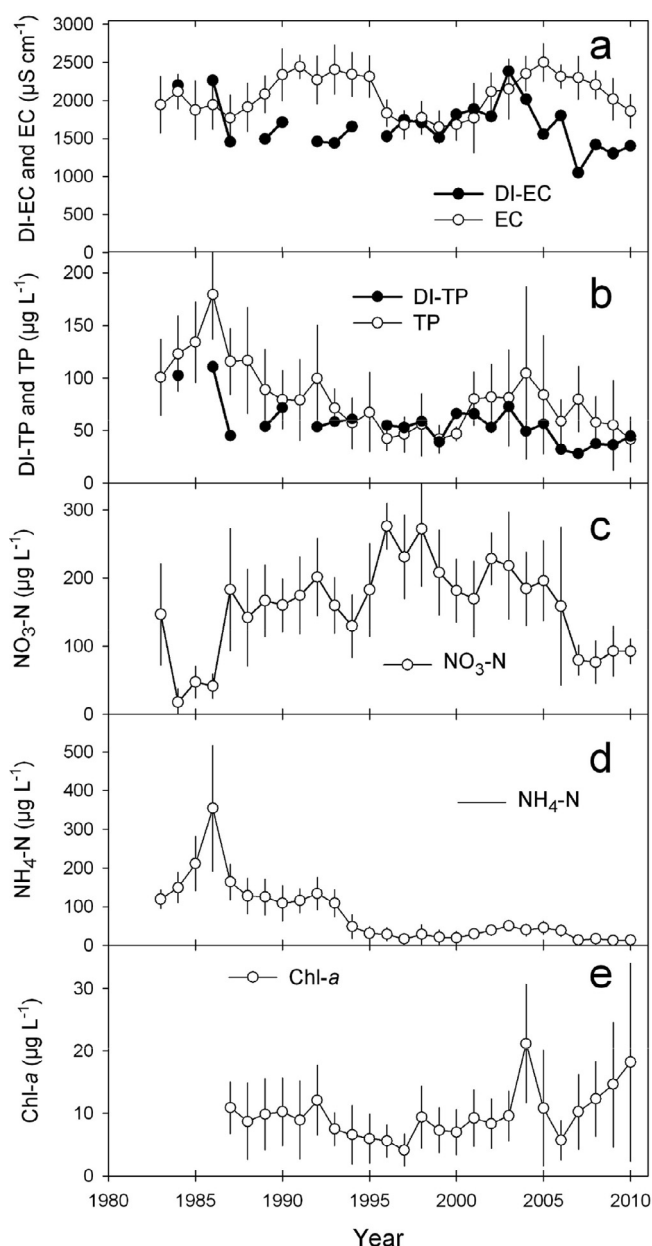
1974). Every second sub-sample along the entire core was analysed for percent weight of total carbon (Tot-C) and nitrogen (TN) with a Perkin-Elmer (Norwalk, CT, USA) PE2400 CHNS/O elemental analyser. Prior to C analyses samples were acidified to remove carbonates according to the "capsule method" described in Brodie et al. (2011), and the percent of inorganic C was calculated as the difference between total % C and the organic % C obtained after acidification.

Biological proxies

Sub-samples for pigment analyses (~3 g of fresh material, FW, weighted at the 4th decimal place) were extracted every four centimetres along the core. Concentrations of total chlorophyll derivatives and carotenoids relative to the organic matter content were determined spectrophotometrically according to Guilizzoni et al. (2011). The ratio of the extract absorbance at 430 and 410 nm provided information on the chlorophyll degradation in the studied core (Guilizzoni et al., 1992), while the concentrations of total carotenoids were used to reconstruct past lake TP level (Guilizzoni et al., 2011). The extracts were then analysed by High Pressure Liquid Chromatography (HPLC) in order to determine the concentrations of singular carotenoids, following the method reported in Milan et al. (2015).

Weighed sediment subsamples (~1 g FW, weighted at the 4th decimal place) for the analysis of sub-fossil diatoms were digested and mounted according to standard procedures (Battarbee et al., 2001). Diatom concentrations were estimated by adding to each cleaned diatom suspension 2.5 ml of a calibrated solution of divinyl-benzene microspheres (mean diameter of ~ 8 µm), and following the method reported in Battarbee et al. (2001). Diatom accumulation rates (DAR) were obtained by multiplying diatom concentrations by the sedimentation rates derived from the radiometric dating. For each sample, at least 500 valves were counted at 1000 magnification under a light microscope (Leica DM 2500, Wetzlar, Germany) equipped with Nomarski differential interference contrast. Diatom identification to the lowest possible taxonomic level was based on standard literature (Krammer and Lange-Bertalot, 1991a; Lange-Bertalot, 2001), integrated with literature on diatoms of European brackish waters by Germain (1981) and Witkowski et al. (2000).

Long term meteorological and limnological data

Long-term homogenized monthly air temperature and precipitation values for the station Eisenstadt-Sopron (~10 km distance from the lake, Fig. 1) for the period 1871–2007 were computed from the HISTALP, 2018 data set. Data for the period 2008–2010 were derived from the Austrian national weather service agency (ZAMG, 2018). Monthly average values of lake water level and temperature measured at the Biological Station Lake Neusiedl, Illmitz, since 1972 and 1991, respectively, were calculated from data provided by the Austrian Hydrographic Service (eHYD, 2018). The same service provided water level data measured at the bathing station Neusiedl am See since 1930 (Fig. 1), which were used to prolong datasets for Illmitz owing to the strong correlations between the two datasets (r = 0.992, p < 0.001, n = 39).

In situ data for lake water chemistry (1983–2007) and phytoplankton biomass and species composition (1968–2006), provided by the Biological Station Lake Neusiedl, Illmitz, rely on samplings at four open water stations close to the coring site. As the measurement frequency was mainly biweekly from spring to autumn and monthly in winter, the average for growing season (April to September) or year (January to December) was calculated by linearly interpolating at daily intervals and then averaging interpolated values over each calendar period for each year. Such an a-priori treatment of time series data is common in ecology and in particular in climate research (e.g. Jankowski et al., 2006; Livingstone, 2003) to overcome biased averages due to inconsistent sampling frequency, irregular sampling time intervals and missing values (Teubner et al., 2018a). Seasonal and annual average values were used to explore the correspondence between palaeo- and limnological data.

Data analyses

Ages and sedimentation rates, provided by the radiometric dating for discrete depths along the core, were interpolated by applying a locally weighted polynomial regression (LOWESS with tension = 0.5, run by the R.3.3.1. software (R Core Team, 2017),*vegan* package (Oksanen et al., 2017), in order to assign an age estimation to each sediment layer.

The binary logarithm-based Shannon Index (Shannon and Weaver, 1949) was adopted to describe the α-diversity of the sub-fossil diatom assemblages, as it does not overweight common and abundant taxa over rare ones (Morris et al., 2014). Ecological preferences of diatoms for lake phosphorus and salinity levels were determined according to Van Dam et al. (1994), as integrated with information on brackish taxa in Bogaczewicz-Adamczak and Dziengo (2003), Witkowski et al. (2000), Zieman et al. (2001). The Halobion Index (Zieman et al., 2001), was calculated for each sediment sub-sample based on the ratio between cumulative abundances of frequency classes of halophilous (including indifferent) and haloxenic taxa. Homogenous diatom zones along the studied core were identified by applying the CONISS method (Grimm. 1992), based on the sum of squares and optimal partitioning criterion, as implemented in the ZONE software (Lotter and Juggins, 1991). The comparison with the broken stick model (Bennett, 1996) identified the number of significant zones.

Non-metric multidimensional scaling (NMDS, Kruskal and Wish, 1978) was applied to a Bray-Curtis dissimilarity matrix on subfossil diatoms with relative abundance (RA) ≥ 0.5% in each sediment sample (Table S1). The NMDS analysis was performed with the R.3.3.1. () *vegan* package (). The function runs several NMDS with random starting configurations and stops after finding twice a similar minimum stress solution, which identifies configuration stability. A scree plot analysis provided the final number of NMDS dimensions to be considered according to Legendre and Legendre (1998). The relation between diatom changes in the sediment of Lake Neusiedl and independent environmental variables was explored by applying the vector and surface fitting procedure (R functions *envfit* and *ordisurf*, respectively, the latter based on a Generalized Additive Model, GAM) to the sample scores of the NMDS configuration. The 54 tested variables included independent and continuous sediment variables (e.g. sedimentation rate, organic, TOC, and TN content), and monthly, seasonal, and annual averages of air temperature and precipitations for the station Eisenstadt-Sopron since the late-19th century (HISTALP, 2018). The vector fitting procedure was applied separately also to the relative abundance of diatom ecological groups identified according to Van Dam et al. (1994)..

The relations between sample scores on NMDS dimensions D1 and D2 and a) discontinuous (i.e. SCPs and pigment concentrations) and diatom-derived sediment variables (e.g. Shannon and Halobion indices, DI-EC and DI-TP values), b) decadal-scale environmental and limnological data collected during the period 1968–2010 at the Illmitz sampling station, were tested through correlation analysis. Since each sediment sample integrates over several years, higher resolution limnological and meteorological data were averaged over each sediment sample time-span to provide a better comparison. The same approach was adopted in order to explore relations between inferred EC and TP values and decadal

environmental and limnological data collected from Lake Neusiedl since 1971, as well as between relative abundances/accumulation rates of key diatom taxa in the sediment samples and relative abundance/biovolume in the modern plankton samples (1968 to 2006). All variables, with the exception of pH and temperature values, and NMDS sample scores on D1 and D2, were log transformed (y = (log(x + 1)) in order to normalize the frequency distribution and reduce the variance within the data set. Pearson (r) or Spearman's rank order (ρ) correlations were selected by testing normality within the datasets with a Kolmogorov–Smirnov distance test. The significance was set at p < 0.05 and values were adjusted according to Benajmini and Hochberg (1995).

Diatom-inferred reconstruction of lake conductivity (DI-EC) and TP (DI-TP) levels were calculated using the software C2 (Juggins, 2007), and based on the training sets available in the European Diatom Dataset (EDDI, Juggins 2001, http://craticula.ncl.ac.uk/Eddi/jsp). For each sample, all diatom taxa occurring with relative abundance ≥ 0.5% were included in the computation independently on the number of their occurrences in the whole dataset (ESM Table S1). DI-EC was inferred based on the locally-weighted weighted average regression model (LWWA) with classical deshrinking applied to the Combined Salinity training set, which includes 387 samples from freshwater to brackish lakes in Spain, N and E Africa, and the Caspian region (Gasse et al., 1983; Gasse, 1987; Reed, 1998). DI-TP was inferred based on the weighted average (WA) regression model with inverse deshrinking applied to the Combined European TP training set, which includes modern samples from 477 European lakes (Battarbee et al., 2001). Training set models and deshrinking methods were selected based on the combination of high regression coefficients and low apparent and prediction errors that reflect the ability to estimate measured values and to predict values of the inferred variables, respectively (Juggins and Birks, 2012). The selected models were validated by comparing the inferred EC and TP values with limnological data recorded since 1983, and applying to the fossil diatom datasets the analogue matching technique (AM), based on squared chi-squared distances between each sediment sample and the five nearest modern analogues in the training sets used (Simpson, 2012).

Results

Sediment chronology

The equilibrium of total and supported ^{210}Pb is likely slightly deeper than the base (68 cm) of the core analysed (ESM Fig. S2a). Unsupported ^{210}Pb (i.e. naturally produced radionuclide derived from atmospheric fallout) activities show little net decline in the top 17 cm, suggesting an increased sediment accumulation in recent years. Higher sedimentation rates also occurred at 36.5 cm depth. Unsupported ^{210}Pb inventory is high (c. 18500 Bq m-2) in the core, corresponding to a mean ^{210}Pb supply rate of 576 Bq m^{-2} yr^{-1} (ESM Fig. S2b). This is higher than the atmospheric ^{210}Pb deposition flux in the region and suggests that the coring location was subject to sediment focusing. The depth profile of ^{137}Cs activity has a well-resolved peak at c. 40.5 cm (ESM Fig. S2c).

The chronology of the core covers the last ~ 140 years (ESM Fig. S3), i.e. the entire period after the last lake desiccation (1865 – 1868). The record starts in 1873 ± 16 yrs, when the refilled lake was already up to 2 m deep (Herzig, 2014). The CRS model places 1963 at 40.5 cm. This suggests that the ^{137}Cs peak was derived from 1963 fallout maximum from the atmospheric testing of nuclear weapons, and the use of the CRS model appears valid for this core. The recent ^{137}Cs inventory of the studied core is high

when compared to ^{210}Pb, thus suggesting a contribution from the 1986 Chernobyl accident. However, the fallout from this event was likely not sufficient to form a clear and separate peak at this site. The CRS model calculation indicates rather high sediment accumulations, which have gradually increased from the 1870s (0.18 g cm^{-2} yr^{-1}) to the present time, with a small peak in the late-1960s, and higher values in the last ten years (average = 0.50 g cm^{-2} yr^{-1}, ESM Fig. S3).

Lithology and geochemistry

The analysed core shows three major sections characterized by different macroscopic aspects: the upper 7 cm are composed of a liquid grey matrix including small reed remains. Between 7 and 42 cm the sediment becomes progressively more compact, while the mineral fraction (silt and sand) progressively increase from 43 cm depth to the core bottom that resembles a terrestrial sandy soil.

Contamination by spheroidal carbonaceous particles (SCPs) predates the base of the analysed core (Fig. 3), and concentrations slowly increase from the late-19th to the mid-20th century, and then more rapidly through to a peak of almost 3000 g DW^{-1} (dry weight) in 1977 ±2 yrs. The successive decline until 1990 is followed by a period of largely consistent SCP concentration through the most recent sediments. Peak SCP accumulation rates of 1120 cm^{-2} yr^{-1} (not shown) occur earlier (1968 ± 3 yrs) due to changes in sediment accumulation rate. Contemporary concentrations and fluxes are back at the level of the early-20th century.

Sediment water content is rather low throughout the core (Fig. 3), ranging from 30% of the wet weight at the core bottom to ~ 80% at the core top. Wet density is accordingly quite high in the deepest sediment layers (up to ~ 1.8 g cm^{-3}, Fig. 3), and gradually decreases to ~ 1.2 g cm^{-3} in the most recent layers. Organic content ranges between 8.6 and 25.7% of dry weight and shows a first increase from the sediment bottom to the mid-1920s, and a second in the layers deposited since the early-1990s (Fig. 3).

The percent weight of total carbon (Tot C) is ~ 4 times higher on average than total organic carbon (TOC, Fig. 3). After a consistent increase in the deepest sediment layers, Tot C only slightly increases towards the core top (i.e. 9.1%), while TOC shows somewhat higher values only during the 1950s. Percent weight of total nitrogen (TN) is particularly low in the deepest core section, and from the early-1960s to the mid-1980s, while values progressively increase up to ~ 0.45% in the recent decades. The values of the TOC: TN are correspondingly low (12–20) from the core bottom to the mid-1940s, show a pronounced increase in the section deposited from the late-1940s to the late-1980s (up to 80 in the late-1940s), and finally decrease down to < 10 in the top core section.

Biological proxies

The average ratio of absorbance at 430 and 410 nm (0.97) indicates a consistent degradation of chlorophyll *a* to phaeopigments, and both these pigments show negligible concentrations in the core section below ~ 20 cm depth (Fig. 3). With regard to the specific algal carotenoids, only fucoxanthin, a proxy for Heterokonta including diatoms, reaches concentrations around 20 nmol g LOI^{-1} in the uppermost core layers, while β-carotene, diatoxanthin (diatoms), zeaxanthin (cyanobacteria) and lutein (green algae) do not exceed 10 nmol g LOI^{-1}. All subfossil pigments show slightly increased values in the 1960s, a pronounced peak in the early-1990s and a gradual increase during the last two decades. The pigment fluxes (not shown) confirm the increase of pigment concentrations after 2000 as real, in agreement with the limnological data (Fig. 2e), and not as an artefact due the higher sedimentation rates in the top core section. Both the low concentration and the scarce
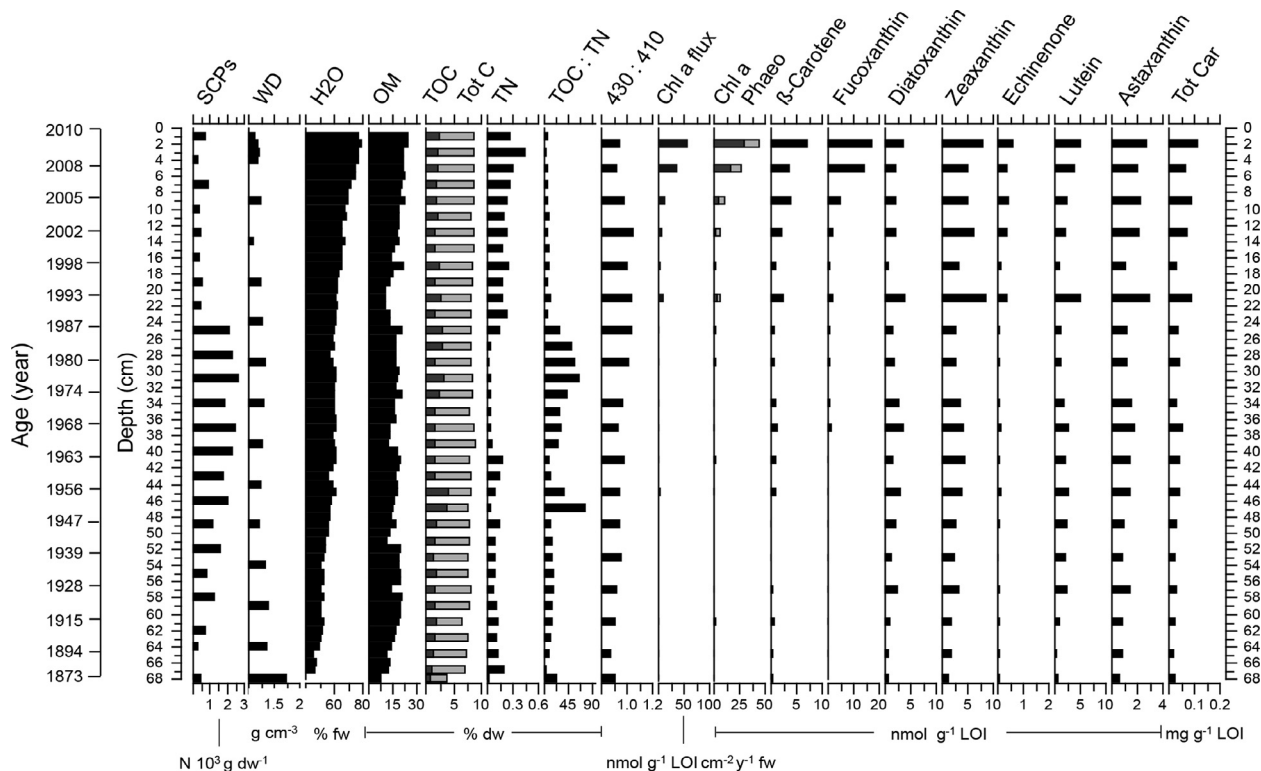
Fig. 3. Geochemical proxies and concentrations of sub-fossil pigments measured in the sediment core collected from Lake Neusiedl. SCPs: spheroidal carbonaceous particles; WD: wet density (x range from 1 to 2 g cm^{-3}); H$_2$O: water content (x range from 40% to 80%); OM: organic matter; TOC: total organic carbon; Tot C: total carbon; TN: total nitrogen; 430:410: ratio between spectrophotometric absorbance of pigment extracts at 430 and 410 nm; Chl a: chlorophyll *a*; Phaeo: phaeophytin; Tot Car: total carotenoid concentration; fw and dw: fresh and dry weight, respectively.

variability of total carotenoids (Tot Car in Fig. 3) prevent a reliable pigment-based reconstruction of lake TP according to Guilizzoni et al., (2011), as inferred values around 7 μg L^{-1} throughout the core are much below the range of variability of annual average TP concentrations measured in the lake water since 1983 (41–180 μg L^{-1}, Fig. 2b).

Identification of sub-fossil diatoms yielded 108 taxa mainly belonging to the fragilarioid and naviculoid groups (n = 19 and 17, respectively), and to the genus *Nitzschia* (n = 17). Diatom accumulation rates (average = 1.9 × 10^6 cm^{-2} yr^{-1}) show minimum values in the deepest 5 cm thick core section, and during the mid-1930s (Fig. 4). Pronounced DAR peaks occur between the early-1960s and the late-1980s (up to 35 × 10^6 valves cm^{-2} yr^{-1} in 1987 ± 2 yrs), while values stabilize around 10 × 10^6 valves cm^{-2} yr^{-1} during the last two decades. Diatom assemblages are particularly diverse at the core bottom and around 2005 ± 2 yrs (Shannon Index up to 3.9), while the index values remain between 1.2 and 3.2 (Fig. 4) in the core section deposited from the early-1930s to the late-1990s. The pattern of the Halobion Index is comparable with the depth profile of diatom diversity, thus suggesting that diatom assemblages richer in halophilous taxa were also more diverse (Fig. 4).

Benthic taxa (including numerous epiphytic and epipelic forms) dominate the diatom assemblages throughout the core, while planktic taxa, including mainly unicellular centrics and fragiloids, account on average for only 9% of the total diatom abundance (Fig. 4). Planktic diatoms reach higher proportions only during the 1930s (up to 50%), with *Cyclotella meneghiniana* Kützing and *C. radiosa* (Grunow) Lemmermann, and again in the first half of the 2000s (up to 23%), with *Fragilaria tenera* (W. Smith) Lange-Bertalot (Figs. 4 and 5). Benthic fragilarioids are strongly dominant in terms of relative abundance (Fig. 4), in particular *Staurosirella*

pinnata (Ehrenberg) Williams and Round, *Pseudostaurosira elliptica* (Schumann) Edlund, Morales and Spaulding, *P. brevistriata* (Grunow) Williams and Round, *Pseudostaurosiropsis geocollegarum* (Witkowski) Morales, *P.* cf. *punctiformis* (Witkowski, Metzeltin and Lange-Bertalot) Witkowski, Seddon and Pliński (Fig. 5) aggr. *Nanofrustulum sopotense* (Witkowski & Lange-Bertalot) Morales, Wetzel & Ector 2019. Relative abundances of non-fragilarioid benthic taxa never exceed ∼ 10% (Fig. 5). Taxa indicated by previous algological studies (e.g. Hustedt, 1959; Padisák, 1982) as characteristic or endemic for Lake Neusiedl (e.g. *Bacillaria paxilliphera* (O.F. Müller) Marsson, *Campylodiscus clypeus* (Ehrenberg) Ehrenberg ex Kützing, *Surirella peisonis* Pantocsek, *Triblionella hungarica* (Grunow) Frenguelli, *Cymbella hungarica* (Grunow) Pantocsek, *Hyppodonta hungarica* (Grunow) Lange-Bertalot Metzeltin and Witkowski, *Craticula halopannonica* Lange-Bertalot) show moderate to low relative abundance throughout the core, but are in general more abundant in the deeper core sections (Fig. 5 and ESM Table S1).

Diatom species composition and abundance identify six major significant zones along the core (DZ1-6), with D6 further divided in two subzones (Figs. 4 and 5).

DZ-1 (68–63 cm depth) includes the core section deposited during the ∼ 40 years after the lake replenishment in the early-1870s (Fig. 5). In the layer deposited just after the lake refilling, halophilous and brackish taxa (including *C. clypeus*, *Rhopalodia gibba* (Ehrenberg) Müller, *T. hungarica*, Fig. 5) account for ∼ 50% of the total diatom relative abundance and are responsible for the Halobion Index high values (Fig. 4). The most abundant taxon is *P. geocollegarum*, a small fragiloid diatom typical of lagoon environments at the lower part of the brackish water-salinity spectrum (Witkowski et al., 2000). This zone is characterized by comparably high proportions of oligo- to meso-traphentic taxa (Fig. 4).
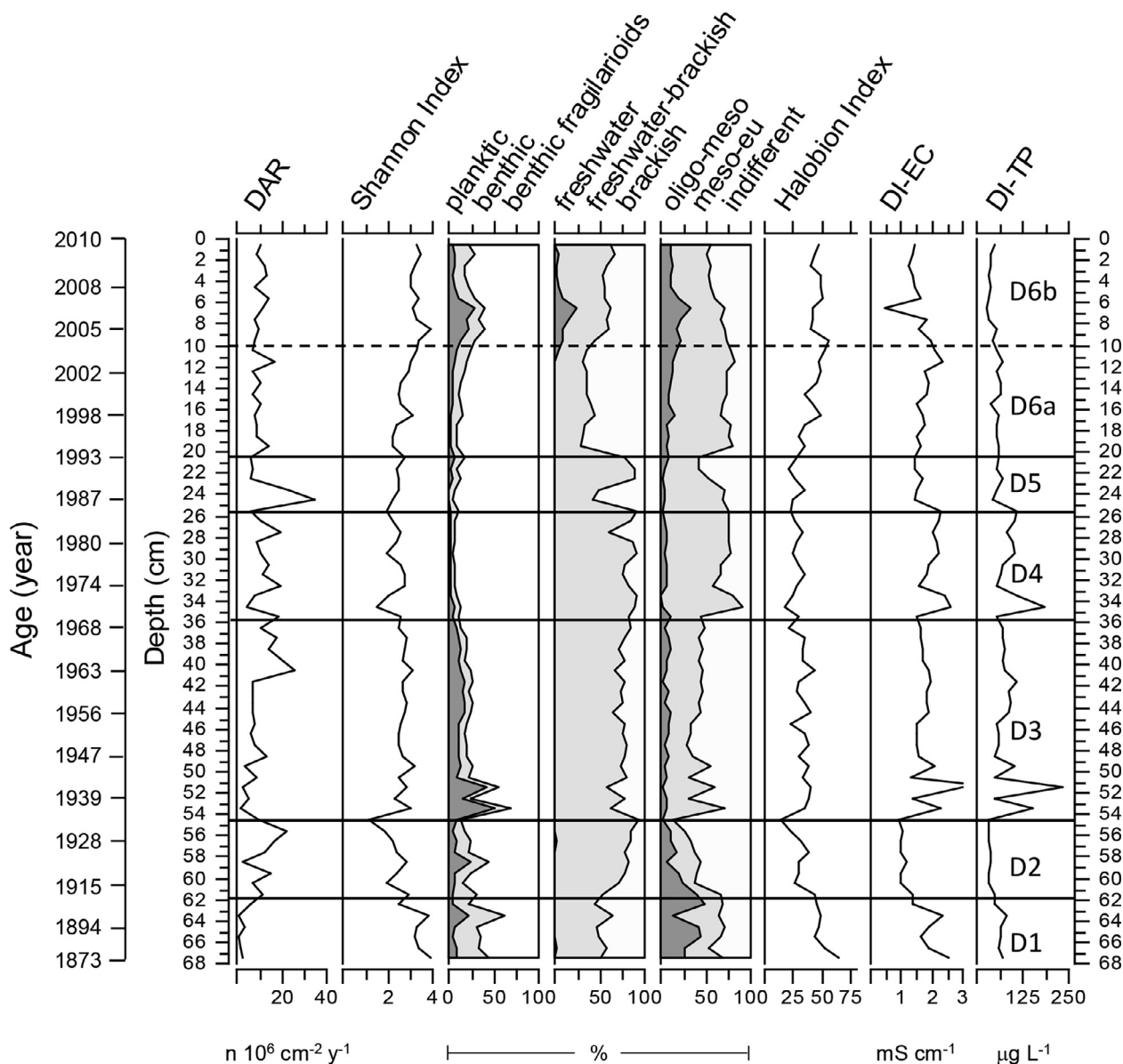
Fig. 4. Accumulation rate (DAR), diversity (Shannon Index) and ecological classification of subfossil sediment diatoms of the Lake Neusiedl, and diatom-inferred lake water conductivity (DI-EC) and total phosphorus (DI-TP). Average standard errors of inferred values as in Fig. 2. Planktic: dark grey; benthic: light grey; benthic fragilarioid: white; freshwater: preferring water salinity < 0.2‰ (dark grey); freshwater-brackish: preferring water salinity between 0.21 and 0.9‰ (light grey); brackish: preferring water salinity between 0.91 and 9.0‰ (white), according to Van Dam et al. (1994); oligo-meso: oligo-mesotraphentic (dark grey); meso-eu: meso-eutraphentic (light grey); indifferent: tolerant to wide TP level (white), according to Van Dam et al. (1994). Halobion Index (Zieman et al., 2001) calculated based on the cumulative abundance of frequency classes of diatom groups with different tolerance to water salinity (from haloxenic to polihalobic). The Halobion Index values are directly proportional to water salinity, with values ≤ 15 being typical for freshwater (β-oligohalobic), values between 16 and 30 and between 31 and 50 indicating, respectively, freshwater with slight to medium salt enrichment (α-oligohalobic and β-mesohalobic), and values > 51 being typical for very salt enriched freshwater (β-mesohalobic).

DZ-2 (62–56 cm), which covers the early decades of the 20th century, is characterized by the substitution of the most halophilous non-fragilarioid taxa by a few dominant taxa that are tolerant towards lake salinity and nutrient level, in particular *S. pinnata* (Fig. 4). Shannon and Halobion Index are consequently lower in this zone (Fig. 4).

DZ-3 (55–36 cm) includes the sediment deposited from the early-1930s to the late-1960s and is characterized by higher proportions of eurihyaline taxa tolerating salinity up to 0.9% and of meso-eutraphentic to indifferent taxa (Fig. 4). *S. pinnata* still represents the most abundant species, but is accompanied by the centric *C. meneghiniana*, several benthic fragiloids (*P. brevistriata*, *P. elliptica*, *P. geocollegarum*), and by *Triblionella apiculata* Gregory,

N. navicularis (Brébisson) Grunow, and *Rhoicosphaenia. abbreviata* (Agadh) Lange-Bertalot (Fig. 5).

DZ-4 (35–26 cm) spans over the period of cultural eutrophication of Lake Neusiedl (i.e. 1970s – 1980s), and is characterized by the lowest proportion (average = 18%) of halophilous taxa and by the lowest values of the Halobion Index (Fig. 4). Meso- to eutraphentic fragilarioid taxa, particularly *Pseudostaurosira parasitica* (W. Smith) Morales, *P. elliptica*, and *S.* cf. *punctifomis* aggr. *N. sopotense* represent the dominant taxa of this zone (Fig. 5).

DZ-5 (25–21 cm) differs from DZ-4 for its higher share of brackish taxa and nutrient-tolerant fragilarioids (Fig. 4), such as *S. pinnata* and *P. brevistriata*, and by the abrupt decrease of *S.* cf. *punctiformis* aggr. *N. sopotense* and *P. elliptica* (Fig. 5).
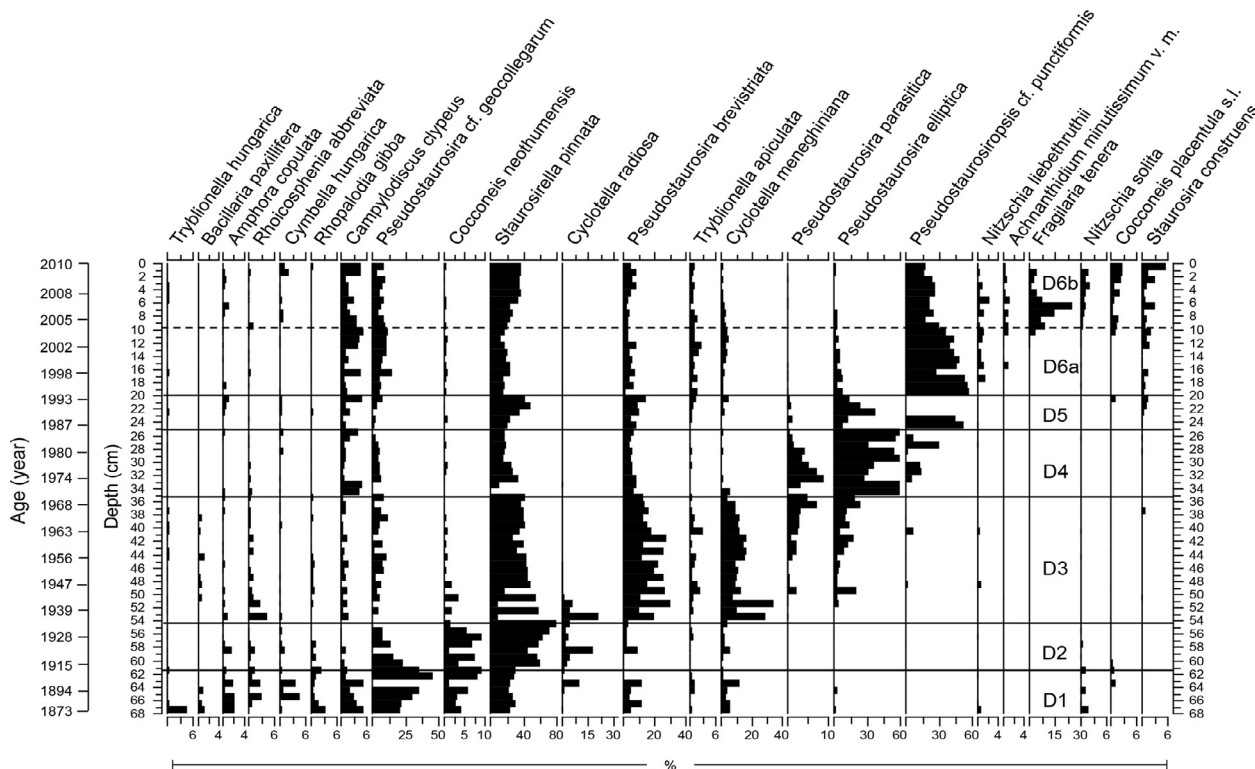
Fig. 5. Depth profile of key subfossil diatom taxa identified in the studied sediment core from Lake Neusiedl. DZ I to IV: homogeneous diatom zones as outlined by the CONISS method, as implemented in ZONE (Lotter and Juggins, 1991). The number of significant zones was established by comparison with the broken stick model (Bennett, 1996). *Pseudostaurosiropsis* cf. *punctiformis* represents the aggregate of this taxon and *Nanofrustulum* cf. *sopotense*; v. m.: variety *minutissimum*.

The top DZ-6 (20–0 cm) include the two decades before the sediment coring, and is characterized by enhanced proportions of halophilous taxa (Fig. 4), especially *C. clypeus*, *N. constricta*, and *N. liebertruthii* Rabenhorst (Fig. 5). The sub-zone DZ-6a is separated from DZ-6b based on the appearance in the early-2000s of *F. tenera* and other taxa (e.g. *Nitzschia solita* Hustedt, *Cocconeis placentula sensu lato* Ehrenberg, and *Staurosira construens* Ehrenberg) responsible for the decrease in the proportion of halophilous and meso-eutraphentic in the topmost core section (Fig. 4).

NMDS and vector fitting

The scree plot analysis indicates a two-dimensional NMDS as sufficient to describe the long-term variability of subfossil diatoms in Lake Neusiedl. The two dimensional ordination explains 92% of the variance in diatom species composition and abundance and shows a low stress (0.13). The smoothed values (running average, n = 5, according to dating errors of ± 2 years in the largest part of the core studied) of sample scores on the two NMDS dimensions are distributed clockwise in the NMDS space from 1873 ± 16 yrs to 2010, with recent samples approaching the oldest ones (Fig. 6a). The sample distribution outlines three stages of major deviation from intermediate species compositions, i.e. those identified by samples located closer to the NMDS axis origin, with maximum deviations broadly corresponding to the 1930s, the 1970s and the mid-1990s/early-2000s (Fig. 6a).

The distribution in the NMDS space of the 65 diatom species with RA ≥ 0.5% in each sample, and the seven significant (p < 0.05) variables fitted to diatoms (Fig. 6b), shows planktic taxa as more abundant in the first half of the 20th century. This period was also characterized by taxa indifferent to nutrient level and preferring fresh to slightly brackish water (e.g. *N. navicularis*, *C. menghiniana*, *S. peisonii*, *Ctenophora pulchella* (Ralfs ex Kützing) Williams

and Round, ESM Table S1). On the contrary, both the oldest and the more recent samples are characterized by higher proportion of oligo-mesotrophic taxa and by species typical for brackish waters (e.g. *C. halopannonica*, *Diatoma elongata* (Lyng.) Agardh, *Haslea stundlii* (Hustedt) Blanco, Borrego-Ramos and Olenici, *N. liebetruthii*, *N. solita*, ESM Table S1). The samples located in the right NMDS quadrants show higher abundance of meso-eutraphentic taxa, such as *Cymbella lacustris* (Agardh) Cleve, *P. parasitica*, *P. elliptica* and *C. clypeus.* (Fig. 6b).

The vector fitting (Fig. 6c-d) outlines significant relations between diatom species composition and abundance and a set of independent variables, i.e. sediment carbon and nitrogen content, sedimentation rate and air temperatures (see ESM Table S2). Sediment carbon shows a positive association with the NMDS axis 1 (D1), with the TOC vector pointing toward the samples deposited during the lake nutrient enrichment (~1970s–1990s, Fig. 6a), while sediment TN concentrations show a negative relation to axis 2 (D2), with recent samples showing the highest values. Vectors of summer, autumn, and annual average air temperature point towards the samples deposited after the mid-1990s that also show the highest sedimentation rate. NMDS sample scores also correlate (Pearson coefficient, Table S3) with the discontinuous SCPs (negatively with D2) and pigment concentrations (positively with D1), as well as to a set of diatom-dependent variables, i.e. Halobion and Shannon Index, and diatom-inferred lake EC and TP values (the latter oppositely correlated with D1 and D2).

The pattern of the TOC surface fitting (Fig. 6c) corroborates the gradual increase in sediment carbon content from the late-19th century till the mid-1980s and the return to intermediate values in the last decades. On the contrary, the surface fitting of average annual air temperature (Tyr, Fig. 6d) indicates that, beside some irregularity, annual temperature progressively increased since the late-19th century to maximum values in the mid-2000s. The
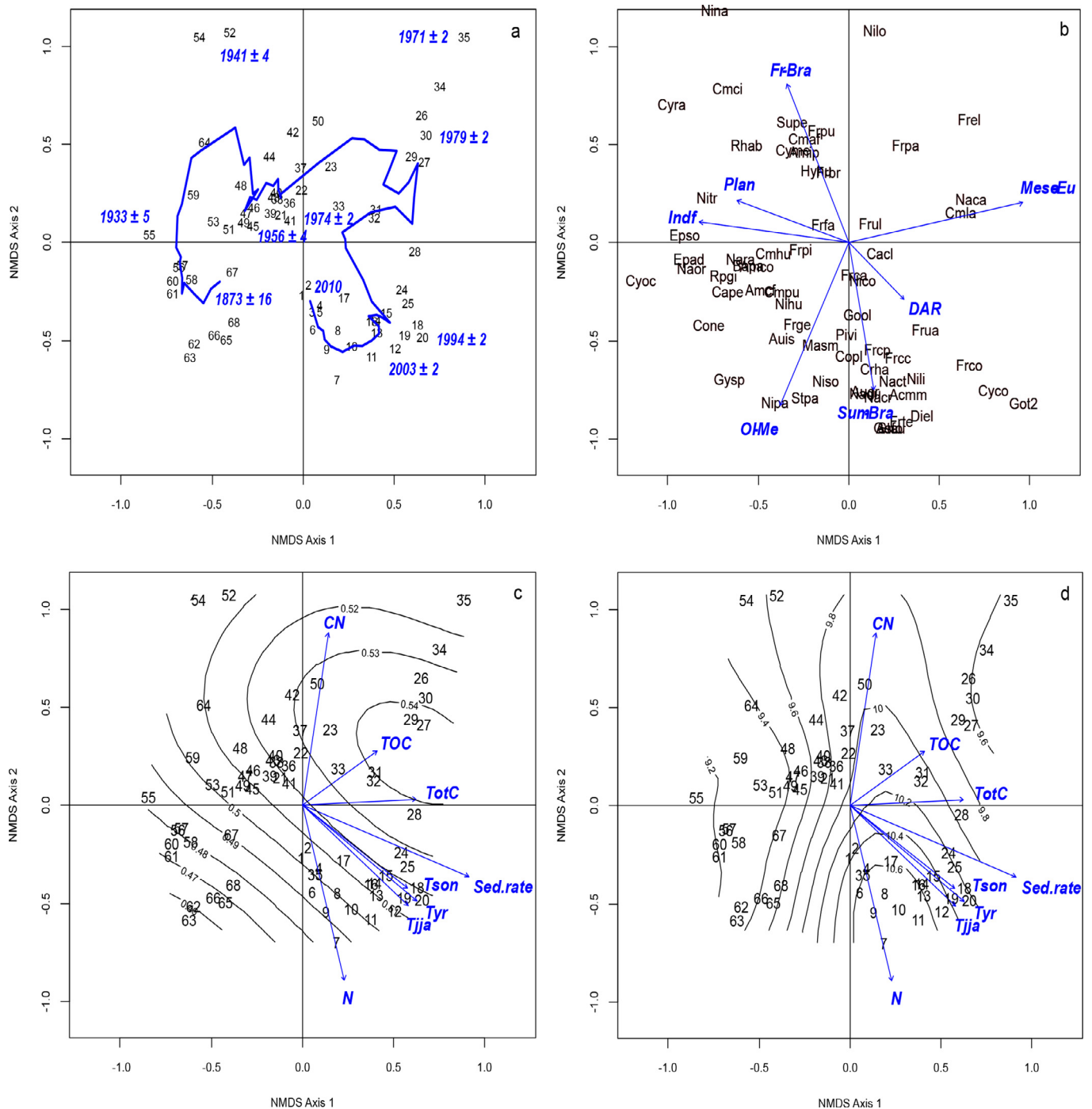
Fig. 6. NMDS ordination of the core samples from Lake Neusiedl based on the 65 diatom taxa used for the DI-EC and TP-Cond reconstruction. a), b): sample and species ordination, respectively. Sample numbers correspond to the sample depth in the core (in cm), the blue line represents the smoothed (i.e. running average, n = 5) sample scores on the two NMDS dimensions, with indication of key sample ages and dating errors. Species abbreviations as in ESM Table S1. Vector fitting shows significant (p < 0.05) variables related to diatoms in b) and to independent sediment analyses and long-term air temperature at the station of Sopron in c) and d). DAR: diatom accumulation rate; Fr-Bra: cumulative RA of freshwater-brackish diatom species; Sum-Bra: cumulative RA of the brackish taxa; Meso-Eu: cumulative RA of meso-eutraphentic taxa; TOC: total organic carbon; TotC: total carbon; Sed.rate: sedimentation rate; Tjja: average air temperature of the period June-August; Tson: average air temperature for the period September-November; Tyr: mean annual air temperature. The vector orientation shows the direction of most rapid change for each fitted variable, while its length is proportional to the correlation between the environmental variable and the sample ordination. The surface fitting is based on the correlation of diatom data with the GAM response surface of TOC in c) and Tyr in d), with numbers on surface lines indicating TOC and Tyr values, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
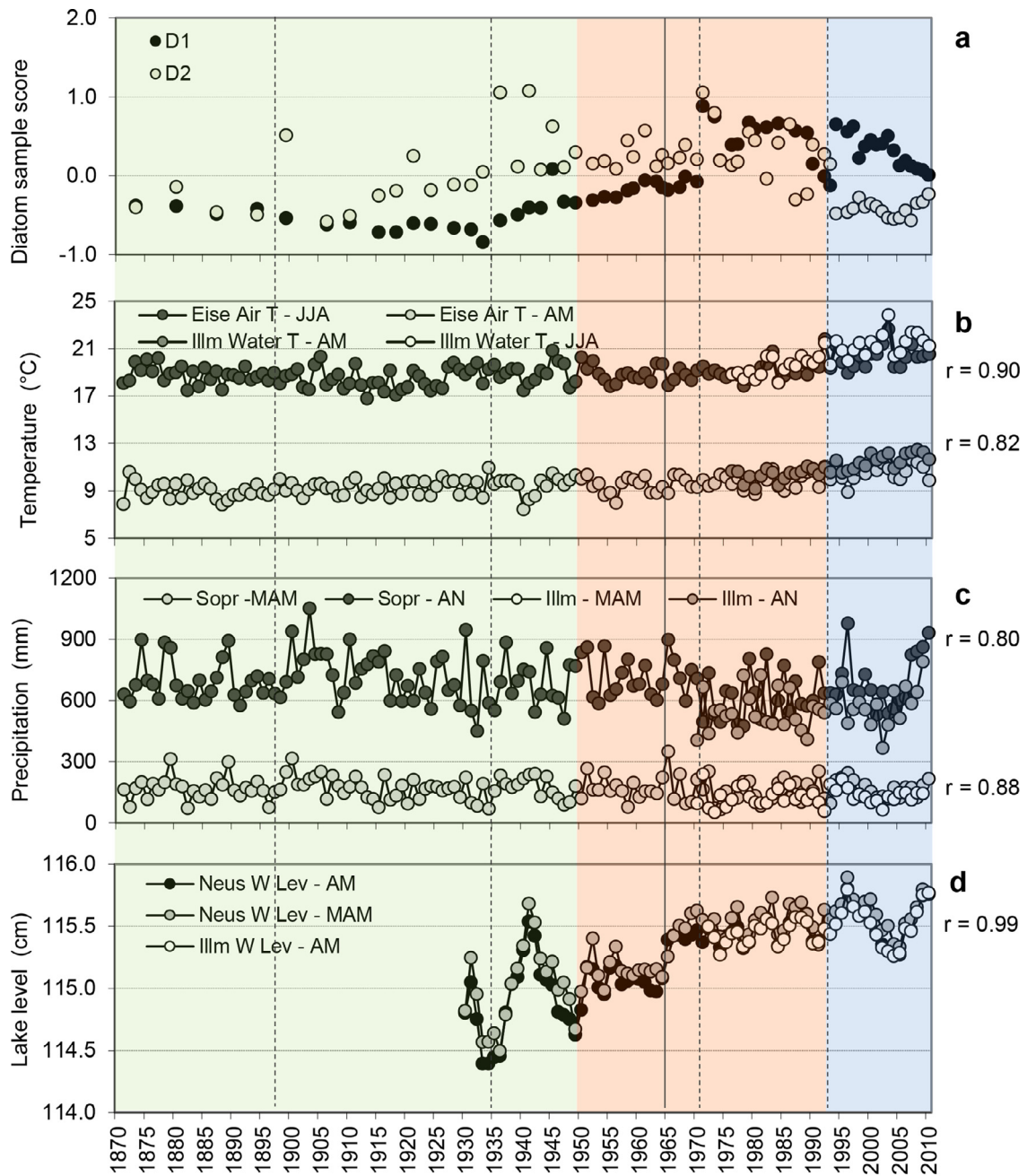
pattern of TN surface fitting, not shown, is almost identical to that of Tyr.

Sample scores on the two NMDS axes also show a number of significant correlations to decadal climate and limnological data (ESM Table S4). In particular, scores on D1 and D2 show opposite

correlation with water temperature measured at the Illmitz weather station since 1976. The plots in Fig. 7 outline that major changes in air temperature and cumulative precipitations occurred after ~ 1970 (Fig. 7b, c), while water level oscillations of Lake Neusiedl became less pronounced after the beginning of the lake

regulation in 1965 (Fig. 7d). Moreover, Fig. 7a underscores that, despite the overall different temporal patterns, the most rapid and pronounced shift in lake diatom assemblages (D1 and D2 scores) is associated with stages of major variability in these climatic-related variables during the 1930s-early 1940s, and the early-1970s and −1990s.

The relation between NMDS sample scores and decadal chemical and biological lake quality (Spearman rank order ρ) is different for the two NMDS dimensions (ESM Table S4). Sample scores on NMDS D1 are more strongly correlated with inferred EC values, those on D2 with inferred TP. Moreover, D1 scores correlate positively with annual average of Mg, dissolved and total organic carbon (DOC and TOC, respectively) and chlorophyll *a*, while D2 scores correlate negatively with the annual average biovolume of total phytoplankton and major algal groups (ESM Table S4).

Diatom-inferred lake EC and TP reconstruction

A total of 54 diatom species, coded by the Combined Salinity Dataset and accounting for an average cumulative relative abundance of 74% (35–99%), could be used for the reconstruction of past conductivity of Lake Neusiedl (ESM Table S1). The fact that *P. geocollegarum* and *P.* cf. *punctiformis* aggr. *N. sopotense* are not included in this training set decreases the cumulative diatom relative abundance available for the EC-inferring, in particular in those layers where these taxa are abundant. The statistical performance of the selected model (LWWA, Table 1) indicates an average standard error of 14.2% for the estimated EC values. The AM technique outlines the presence of a very few close and very good analogues (below the 1st percentile), all located in the central part of the core (ESM Fig. S4) and corresponding to lakes in the Caspian region, and secondarily in eastern Africa. The pattern of the average distance of the five closest analogues for each sediment sample confirms the scarce quality of analogues (distance above the 10th percentile) especially in the deepest and top core sections. The DI-EC depth profile (Fig. 4) shows oscillating values during the period 1870s–2010, with values above ~ 2 mS cm^{-1} in the sediment layers deposited just after the lake refilling in the early-1870s, and during the periods 1930s–1940s (up to ~ 3.2 mS cm^{-1}), early-1970s – mid-1980s, and early-2000s (up to 2.4 mS cm^{-1}). Layers deposited in the first decades of the 20th century and after 2003 show low DI-EC, down to 1.4 and 0.9 mS cm^{-1}, respectively.

Cumulative relative abundances of the 54 diatom taxa coded by the European Combined TP Dataset (ESM Table S1) in each sediment subsample range between 34 and 99% (average = 74%). Percentages are lower for those samples with higher proportion of halophilous taxa typical for the Pannonian steppe lakes, and of the small non-coded fragiloid taxa *P. geocollegarum* and *P. punctiformis* aggr. *N. sopotense.* The AM technique outlines the presence of a few close analogues, but the average distance of the five closest analogues indicates their overall good quality in the upper 50 cm of the sediment core (distance below or close to the 5th percentile, ESM Fig. S4). Analogues are located in several European regions, in particular in Switzerland, France, Sweden and Northern Ireland. The reconstructed DI-TP values show an average standard error of 22.8% (Table 1). The DI-TP depth profile (Fig. 4) indicates values decreasing from 73 μg L^{-1} after the lake replenishment to 30 μg L^{-1}, i.e. down to moderately eutrophic level (ÖNORM M261, 2001), in the late-1920s. The successive two decades show

Table 1

Logarithm errors of estimation (apparent) and of prediction (jack-knifed) relative to diatom-inferred lake conductivity (DI-EC) and total phosphorus (DI-TP) reconstructed for Lake Neusiedl since the last desiccation period. LWWA: Locally Weighted Weighted Average; WA: weighted average; class.: = classical deshrinking; inv.: inverse deshrinking; RMSE: Root mean squared error of the model; Av-bias, M-bias: average and maximum bias of the model, respectively; Av. SE %, Range SE %: average and range standard error as % of reconstructed DI-EC and DI-TP values, respectively.

| Variable | DI-EC | DI-TP | |
| Model Deshrinking | LWWA class. | WA inv. | |
Error	Prediction Estimation	Estimation	Prediction
r^2	0.741	0.710	0.334
RMSE	0.471	0.298	0.637
AV-bias	0.023	$-4.682\ e^{-8}$	0.003
M-bias	0.877	0.367	0.720
AV. SE %	14.2		22.8
Range SE %	13.1–14.5		17.2–29.8

pronounced oscillations, with peaks up to ~ 230 μg L^{-1}. From the late-1940s until the late-1980s, DI-TP ranges between ~ 50 and 100 μg L-1, with a sharp peak the early-1970s up to hypertrophic levels (~180 μg L^{-1}), while they rapidly decrease during the mid-1980s and stabilize around or slightly below 50 μg L^{-1} till 2010 (i.e. towards moderately eutrophic status according to ÖNORM M261, loc. cit.).

Inferred DI-EC and DI-TP values for the whole core are strongly correlated to each other (r = 0.86, p < 0.001, ESM Table S3), as well as diatom-inferred and measured lake TP concentrations when considering the entire monitoring period 1983–2010 (r = 0.57, p < 0.01, Table 2). On the contrary, DI-EC and EC significantly correlate only when considering the period 1994–2004 (r = 0.43, p < 0.05, Table 2). Both DI-EC and DI-TP are inversely related to annual and seasonal averages of lake water level and temperature values, while only DI-EC is related to annual and April-September cumulative precipitation (Table 2). Relation to the water level is stronger for DI-EC values, while DI-TP appears more correlated to water temperature, especially in spring. This pattern is only partially maintained when considering correlations of EC and TP values (1983–2010) with the same environmental variables, as lake EC is not significantly related either to lake water temperature or precipitation. TP concentrations are more strongly correlated with water level than EC values, and also show negative correlation to spring and summer water temperature (Table 2). When considering the relations to chemical and biological variables, only DI-TP is related positively to carbonate concentrations and negatively to DOC and TOC concentrations, as well as to annual mean biovolume of total phytoplankton and sum of chlorophytes and euglenophytes (Table 2). Measured EC and TP values show a rather different correlation pattern, with TP values related to Ca and CO$_3$, total phytoplankton, centric diatoms, and sum of chlorophytes and euglenophytes, and both EC and TP positively related to water pH. EC shows a further positive relation to DOC concentration (available only since 1997).

◄

Fig. 7. Overview of environmental (Env) and biological (Biol) variability of Lake Neusiedl since the end of its last complete desiccation (1873 ± 16 yrs – 2010). a) Scores of subfossil diatom samples from Lake Neusiedl on the two NMDS dimensions (D1, D2); b) HISTALP average annual and summer (AM and JJA, respectively) air temperature for the station Eisenstadt-Sopron (Eise) during the period 1870–2010, and average annual and summer (AM and JJA, respectively) lake water temperatures measured at the Biological Station Lake Neusiedl, Illmitz (Illm) since 1976; c) HISTALP spring (MAM) and annual (AN) cumulative atmospheric precipitation for the station Sopron (Sopr) during the period 1970–2010, and values measured at the station Illmitz (Illm) since 1971; d) annual and spring (MAM) average lake water levels (WL) measured at Neusiedl am See (Neus) since 1930, and annual average levels measured at Illmitz since 1972. r values refer to Pearson correlation coefficients between long term and decadal data sets of air temperature and precipitation, and between the different historical water level data sets (p < 0.001). Coloured shadings identify the three major stages in the lake development during the studied period; green: pre-disturbance trophic conditions and first climate-driven changes; orange: cultural eutrophication; blue: lake recovery. Trophic classification based on the combination of measured and diatom-inferred TP (ÖNORM M6231, 2001) and diatom ecological preferences. Dashed lines: periods of major shifts in samples scores on D1 or D2; solid line: building of the Einser canal in 1965; black triangles: documented periods of low lake water level; ↑: increasing; ↑↑: strongly increasing; ↓: decreasing; Δ: changing. Reeds: extension of the reed belt, Cya; cyanobacteria, other abbreviations as in Table 2 and Figs- 2–6. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Pearson correlation coefficients (r) of diatom-inferred and measured lake conductivity values (DI-EC and EC, respectively) and total phosphorus concentrations (DI-TP and TP, respectively) versus a set of environmental and limnological variables measured at the Biological Station Lake Neusiedl, Illmitz. Phytoplankton data available since 1968, water level (WL) and temperature (WT) values since 1976, CP (cumulative precipitations) since 1971, lake water EC values and nutrient concentrations available since 1983, major ions since 1988, DOC and TOC since 1998. N: number of observations available for each variable pair; significant coefficients with p < 0.05 after Benjamini-Hochberg adjustment; n.s.: not significant; AM: annual average, Am: annual minimum, Amax: annual maximum, MAM, DJF, SON, AS: average values for the periods March-May, December-February, September-November and for the vegetative period April-September, respectively; Tot-Phy, Dia-Cen, Chl-Eug: annual average values of total phytoplankton biovolume, centric diatoms and Chlorococcales + Euglenoid algae, respectively. All data but water temperature and pH transformed according to y = log(x + 1). Lake TP and EC values are significantly correlated only when considering the period 1988–2010 (r = 0.560, p < 0.05), DI-EC and EC only in the period 1994–2004 (r = 0.497, p < 0.05).

Variable	Unit	N	DI-EC	DI-TP	N	EC	TP
WL-AM	cm	28	−0.569	−0.414	28	−0.378	−0.678
WL-Am	cm	28	−0.577	−0.448	28	n.s.	−0.691
WL-AMax	cm	28	−0.517	n.s.	28	−0.489	−0.638
WL-SON	cm	28	−0.563	−0.429	28	n.s.	−0.682
WL-AS	cm	28	−0.517	n.s.	28	−0.436	−0.552
WT-AM	°C	28	−0.459	−0.718	28	n.s.	−0.665
WT-Am	°C	28	−0.431	−0.693	28	n.s.	−0.446
WT-MAM	°C	28	−0.536	−0.746	28	n.s.	−0.750
WT-DJF	°C	28	−0.386	−0.687	28	n.s.	−0.448
WT-AS	°C	28	−0.434	−0.670	28	n.s.	−0.667
CP	mm	31	−0.421	n.s.	28	n.s.	−0.383
CP-AS	mm	31	−0.358	n.s.	28	n.s.	−0.463
pH		23	n.s.	n.s.	28	0.432	0.803
Ca	mg L^{-1}	21	n.s.	n.s.	24	n.s.	−0.841
CO$_3$	mg L^{-1}	20	n.s.	0.631	23	n.s.	0.601
EC	mS cm^{-1}	23	n.s.	n.s.	28	–	n.s.
TP	µg L^{-1}	23	0.445	0.572	28	n.s.	–
DOC	mg L^{-1}	13	n.s.	−0.591	13	0.882	n.s.
TOC	mg L^{-1}	13	n.s.	−0.643	13	0.737	n.s.
Tot-Phy	mm^{3}L^{-1}	25	n.s.	−0.552	22	n.s.	−0.732
Dia-Cen	mm^{3}L^{-1}	25	n.s.	n.s.	22	n.s.	−0.856
Chl-Eug	mm^{3}L^{-1}	25	n.s.	−0.496	22	n.s.	−0.421

The pairwise comparison of the abundances of key diatoms taxa in the plankton (biovolume) and in the sediment (relative abundance) samples, aimed at testing to what extent subfossil diatoms are representative of the whole diatom assemblages of Lake Neusiedl, outlined significant direct relations only for the genera *Nitzschia* and *Campylodiscus* (ESM Table S5). A few further relations between taxa abundances in the plankton are maintained in the sediment, e.g. between the cumulative abundance of benthic Fragilariaceae and centric taxa and *Navicula* s.l. (ESM Table S6). Benthic diatom taxa show several significant relations with lake EC and TP and NO$_3$-N level, with a few concordant relations in plankton and sediment (ESM Table S6).

Discussion

The studied sediment core from the large and extremely shallow Lake Neusiedl shows an orderly sedimentation during the period 1873 ± 16 yrs – 2010, i.e. since the end of the last complete lake desiccation that occurred from 1865 to 1868 (Herzig and Dokulil. 2001). The present multi-proxy palaeolimnological study of Lake Neusiedl, including the multivariate analyses and the diatom-based reconstruction of past lake water properties, outlines three major stages in the evolution of the lake during the period covered by the core chronology. In the following paragraphs, we first discuss these major evolution stages of the lake, and then critically evaluate the reliability of biological sediment proxies for palaeolimnological reconstruction at Lake Neusiedl and shallow lakes in general. Finally, we use the results of this study to evaluate the current and future vulnerability of Lake Neusiedl towards climate-related hydrological variability.

Ecological evolution of Lake Neusiedl from 1873 ± 16 yrs to the 1940s

Our sediment record suggests that Lake Neusiedl experienced moderate chemical and biological variations over the

first ~ 50 years after its refilling. The sediment density rapidly decreased after the restoration of lacustrine conditions, while the decrease of TOC:TN values down to ~ 10 indicates microalgae as rapidly becoming the principal source of sediment organic matter. The reciprocal proportion of subfossil pigments suggest phytoplankton assemblages as mainly consisting of cyanobacteria, diatoms, and, later on, green algae, in accordance with the high average diatom-inferred lake TP level (~ 60 mg L^{-1}, Fig. 4). This extends the limnological records that report the dominance of these three algal groups since the late-1960s (e.g. Padisák and Dokulil, 1994). Immediately after the lake refilling, diatoms were scarce though diverse, and halophilic taxa typical for Lake Neusiedl (e.g. *C. clypeus, C. hungarica, S. peisonii*), and *P. geocollegarum*, were dominant. DAR and diatom taxa indifferent to the nutrient level rapidly increased, while halophilic diatom taxa markedly decreased from the turn of the century. The diatom inferred TP values steadily > 30 µg L^{-1}, combined with the taxonomical composition and ecological preferences of subfossil phytoplankton and sediment diatoms, suggest moderate eutrophic conditions already in the first decades after the lake refilling. The increase in brackish diatom taxa and inferred EC and TP levels around the turn of the century agrees with the stage of low water level and high salinity (i.e. 13 g L^{-1}, corresponding to 19.5 mS cm^{-1} 20 °C) reported in historical archives around 1902 (Berger and Neuhuber 1979; Österreichisch-Ungarische Gewässerkommission, 1996), and underscores a prompt response of the lake biota to short-term hydrological changes (Fig. 7).

The first evident ecological shift of Lake Neusiedl occurred during the 1930–40s and mainly consisted of a decrease in the DAR values since the late-1920s, accompanied by the pronounced increase in the proportion of halophilous and meso- to eutraphentic taxa (especially the planktic *C. meneghiniana* and the benthic *P. brevistriata*). Historical information suggests these changes as related to the high annual and summer mean air temperature and scarce precipitation recorded over Europe and the region of Lake Neusiedl since the mid-1930s (Böhm, 2012; HISTALP, 2018).

This situation likely affected the lake evapotranspiration rates that, in turn, triggered a pronounced decrease in lake water level in the early-1930s (Fig. 7), and the increase in water salinity up to 16 g L^{-1} (23.6 mS cm^{-1} 20 °C, Berger and Neuhuber, 1979) and in nutrient concentrations in absence of major inputs form the catchment (Herzig, 2014). Coherent lake responses to the warmer and drier conditions that characterized Europe in the 1930–40s are evident in sediment records from temperate and mountain lakes of the Alpine region (e.g. Bruel et al., 2018; Koinig et al., 2002; Milan et al., 2015; Thies et al., 2012; Tolotti, unpublished data). In general, these lakes mimicked the effects of nutrient enrichment, with moderate increase in subfossil photosynthetic pigments, TP level or organic matter that were, however, mediated by specific hydrological and thermal dynamics in a period where anthropogenic inputs were still low (Tolotti et al., 2018). In the studied core, the low variability of sedimentation rate and wet density during the 1930–40s support the biological responses of Lake Neusiedl in this period as not principally triggered by inputs from the catchments but by changes mediated by water level fluctuations (Dokulil et al., 2010).

Cultural eutrophication of Lake Neusiedl (1950s–1980s)

Similarly to the majority of European temperate lakes (Bennion et al., 2011; Dokulil et al., 2010; Tolotti et al, 2018), the 1960s represented a milestone for the ecological evolution of Lake Neusiedl. The expanding settlements and recreational activities within the lake catchment during the post-war economic boom, along with the progressive substitution of pastures and meadows by intensive crops and vineyards (Löffler, 1979), led to the cultural eutrophication of Lake Neusiedl (Herzig and Dokulil, 2001), as witnessed by changes in geochemical and biological sediment proxies since the late-1950s.

Subfossil pigment profiles confirm cyanobacteria, green algae and diatoms, in this order, as the dominant algal groups in Lake Neusiedl during the eutrophication. This agrees with the increasing density of green algae *sensu lato* and cyanobacteria reported since the 1970s (Herzig, 2014; Herzig and Dokulil, 2001), when considering that zeaxanthin, echinenone and lutein are characterized by higher molecular stability in comparison to the diatom-specific carotenoids (Leavitt and Hodgson, 2001).

The proportion of meso- to eutraphentic diatom taxa (especially *P. elliptica*, *P. parasitica*, and the non-coded *P.* cf. *punctiformis* - aggr. *N. sopotense*) abruptly increases in the core section deposited after the late-1960s, thus explaining the high diatom-inferred lake TP values from the early-1970s to the late-1980s. Although the validation of these values is possible only after 1983 (when the regular monitoring of lake water chemistry was initiated), the average DI-TP values for the period 1968–1985 (i.e. 92 ± 2.5 μg L^{-1}) agree with early limnological information reporting annual lake TP concentration > 100 μg L^{-1} (i.e. within the hypertrophic level) until 1988 (Herzig and Dokulil, 2001).

Despite the small changes in the sediment content of carbon and organic matter during the lake eutrophication, the percent weight of TN was particularly low during the period 1960–1980s. Microbial denitrification of sediment organic matter can hardly explain the N decrease, considering that the open water of Lake Neusiedl is well oxygenated throughout the year (Löffler, 1979), and that the sediment is not anoxic, as confirmed by its light colour. Moreover, NH_4^+ ions resulting from denitrification are mainly absorbed by sediment clay minerals, thus preventing a substantial decrease in sediment TN content (Meyers and Lallier-Verges, 1999). On the contrary, the decrease in sediment TN fits well with an enhanced uptake by the reed belt (Löffler, 1979) that expanded during the 20th century and reached its maximum during the late-1960s (Herzig, 2014). The highest TOC:TN values during the lake

eutrophication (~70, Fig. 4) suggest a dominant contribution of facultative C4 plants, such as *Phragmites australis* (Cav.) Trin. ex Steudel, to the sediment organic matter (Meyers and Teranes, 2001). The reed development does not disagree with observations from eutrophic shallow lakes that often report a shift from dominant macrophytes to phytoplankton during nutrient enrichment stages (Beklioglu et al., 2011; Dokulil et al., 2011; Sheffer, 1999; Teubner et al., 2018b, 2020). In fact, emerged macrophytes have a competitive advantage over both submerged macrophytes and phytoplankton in the naturally turbid Lake Neusiedl (Herzig and Dokulil, 2001; Padisák and Dokulil, 1994). Because nutrient demand of rooted macrophytes is supposed to be largely supplied by the sediment (Hupfer and Hilt, 2008), the reed expansion in Lake Neusiedl was likely triggered by low lake water levels and a decrease in the traditional reed harvest during the first half of the 20th century (Löffler, 1979). The introduction of lake level regulation (Einser Kanal in 1965, Fig. 7), that imposed an increase in lake water level of ~ 30 cm, and of reed management measures (Herzig, 2014; Löffler, 1979) stopped the reed expansion and likely contributed to the sediment TOC:TN decrease after the early-1990s.

Restoration and recent development of Lake Neusiedl (1990s–2010)

The sediment record agrees with limnological observations in identifying the early-1990s as the beginning of a new ecological stage for Lake Neusiedl (Fig. 7). The lake restoration started in the 1980s (Dokulil and Herzig, 2009) resulted in a rapid decrease in the lake DI-TP level down to pre-disturbance levels (Fig. 2b), while the sediment TN content increased from the late-1980s to the mid-2000s, in agreement with the limnological records of lake N level (Fig. 2c). The estimated average load of inorganic nitrogen to the surface of Lake Neusiedl amounted to ~ 233 t N y^{-1} in the period 1990–2010s (Soja et al., 2014). Close attention has been given to atmospheric deposition that annually amounted to 2–3 kg NO_3-N ha^{-1} and 5–6 kg NH_4^+-N as wet deposition, and to 5–6 kg N ha^{-1} as dry deposition of NO and NO_2 (Spangl and Nagl, 2011). The increase in sediment N contributed to the stabilization of TOC:TN values below 10 after the early-1990s, thus suggesting phytoplankton as the major source of sediment organic matter in this period (Meyers and Teranes, 2001). Indeed, the peak in sediment pigment concentrations found in the early-1990s corresponds with the maximum phytoplankton biomass recorded in 1991 (Dokulil and Padisák, 1994) in conjunction with high P an N availability and low salinity (Fig. 2). Both pigment concentrations and fluxes confirm the increase in algal biomass after 2000 as principally driven by green algae, cyanobacteria and Heterokontae (i.e. diatoms and Chrysophyceae), as reported in Herzig (2014) and confirmed by a peak in DAR in the late-1980s.

Since the early-1990s, the increased proportion of oligo-mesotraphentic and, especially, of phosphorus indifferent subfossil diatom taxa led to diatom-inferred TP values oscillating around ~ 50 μg L^{-1}, in good agreement with monitoring data (Dokulil and Herzig, 2009). The proportion of halophilous taxa, including several of the species abundant in the deeper core sections, remained > 50% until the early-2000s. However, the diatom-inferred EC (around 1.5 mS cm^{-1}) underestimates the measured EC values during the 1990s and again since 2003 (2.0 – 2.5 mS cm^{-1}). The recent decline in DI-EC depends on the appearance of haloxenic fragilarioid taxa, especially *Fragilaria tenera* and, to a lesser degree, *F. acus* and *F. ulna* in the top section of the studied core. In a number of lakes of the northern hemisphere the development of planktic Fragilariaceae has been put in relation to enhanced N availability (e.g. Saros et al., 2005; Tolotti et al., 2007; 2012; Williams et al., 2016). However, considering the recent decrease in NO_3-N concentrations in Lake Neusiedl, the

increase in Fragilariaceae seems related to the combination of lower nutrient availability and low lake salinity since the mid-2000s.

Reliability of sediment proxies for palaeolimnological reconstruction of shallow lakes

In contradiction with previous expectations (e.g. Löffler, 1991), the orderly sedimentation of the studied core from the shallow Lake Neusiedl indicates that wind-driven sediment resuspension is sufficiently reduced at sheltered places along the eastern shore of the lake to make cores taken in this area representative for the pelagic zone. Nevertheless, the extreme shallowness of Lake Neusiedl, its unique chemical nature, and the related features (e.g. water turbidity, alkaline pH), represent a challenge for palaeolimnological reconstructions, as they can affect both quantity and quality of abiotic and biotic proxies.

The SCP concentration profile does not substantially contribute to the dating of the studied core, as it only becomes interpretable when plotted against the core chronology. Although comparable data are limited, the SCPs in Austrian lakes show a first appearance between 1850 and 1880 (e.g. Rose et al., 1999; Thies et al., 2012), so the record in Lake Neusiedl could likely be extended back a decade or two further if the core were longer. Moreover, the usual rapid increase in concentration at around 1950 appears muted by the increase in sediment accumulation rates (ESM Fig. S3 and Fig. 3). Nonetheless, the SCP sediment profile confirms the increasing atmospheric contamination in the region of Lake Neusiedl since the mid-20th century. The peak SCP contamination in Lake Neusiedl (1960s – 1970s) currently represents the highest observed level for Austrian lakes (Koinig et al., 2002; Thies et al., 2012), and is likely related to the rapid industrial development of the region between Vienna and Wiener Neustadt, located 30–50 km west of the lake, and the subsequent transport and deposition of atmospheric pollutants to the site. As is typical for Europe (Rose and Monteith, 2005), SCP concentrations have strongly declined in the last few decades, and are now comparable to those of the early-20th century because of the introduction of particle filtering technology in major fossil-fuel combustion plants, and of the general decline of heavy industry in Austria as well as in other European regions (Rose, 2001).

Usually, N sediment concentration is not a reliable proxy due to the complex chemical and biological exchanges between the sediment and water lake column (Talbot, 2001). However, the TN content of the core from Lake Neusiedl agrees with the decadal limnological records in tracking increased lake N level in the last decades of the 20th centuries, and, in combination with organic carbon content, provides useful information on the origin of the organic matter stored in the sediment.

Concentrations of sub-fossil pigments are lower in Lake Neusiedl than in other meso-eutrophic lakes of the Alpine region (e.g. Guilizzoni et al., 2011; Milan, 2016; Schneider et al., 2018). This is likely caused by high post-depositional degradation in both the water column and the sediment due to aggressive physical and chemical conditions (Leavitt and Hodgson, 2001), including high summer water temperature, high pH and oxygenation, and high mineral turbidity caused by water turbulence and sediment resuspension. As observed in other productive shallow lakes (e.g. Guilizzoni et al., 2011), sediment pigment profiles from Lake Neusiedl are smoothed and poorly reflect the changes in total phytoplankton biomass documented in the past decades, so that they are not reliable for inferring past lake TP. Nevertheless, their depth profiles still allow an evaluation of the relative proportion of different algal groups when taking into account the resistance of different pigments toward chemical degradation (McGowan, 2007).

Sub-fossil diatoms represent a key biological proxy for sediment studies as they can provide a large set of information on environmental and ecological lake evolution (e.g. Hall and Smol, 2010; Tolotti et al., 2018). In Lake Neusiedl the DAR sediment profile suggests a postponed negative effect of nutrient enrichment on diatom production that may be mediated by the particular lake environmental settings. In fact, despite the mineral water turbidity of Lake Neusiedl, phytoplankton growth positively responds to enhanced nutrient availability (Dokulil et al., 2010). The phytoplankton pulses can contribute to furtherly enhance the water turbidity and the light limitation of periphytic diatoms. Stages of dry weather and increased evapotranspiration concentrate the in-lake nutrient pool and increase the wind-driven resuspension (Padisák and Dokulil, 1994), but, at the same time, decrease the nutrient input from the catchment (Herzig, 2014). This appears potentially relevant especially for silica due to its slow turnover (Reynolds, 2006). However, as monitoring data on silica in Lake Neusiedl are available only since 2000, its ecological role in regulating diatom growth in this lake is still poorly known, and might be explored in future research.

The classification of the sub-fossil diatom taxa according to their preference for habitat (benthic vs. planktic), water TP (Van Dam et al., 1994) and salinity (Zieman et al., 2001) allowed the reconstruction of long-term ecological changes in both the periphytic and planktic diatom assemblages of Lake Neusiedl, thus providing an additional validation tool for the diatom-based reconstruction of lake chemistry. This is crucial for Lake Neusiedl, where diatom inferred EC and TP reconstructions have differing reliabilities and outline a set of biases related to both site peculiarity and methodological background. In the absence of training sets specific for Lake Neusiedl, the reconstruction of past EC levels was based on the Combined Salinity training set (Gasse et al., 1983), that includes several brackish to hypersaline marshes, temporary ponds and small lakes in Africa, Europe and the Caspian region. Although the salinity values of Lake Neusiedl are well represented in this training set, large shallow lakes are not. Consequently, the diatom taxa composition of Lake Neusiedl is scarcely represented in the training set, as confirmed by the small number and scarce quality of modern analogues outlined by the AM techniques (ESM Fig. S4). Several taxa, but in particular the two most abundant fragilarioid *P. geocollegarum* and *P.* cf. *punctiformis* aggr. *N. sopotense,* are unavailable for reconstruction purposes as they are not coded in any of the considered training sets. Both taxa are typical of brackish habitats, such as the Baltic Sea (Germain, 1981; Witkowski et al., 2000), or productive highly mineralized lakes in South America (Morales, 2002), and in Lake Neusiedl they were most abundant in the deepest core section (1873 ± 16 yrs-1910s) and after the late-1980s. The cumulative diatom relative abundance available for the reconstruction is, therefore, low (35–70%) in both these core sections, and this heavily affects the reconstruction of the past EC of Lake Neusiedl, with inferred values underestimating both the Halobion Index in the top and bottom core sections, and the EC values recorded during the monitoring period (1983–2010).

The same small fragilarioid taxa are not coded also in the Combined European TP training set (Battarbee et al., 2001). However, as Fragilariaceae are considered as poor trophic indicators due to their wide tolerance to water nutrient level (Bennion et al., 2010), the diatom-inferred past TP levels of Lake Neusiedl still remain reliable, as outlined by the large pool of modern analogues of good quality (ESM Fig. S4) located in different European regions. In addition, the inferred TP values agree in magnitude and directly correlate with the annual average lake TP concentrations measured in the lake since 1983. Because taxa with higher TP and EC optima generally coincide in the two training sets used in this study, diatom-inferred EC and TP values positively correlate to each other,

as expected for highly productive lakes (Wetzel, 2001). The same, however, is not true for monitored EC and TP values that positively correlate only in the period 1997–2003, while they are decoupled during the lake eutrophication stage due to the increased TP input from the catchment. These aspects outline that only the TP values inferred from the sediment diatoms are reliable for Lake Neusiedl, while the interpretation of inferred EC needs the support of additional metrics, such as the Halobion Index.

The diatom taphocoenoses of Lake Neusiedl appear scarcely representative of the living planktic assemblages determined during the monitoring period, while sparse information is available for littoral periphytic assemblages (e.g. Hustedt, 1959). In particular, some centric and pennate taxa reported in the literature as frequent in the plankton samples (Dokulil and Herzig, 2009; Padisák and Dokulil, 1994) are underrepresented (e.g. *Bacillaria*, and long *Synedra* and *Nitzschia* species), or absent (e.g. *Chaetoceros muelleri* and small *Cyclotella* spp.) in the sediment. Standard enumeration protocols (Battarbee et al., 2001) imply the underestimation of large taxa, and frustules of scarcely silicified taxa, such as *Chaetoceros*, can be damaged/dissolved by the sample treatment with H_2O_2. In addition, the high alkalinity and mineral turbidity of Lake Neusiedl likely contribute to a rapid post-depositional silica dissolution of the most delicate frustules. Eroded diatom frustules are indeed present in the whole core, though especially in the oldest section (below 57 cm). As typical of shallow lakes (Bennion et al., 2010), diatom sediment assemblages of Lake Neusiedl mainly consist in a mix of periphytic taxa (epipelic and epiphytic), while average abundance of planktic taxa is 9%. This can explain the differences with the phytoplankton samples, where planktic and meroplanktic taxa dominate (Löffler, 1979; Padisák and Dokulil, 1994). In addition, the phytoplankton dataset outlines changes in the counting and identification criteria since the beginning of monitoring. For example, the key planktic taxon *C. meneghiniana* was identified at species level until 1990 and then as part of the group "small-size centrics". Further, the identification at species level of diatom taxa is hardly possible when following the standard counting protocols for phytoplankton samples, i.e. the inverted microscope technique by Utermöhl (1958). In particular, small *Nitzschia*, *Fragilaria* and *Achnanthidium* species are hardly distinguishable from each other, while the very small and rounded *P.* cf. *punctiformis* aggr. *N. sopotense* can be easily confused with small coccal green specimens, thus leading to erroneous quantification.

The poor comparability of subfossil and modern diatom assemblages implies that the validation of the diatom-based palaeolimnological reconstructions for Lake Neusiedl must rely on the comparison between inferred and measured limnological data. The adoption of the multi-proxy palaeolimnological approach proved crucial for partially surpassing these methodological shortcomings, some of which are common to shallow lakes (Bennion et al., 2010), and for obtaining an acceptable reconstruction of the major evolutionary steps of Lake Neusidl since the end of its last complete desiccation (1865–1868).

Current and future vulnerability of Lake Neusiedl towards climate-related hydrological variability

The present palaeolimnological study of Lake Neusiedl allows an evaluation of its recent ecological status against inferred past conditions, and the forecasting of future possible algal responses to climate-driven variability in water solutes by analogy with past changes.

The multivariate analyses (Fig. 6) suggest two modes of diatom response to environmental changes, consisting of: a) three stages of increased variability (i.e. in the 1930–40 s, 1970s and 1990s/early 2000s, respectively) that appear related to major changes in lake hydrology and phosphorus concentrations; b) a gradual shift

in taxonomical composition from the late 19th century to 2010 in response to lake warming, and enhanced nitrogen availability since the 1980s (Herzig, 2014; Soja et al., 2014). The first mode of variability underscores that episodes of low water level associated with dry and warm periods, as recorded during the 1930s and in the 1990s/early-2000s, are sufficient to induce a prompt response of diatom species composition mediated by the concentration of lake water solutes following the volume reduction of Lake Neusiedl (Löffler, 1979). However, chemical and ecological sensitivity of Lake Neusiedl towards climate driven changes (Soja et al., 2013) appears more pronounced during stages of moderate nutrient load, as reported also for deep lakes (Tolotti et al., 2018). Periods of higher water level, as occurred after the construction of the Einser Kanal in 1965, and in the late-2000s, are associated with smaller changes.

The biological variability of Lake Neusiedl at decadal scale agrees with the resilient behaviour of shallow lakes towards the frequent hydrological variations that typically characterize them (Salmaso and Tolotti, 2021). In addition, water quality of shallow lakes often shows a good recovery capacity after reduction of human disturbances, such as cultural eutrophication (Sheffer, 1999; Tolotti et al., 2018), in contrast to deep large lakes that typically show a more pronounced inertia towards climate related variability, and longer recovery time (Tolotti et al., 2018). The resilience of Lake Neusiedl conforms to the observation that its phytoplankton follows an approximatively decennial cyclic development (Padisák and Dokulil, 1994), in conjunction with the cyclical variability of EC (Fig. 2a), and with the high proportion of sediment diatoms tolerant to nutrients and salinity. In turn, this agrees with the phytoplankton intermediate disturbance hypothesis, which defines resilience of algal communities as a function of the frequency of disturbances that impose a community reorganisation and the interruption of developing trends toward climax conditions (Reynolds, 2006). Nonetheless, the second mode of diatom variability recorded in Lake Neusiedl indicates an incomplete ecological recovery after each of the major variable stage due to superimposed effects of global warming and variability of nitrogen inputs to the lake. This determined gradual changes in the relative abundance of dominant taxa, and the appearance of taxa new for the lake (e.g. *F. tenera*, *S. construens*) since the early-2000s. In other words, the ecological evolution of Lake Neusiedl shows the hysteresis that commonly characterizes both shallow (Sheffer, 1999; Dokulil and Teubner, 2005; Tolotti et al., 2018), and deep lakes (Salmaso and Tolotti, 2021).

The recent ecological variability of Lake Neusiedl appears of crucial importance for future lake management in the expected context of reduced nutrient inputs from point-sources, high atmospheric deposition, and global warming. The present lake TP concentrations are back to the diatom-inferred pre-1960s level, thus confirming the success of the restoration measures launched in the 1980s (Herzig and Dokulil, 2001). However, the P storage pool in the sediments is still large, and Wolfram et al. (2007) have estimated a further increase by 300 t P between 1992 and 2006 in spite of successful input reductions. The N cycle has been recognized as out of equilibrium at a global scale because of the increasing production and release to the atmosphere of reactive N derived from fossil fuels and artificial fertilizers since the 1950s (Rockstrom et al., 2009), and increased N depositions represent a common feature of catchments of the northern hemisphere (Holtgrieve et al., 2011). Despite the leading role of P in controlling algal biomass (Schindler, 2012; Schindler et al., 2016), freshwater ecosystems are sensitive also to changes in N availability (e.g. Lewis et al., 2011; Moos, 2012; Paerl et al., 2011). The changing phytoplankton biomass and/or biodiversity observed in several lakes of the northern hemisphere without concomitant major changes of lake TP has been explained by changing nutrient ratios

due to increasing N load from industry and agriculture (Saros et al., 2005; Wolfe et al., 2001, 2013), or to decreasing nutrient load in recovering lakes (Tolotti et al., 2012). Lake Neusiedl is exposed to high nitrogen emissions from intensive agriculture and industry and represents one of the Austrian regions with the highest average annual nitrogen air concentrations (8.3 $\mu g\ m^{-3}\ NO_2$, 9.1 $\mu g\ m^{-3}$ NO_x, Spangl, 2019). Although Soja et al. (2014) showed that most of the N load entering the biological lake nitrogen cycle is finally released as N_2 and in minor proportions as N_2O, changes in the N:P ratio may contribute to modulate phytoplankton biomass and species compositions in Lake Neusiedl, as observed in other lakes (Salmaso and Tolotti, 2021). Information is not yet sufficient for definitive assertions due to missing experimental evidence, but the results of the present study underscore the high sensitivity of this shallow lake to changing nutrient availability in relation to climate and hydrological dynamics.

Air temperatures in the region of Lake Neusiedl have been steadily increasing since the 1970s and regional climate scenarios project a decrease in summer precipitation up to 40% for the second half of the 21st century (Soja et al., 2013). Through its control over the hydrological dynamics of Lake Neusiedl, climate change may be very effective in controlling this lake's nutrient status. Moreover, although the inorganic water turbidity represents a protection against extensive algal blooms (Herzig and Dokulil, 2001), Lake Neusiedl may still undergo critical ecological transitions (Bruel et al., 2018) in relation with enhanced phosphorus release from the sediment storage, e,g. in warm and less oxygenated sheltered portions of the lake (Löffler, 1979), or if high N atmospheric deposition will persist over the region (Spangl, 2019).

Conclusion

The palaeolimnological study of pelagic sediments from Lake Neusiedl allowed a reconstruction of the evolution of the largest European shallow lake since the late 19th century. The extension of the temporal perspective to the secular scale outlined the succession of three major ecological and trophic stages after the last major lake desiccation (1865–1868), and allowed the identification of pre-disturbance lake trophic conditions during the first half of the 20th century. The study underscores that, despite their great potential to reveal past lake ecological changes, sub-fossil diatoms are not sufficient for a reliable reconstruction of past water salinity in shallow lakes in the absence of site-specific training sets. This confirms the multiproxy approach as an indispensable and powerful tool to improve the reliability and the prediction potential of sediment studies in general, and of challenging shallow lakes in particular.

In agreement with the limnological surveys, the sediment records corroborate the high vulnerability of Lake Neusiedl, both in present and past times, towards climate-driven changes in water level and salinity. Concentration processes of solutes during low lake level stages appear more effective in inducing biological responses than dilution processes during high lake level conditions. As water turbidity of Lake Neusiedl limits the phytoplankton growth, nutrient input can be considered a secondary risk factor for the conservation of the lake ecological functionality, at least as long as lake management ensures moderate P-load. However, the present study suggests that nitrogen inputs to the lake from non-point sources (i.e. agriculture, industry, and traffic) may represent an additional stressor for future lake development under moderately eutrophic conditions. As nitrogen input revealed to be crucial in driving ecological responses in lakes located in other densely populated regions of the northern hemisphere, nitrogen control should represent a focus of future lake management, together with the mitigation of global warming effects, considering

that the location of Lake Neusiedl makes it particularly exposed to airborne pollution.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jglr.2021.06.004.

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