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A diatom-based predictive model for inferring past conductivity in Chadian Sahara lakes

Remadji Rirongarti · Florence Sylvestre · Françoise Chalié · Christine Paillès · Jean-Charles Mazur · Abdallah Mahamat Nour · Wulfran Barthelemy · Hélène Mariot · Thijs Van der Meeren · Chloé Poulin · Pierre Deschamps · Moussa Abderamane

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Abstract For decades, diatoms have been recognized as powerful bio-indicators of modern water quality. They have also been utilized in the design of transfer functions, which can be applied to diatom assemblages in lake sediment cores to infer aspects of past lake hydrochemistry and estimate variables that can be incorporated into paleohydrology models. The Ounianga lakes, in the heart of the Chadian Sahara, possess unique and well-preserved sediment records that extend back beyond the middle Holocene. Today, the lakes display a range of hydrochemical conditions, from fresh to hypersaline. Mainly fed by fossil

groundwater that originates in the Nubian Sandstone Aquifer System, measured conductivity across these lakes varies from 217 to 352,000 $\mu\text{S cm}^{-1}$, values that are influenced by factors such as hydrology, local geomorphology (e.g., depth and area), and aquatic vegetation. Although these lakes have been on the UNESCO World Heritage List since 2012, they have never been studied in detail because they are located on the fringes of the Chadian Sahara. The distribution of diatom taxa in the lakes today is closely linked to water-column physical and chemical conditions, especially conductivity. Whereas each lake has particular features that influence its diatom flora, diatoms across a conductivity gradient enabled identification of three distinct waterbody types, freshwater lakes, meso-saline to hyper-saline lakes, and freshwater springs. Relationships between diatom species distributions and environmental variables were examined using multivariate analysis, which revealed that conductivity is the variable that explains most of the variance in the diatom flora. We used modern diatom assemblages from the lakes to develop a predictive model (transfer function) for conductivity, using the weighted averaging method. Our conductivity prediction model is strong, with a coefficient of determination (R^2) of 0.89 between estimated and measured values, and a value of 0.78 using jackknife estimates of prediction. This study better constrained conductivity optima and tolerance values for diatom species found in the Ounianga lakes, thereby enabling development of a model that will yield better inferences for

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past conductivity, using diatoms from lake sediment records in the region.

Keywords Sahara · Chad · Lake · Diatoms · Conductivity · Transfer functions

Introduction

The lakes of Ounianga, in northeast Chad, were added to the UNESCO World Heritage List in 2012 (UNESCO 2015). The desert water bodies form a hydrological system that is unique in the world (Kröpelin 2007). They are composed of a series of lakes and oases in the Chadian Sahara, one of the most arid desert regions on Earth. The area features extraordinary geological structures, e.g., Nubian Sandstone, and the diverse local landscape types are recognized for their beauty (Fig. 1).

Few studies have been conducted on these lakes because access to the region is difficult. A monograph from the early 1960s described the geography, climate and biogeography of the region (Capot-Rey 1961). Only one paper reported diatom observations, carried out on samples collected during an expedition in 1957 (Round 1961). More recently, paleolimnological study of a sediment core from one of the lakes, Lake Yoa, was used to infer paleoenvironmental changes in the area over the last 6000 years (Kröpelin et al. 2008). The lake displayed strong hydrological variability through time. Whereas it was a freshwater system during the middle Holocene wet period, that interval was followed by a period of lake level decline and strong salinization (Kröpelin et al. 2008). Other studies were carried out to assess changes in the zoobenthos and zooplankton communities of Lake Yoa (Eggermont et al. 2008; van Bocxlaer et al. 2011), shifts in the terrestrial environment (Lézine et al. 2011), and lake sediment dynamics (Francus et al. 2013). These studies were supplemented with an analysis of surface hydrological connections in the Ounianga lakes catchment zone during the Holocene (Grenier et al. 2009). Another study focused on three other lakes in the Ounianga hydrologic system, Edem, Hogou and Agouta, using sediment cores spanning shorter periods (<500 years) (Creutz et al. 2016). These early studies were complemented by more recent investigations of the modern hydrology and

ecology of the lakes (Poulin 2018; van der Meeren et al. 2019), and a paleoenvironmental reconstruction spanning the last 3000 years (van der Meeren et al. 2022).

Despite increased interest in the lakes of Ounianga over the last couple of decades, modern phytoplankton, especially diatoms in the waterbodies, have not been the subject of in-depth study. Nonetheless, the water conductivity inference in Kröpelin et al. (2008) was based, to a considerable extent, on the ecology of the phytoplankton community, including diatoms. That quantitative inference of water conductivity was achieved using a transfer function based on a calibration dataset compiled at the scale of Northern Hemisphere Africa (Gasse et al. 1995). Some 20 diatom samples from the lakes of Ounianga were added to the database, but those did not reflect the full range of modern limnological conditions in the area (Kröpelin et al. 2008). Today, conductivity across the lakes of Ounianga ranges from 217 to 352,000 $\mu\text{S cm}^{-1}$. The limited number of samples from the lakes of Ounianga (20), compared to the 389 that form the African database, which covers East Africa, the Maghreb and the Sahel, suggests that application of transfer functions from the broader region in Africa, to diatom assemblages in sediment cores from the Ounianga lakes, could yield large uncertainties for inferred values. Furthermore, it has been shown, in various contexts, that diatom-based quantitative inferences are much improved when local conditions are taken into account (Sylvestre et al. 2001; Mills and Ryves 2012).

The goal of this study was to develop a diatom-based model for inferring past environmental changes and diatom ecology, especially conductivity, which appeared to be the main variable explaining the distribution of diatom floras from the lakes of Ounianga. An extensive dataset was built for each lake, including information on the diatom floras and several measured limnological variables. The acquired datasets were used to explore the relationship between diatom species and environmental factors that determine their distribution in these aquatic systems. The relationship between diatoms and conductivity was used to develop a transfer function that calculated conductivity values from diatoms that are commonly observed in African lakes and elsewhere and can be used to infer past lake water conductivity from diatom assemblages in sediment cores from local water bodies.

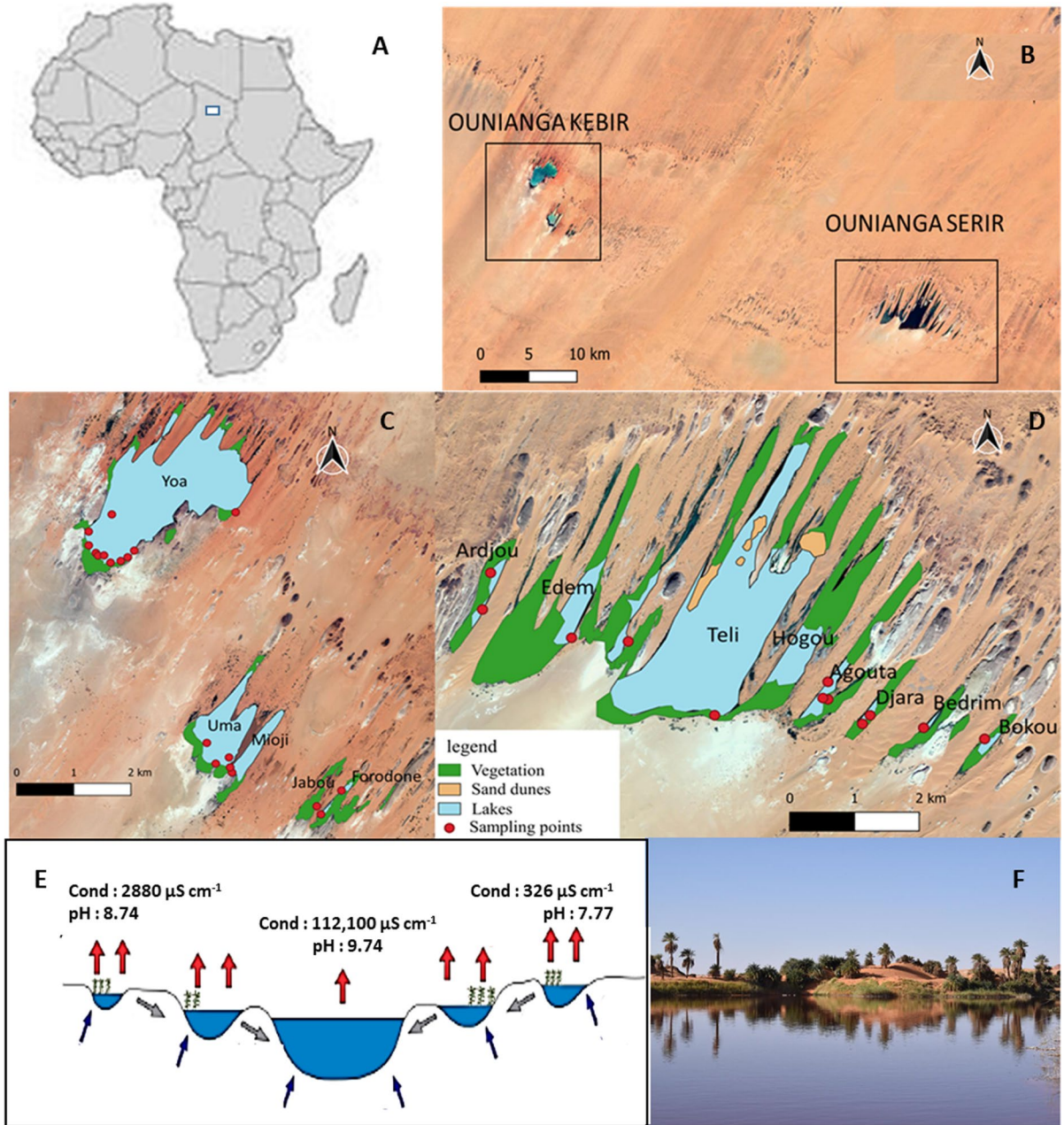


Fig. 1 A, B Location of the Ounianga lakes in central Sahara (rectangle on map of the continent). Location of the sampling points in C Ounianga Kebir and D Ounianga Serir. E Diagram of hydrologic inputs and outputs in the Ounianga Serir (modi-

fied after Poulin [2018]). Red arrows indicate evaporation, blue arrows groundwater and grey arrows infiltration of water through lakes. F Photograph of Lake Jabou, Ounianga Kebir, taken during sampling in 2016 (credit @ F Sylvestre)

Study site

The Ounianga region is located between the Tibesti volcanic mountain range and the Ennedi mountains,

and is backed up against the Erdis sandstone plateau, in one of the most arid regions of the Chadian Sahara. Located at 19° N latitude and 20° E longitude, this region of northeast Chad features lakes that lie below

narrow sandstone escarpments that were carved by the wind (Fig. 1A). The region hosts the largest lake system in the Sahara and includes two sub-basins. To the west, the Ounianga Kebir is comprised of five lakes (19°03'18''N, 20°30'20''E) (Fig. 1B). The Ounianga Serir lakes are located 50 km east (18°55'45''N, 20°51'01''E), in what is probably an aeolian depression that runs NE-SW for about 10 km. The Serir group consists of seven lakes, aligned in parallel and separated by sand dunes (Fig. 1C). All these lakes receive hydrologic input from fossil water of the Nubian Sandstone Aquifer System (NSAS), through springs located around lakes (Poulin 2018).

The region of Ounianga is characterized by a hyper-arid Saharan climate. It is marked by long periods of drought and almost no rain. Average precipitation recorded in the 1960s was $<5 \text{ mm yr}^{-1}$, whereas potential evaporation was about 6 m yr^{-1} (Capot-Rey 1961). Extreme evaporation from the lakes is compensated by groundwater inflow from the NSAS, which enables the water bodies to persist in spite of the arid climate (Kröpelin 2007; Poulin 2018).

The mean daytime temperature in the region is $40 \text{ }^\circ\text{C}$ during summer (June to August) and $25 \text{ }^\circ\text{C}$ during winter (December and January) (Capot-Rey 1961). There is vegetation only around the lake shores and it is composed mainly of *Phoenix dactylifera* (date palms). The region is subjected to very strong north-easterly winds throughout much of the year. This is reflected in the arrow-shaped sand dunes that fill in the lakes (Fig. 1A). The absence of precipitation and silting makes observation of the hydrologic network difficult (Grenier et al. 2009). The lakes are not connected to an active hydrologic network today. Rather, they are isolated in depressions $>50 \text{ m}$ below sandstone escarpments that are several km long.

The local geomorphology has contributed to the Lakes of Ounianga Kebir all being extremely saline, with conductivities ranging from $64,000$ to $352,000 \text{ } \mu\text{S cm}^{-1}$, despite the fact that the spring water that flows into them is fresh, $217 \text{ } \mu\text{S cm}^{-1}$. Lake Yoa is the largest Ounianga Kebir lake, with an area of 3.58 km^2 and maximum depth of $\sim 27 \text{ m}$. It is the deepest of the five lakes that form the Ounianga Kebir system and has never desiccated in the past 6000 years (Kröpelin et al. 2008).

The Ounianga Serir lakes are located in a 10-km-wide depression and display distinct hydrologies because of their parallel alignment and their

'staircase' positions at different elevations. The topography enables water to flow through dunes from one lake into another (Fig. 1D). Lakes at the outer margin are totally or partially covered by aquatic vegetation and fed by numerous springs. They are fresh, as indicated by the reeds that grow in them. The fresh water flows from lake to lake, gradually becoming more saline, and ultimately reaches central Lake Teli, which lies at the lowest point in the centre of the depression (Fig. 1D). Lake Teli is extremely saline ($112,100 \text{ } \mu\text{S cm}^{-1}$), with a surface area of 4.36 km^2 and a maximum depth of 5 m . The intense evaporation of the lake is compensated for by groundwater from the NSAS and by steady flow of water from the neighbouring lakes, through the dunes (Poulin 2018). The groundwater inputs and hydrologic connectivity result in constant water levels in the lakes (Kröpelin 2007). These factors are also responsible for the salinity gradient from the peripheral to the central lakes. Lake Bokou to the east has a conductivity of $326 \text{ } \mu\text{S cm}^{-1}$ and Lake Ardjou to the west has a conductivity of $2880 \text{ } \mu\text{S cm}^{-1}$, whereas centrally positioned Lake Teli has far more dissolved ions in its water ($112,100 \text{ } \mu\text{S cm}^{-1}$).

Materials and methods

Field sampling

Field missions were undertaken in 2015 and 2016, under the auspices of the 'Grands Ecosystèmes Lacustres Tchadiens (GELT)' project. During those field campaigns, we took in situ samples of water, phytoplankton and surface sediment in each lake of the Ounianga Kebir and Ounianga Serir (Fig. 1B, C; Table 1). At each site, we collected a surface sediment sample from the sediment/water interface (topmost $<1 \text{ cm}$) by scraping if the lake was shallow, or with a grab-sampler if the lake was deep and required use of a boat. At the same time and site, we collected water to measure physical and chemical variables. When conditions in the field permitted access, diatoms in surface water were collected using a phytoplankton net with $5 \text{ } \mu\text{m}$ mesh. Aquatic vegetation was also sampled by scraping, using a spatula; in some cases, we collected a piece of vegetation, to be dealt with later, in the laboratory. Water temperature, pH and conductivity (i.e., specific conductance)

Table 1 List of the samples collected in the Ounianga Kebir and Ounianga Serir lakes. (a) lake names (b) sample names (c) geographic coordinates (d) type of sample; M: macrophytes, L: water column, S: sediment (e) year of sampling (f) alkalinity in mol/L (g) major anions in mg/L (h) major cations in mg/L (i) conductivity in $\mu\text{S cm}^{-1}$ (j) pH (k) temperature in $^{\circ}\text{C}$

a Site name	b Sample name	c Latitude (N)	d Longitude (E)	e Year of sample	f Alkalinity (mol/L)	g Cl ⁻ (mg/l)	h		i cond ($\mu\text{S cm}^{-1}$)	j pH	k Temp ($^{\circ}\text{C}$)				
							SO ₄ ²⁻ (mg/l)	Ca ²⁺ (mg/l)							
Ouni- anga Kebir	Spring Yoa	19.044702	20.496489	2015	184	7	22	6	6	3	8	217	7.4	24.4	
	Spring Yoa	19.047562	20.492858	2016	84	47	37	11	5	50	4	344	6.98	31.2	
Spring Yoa	YOs1-16	19.044965	20.498185	2016	84	47	37	11	5	50	4	344	6.98	26.6	
	YOs4-16	19.05306	20.51729	2016	84	47	37	11	5	50	4	344	6.98	26.6	
Spring Uma	YOs3-15	19.045600	20.499347	2015	202	17	61	19	5	42	12	362	6.9	31.1	
	YOs2-15	19.046695	20.500436	2015	202	17	61	19	5	42	12	362	6.9	31.1	
	Yoa-A2m	19.045872	20.494408	2016	84	47	37	11	5	50	4	344	6.98	31.2	
	Yoa-A3m	19.046291	20.494045	2016	84	47	37	11	5	50	4	344	6.98	31.2	
	Yoa-A3m1	19.046291	20.494045	2016	84	47	37	11	5	50	4	344	6.98	31.2	
	UMs1-15	19.011352	20.513986	2015	201	10	13	13	4	30	7	234	7	29.3	
	MI4-16	19.00986	20.51670	2015	478	22	95	44	10	76	9	623	7.9	29.51	
	Lake Yoa	MI5-16	19.00986	20.51670	2015	478	22	95	44	10	76	9	623	7.9	29.51
		Yoa-Cm	19.049856	20.492846	2015	48,800	9656	15,744	159	19	22,425	3186	64,900	10.11	26.4
	Lake Uma	YO12-16	19.0459	20.4954	2015	48,800	9656	15,744	159	19	22,425	3186	64,900	10.11	26.6
YO13-16		19.0527	20.4967	2015	48,800	9656	15,744	159	19	22,425	3186	64,900	10.11	26.6	
Lake Mioji	UMI2-16	19.012372	20.516206	2015	124,282	80,844	41,476	73	19	107,313	10,188	352,000	10.3	25.53	
Lake Mioji	Mioj-Bm	19.01072	20.51639	2016	25,956	21,557	10,606	231	19	29,647	2899	124,000	9.03	23.76	
Lake Mioji	Mioj-Cm	19.01072	20.51639	2016	25,956	21,557	10,606	231	19	29,647	2899	124,000	9.03	23.76	
	MJI1-16	19.01072	20.51639	2016	25,956	21,557	10,606	231	19	29,647	2899	124,000	9.03	23.76	
	MJI2-16	19.01072	20.51639	2016	25,956	21,557	10,606	231	19	29,647	2899	124,000	9.03	23.76	
Lake Mioji	MJI3-16	19.01072	20.51639	2016	25,956	21,557	10,606	231	19	29,647	2899	124,000	9.03	23.76	

Table 1 (continued)

a	b	c	d	e	f	g	h	i	j	k				
Site name	Sample name	Latitude (N)	Longitude (E)	Type of sample	Alkalinity (mol/L)	Cl ⁻ (mg/l)	SO ₄ ²⁻ (mg/l)	Ca ²⁺ (mg/l)	Mg ²⁺ (mg/l)	Na ⁺ (mg/l)	K ⁺ (mg/l)	cond (μS cm ⁻¹)	pH	Temp (°C)
Lake Jabou	JAB11-16	19.00425	20.53079	S	118,177	105,867	79,075	159	19	140,192	25,935	82,700	8.2	30.84
Lake Forodone	JAB12-16	19.00425	20.53079	S	118,177	105,867	79,075	159	19	140,192	25,935	82,700	8.2	30.84
	FOR11-16	19.00687	20.53490	L	5	190	269	20	42	604	77	3000	9.1	23.05
Ouni-anga Serir	Fo-Cm	19.00292	20.53149	M	4809	250	129	30	64	3593	421	11,115	9.6	23.05
	FOR12-16	19.00292	20.53149	S	4809	250	129	30	64	3593	421	11,115	9.6	23.05
Lake Bokou	Bok-Bm	18.91546	20.91156	M	126	12	27	44	6	12	2	326	7.77	23.3
Lake Bedrim	BK11-16	18.91546	20.91156	L	126	12	27	44	6	12	2	326	7.77	23.3
	BK12-16	18.91546	20.91156	S	126	12	27	44	6	12	2	326	7.77	23.3
Lake Bedrim	Bed-Bm	18.91709	20.90261	M	29	65	63	43	15	60	10	737	8.03	24
Lake Djara	BED11-16	18.91709	20.90261	S	29	65	63	43	15	60	10	737	8.03	24
	Dja-Am	18.918912	20.894770	M	71	126	4	26	48	127	32	1343	7.97	23.1
Lake Agouta	DJ11-16	18.917662	20.89364	S	71	126	4	26	48	127	32	1343	7.97	23.1
	Agou-Bm	18.921258	20.88858	M	62	250	129	30	69	209	46	1807	8.33	23.6
	AG12-16	18.92384	20.88858	L	62	250	129	30	69	209	46	1807	8.33	23.6
	AG11-15	18.921457	20.887824	S	1013	221	142	37	47	202	47	1833	8.1	17.4
	AG11-16	18.92384	20.88858	S	62	250	129	30	69	209	46	1807	8.33	23.6
	AG13-16	18.92384	20.88858	S	62	250	129	30	69	209	46	1807	8.33	23.6
Lake Teli	TL11-16	18.91893	20.87196	S	46,726	23,817	12,750	159	19	34,500	10,920	105,100	10.2	25
Lake Edem	ED12-16	18.93029	20.85097	L	345	23	11	32	22	67	26	678	8.6	23.7
	ED11-16	18.929761	20.859285	S	461	33	26	34	32	99	41	896	8.49	23.7

Table 1 (continued)

a	b	c		d	e	f	g		h			i	j	k	
Site name	Sample name	Latitude (N)	Longitude (E)	Type of sample	Year sampling	Alkalinity (mol/L)	Cl ⁻ (mg/l)	SO ₄ ²⁻ (mg/l)	Ca ²⁺ (mg/l)	Mg ²⁺ (mg/l)	Na ⁺ (mg/l)	K ⁺ (mg/l)	cond (µS cm ⁻¹)	pH	Temp (°C)
Lake Ardjou	18.934450	20.837915	M	2016	965	316	175	9	32	490	147	2880	8.74	22.2	
Ardj-A2m	ARJII-16	18.93979	20.839101	S	2016	965	316	175	9	32	490	147	2880	8.74	22.2

were measured in situ, using a portable WTW 350i multi-meter. Twenty-six samples were collected at Ounianga Kebir and 17 samples at Ounianga Serir (Table 1). These 43 samples cover the range of all modern environments in these lakes. At some lakes and springs, at the same site with the same physical and chemical conditions, we collected multiple samples from different habitats (surface sediments, macrophytes). This was done in an effort to recover samples that spanned the broadest possible range of conditions today, and we hope, in the past.

Laboratory analyses

Water samples for elemental analysis were filtered in the field using a 0.45-µm membrane filter. Samples for cation analysis were acidified using ultrapure nitric acid. Total alkalinity of all water samples was analysed by titration (Hach). Concentrations of major elements were determined using a Thermo Scientific Dionex Aquion ion chromatography system at CEREGE (Aix-en-Provence, France). Exceptionally high concentrations of sodium and chlorine in Lakes Uma, Mioji, Forodone, Jabou and Teli made measurement of some elements, especially magnesium, impossible. The dilution required (up to 50,000x) precluded detection of other ions. Missing values for these samples were interpolated by the best analogue method, using XLStat 2019.3.1 software (Addinsoft 2019).

Preparation of samples for diatom analysis consisted of removing all sediment components other than silica. Treatment at 50 °C with hydrochloric acid (HCl) and hydrogen peroxide (H₂O₂) was done to eliminate carbonates and organic matter, respectively, and to deflocculate clays. After the chemical treatments, samples were rinsed several times in distilled water (H₂O) to remove suspended particles. An aliquot of each sample was then mounted on a slide with a coverslip and fixed with Naphrax™.

The number of species in each sample was evaluated by identification under a Nikon 80i photon microscope, at 1000× magnification, using oil immersion. Diatom counts were performed along randomly selected vertical transects. At least 400 valves were enumerated per sample.

Species were identified mainly using Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b), Germain (1981) and Gasse (1980; 1986). Species with

uncertain identification were assigned open nomenclature (sp. aff.). Taxonomic synonyms were dealt with using the revised taxonomy of Round et al. (1990).

Diatom distributions related to limnological variables and development of the diatom-based transfer function

Correspondence analysis (CA) was performed on the diatom flora with the software XLSTAT 2019.3.1 (Addinsoft 2019), to rank data and show relationships between samples and species. CA was performed using 42 selected taxa, defined by their relative abundance in 43 samples (Electronic Supplementary Material [ESM] Table S1). Taxa with <3% relative abundance and number of occurrences <2, were removed from the abundance table. This cutoff criterion was applied because in cases of species that occur in low numbers, an optimum value for an environmental variable cannot be determined accurately from the species distribution along the environmental gradient. In cases of relatively low species percentages, the optimum value for a variable could be inferred poorly. Two species that were encountered in only a single sample, but were strongly dominant (>50%), were kept (AMIJ et CAMPY; (Electronic Supplementary Material [ESM] Table S1). Such overwhelming dominance is indicative of the strong relation between the species and its environment, and we felt it was important to include these taxa in the dataset. In this specific case, the high percent abundance suggests that the species meet their optimum conditions, hence making it possible to determine the species environmental optima.

The relationship between diatom flora and environmental variables was then explored with variance partitioning, and by Canonical Correspondence Analysis (CCA), using the software CANOCO (Ter Braak 1986; <http://www.canoco5.com/>). CCA was performed on the same diatom data set used in the CA. Variables measured in the field (conductivity, pH, alkalinity) and the laboratory (Na^+ , K^+ , Mg^{2+} , Ca^{2+} , Cl^- , SO_4^{2-}) were included in the analysis. Conductivity is expressed as \log_{10} (LogCond) to reduce data dispersal, given the broad range of measured values. The log-transformed values of conductivity were used to examine a species *versus* conductivity distribution,

to conform to requirements of the statistical analysis (Feng et al. 2014).

Cation and anion concentrations were expressed in terms of relative abundance (%) with regard to total cation and anion concentrations, respectively. Ion ratios were used to describe the hydrochemical facies of the water, and expressed as the cation ratio ($\text{RC} = \text{Na}^+ + \text{K}^+ / \text{Ca}^{2+} + \text{Mg}^{2+}$) and anion ratio ($\text{RA} = \text{total alkalinity} / \text{Cl}^- + \text{SO}_4^{2-}$).

For developing the transfer functions, we selected the ordinary weighted-averaging (WA) and the tolerance-downweighted WA (WA-Tol) methods (Ter Braak and Looman 1986). We used the C2 software of Juggins (2003), which can be found at <https://www.staff.ncl.ac.uk/stephen.juggins/software/code/C2Description.pdf>. This method is particularly well adapted to these extreme environments, as optimum and tolerance for each species are calculated on the basis of species abundance relative to the environmental variable across the modern reference database. The optimum is a theoretical value of the environmental variable, at which conditions are optimal for the development of a species. The tolerance describes a theoretical value that represents the ability of the species to survive under conditions that diverge from the optimum value of the environmental variable. We present results for both ‘apparent’ estimates (the two datasets used to infer estimates and to test predictive ability are the same) and jackknife estimates. The deshrinking procedure, used to minimize bias, was applied for both classical and inverse methods. Transfer function performance was evaluated using several parameters. RMSE is the root mean square error for the estimates. R^2 is the coefficient of determination between diatom-inferred and observed (measured) values of a given environmental variable. Maximum bias indicates transfer function predictability.

Results

Environmental variables

Field measurements of physical and chemical variables, and results of laboratory chemical analyses of major elements in water samples collected in the Ounianga Kebir and Serir lakes, are shown in Table 1. The pH of the lakes ranged from 6.90 to 10.11. Conductivity displayed a range from 217 to

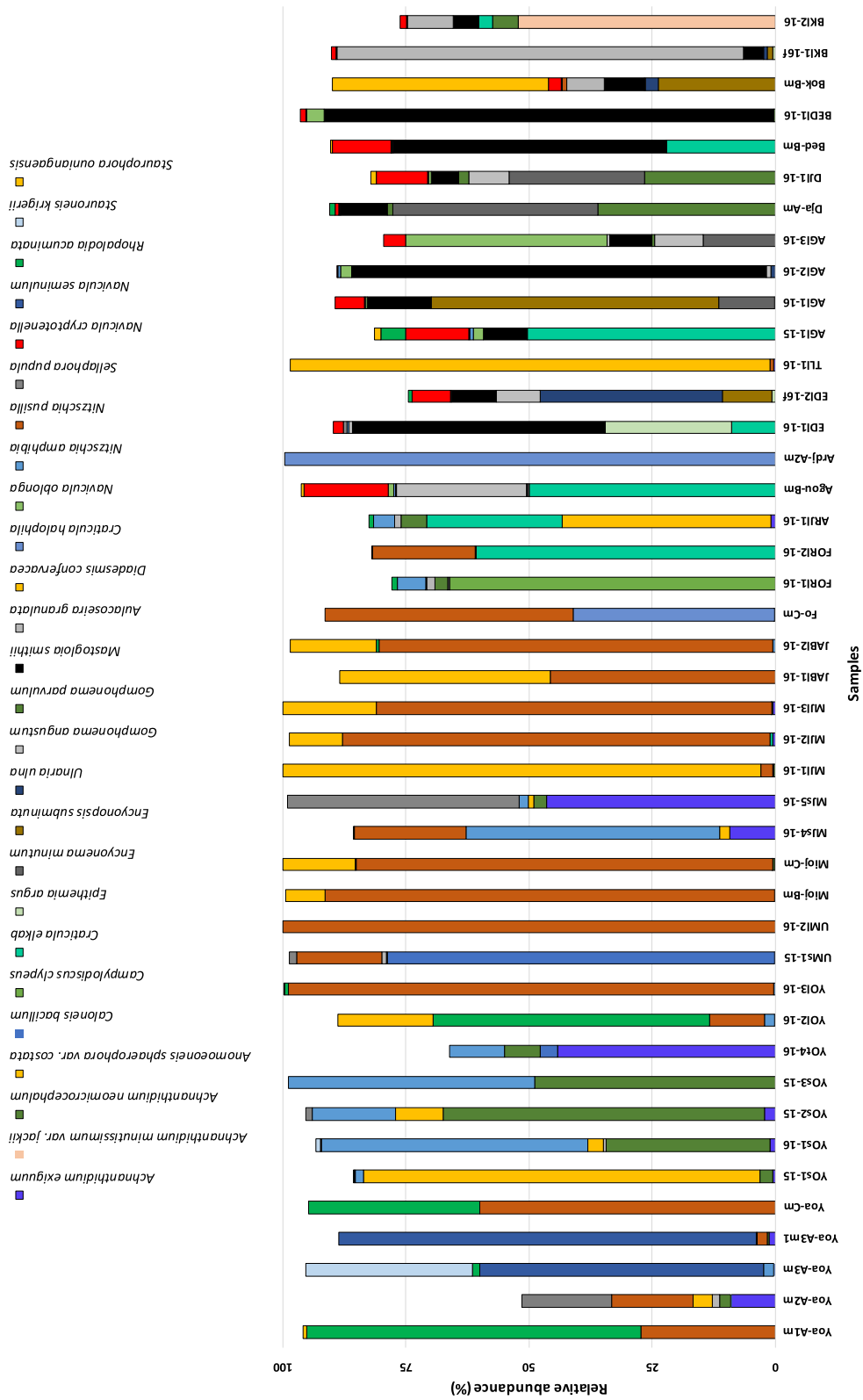


Fig. 3 Composition of the diatom flora for each sample studied in the Oumianga Kebir and Oumianga Serir lakes

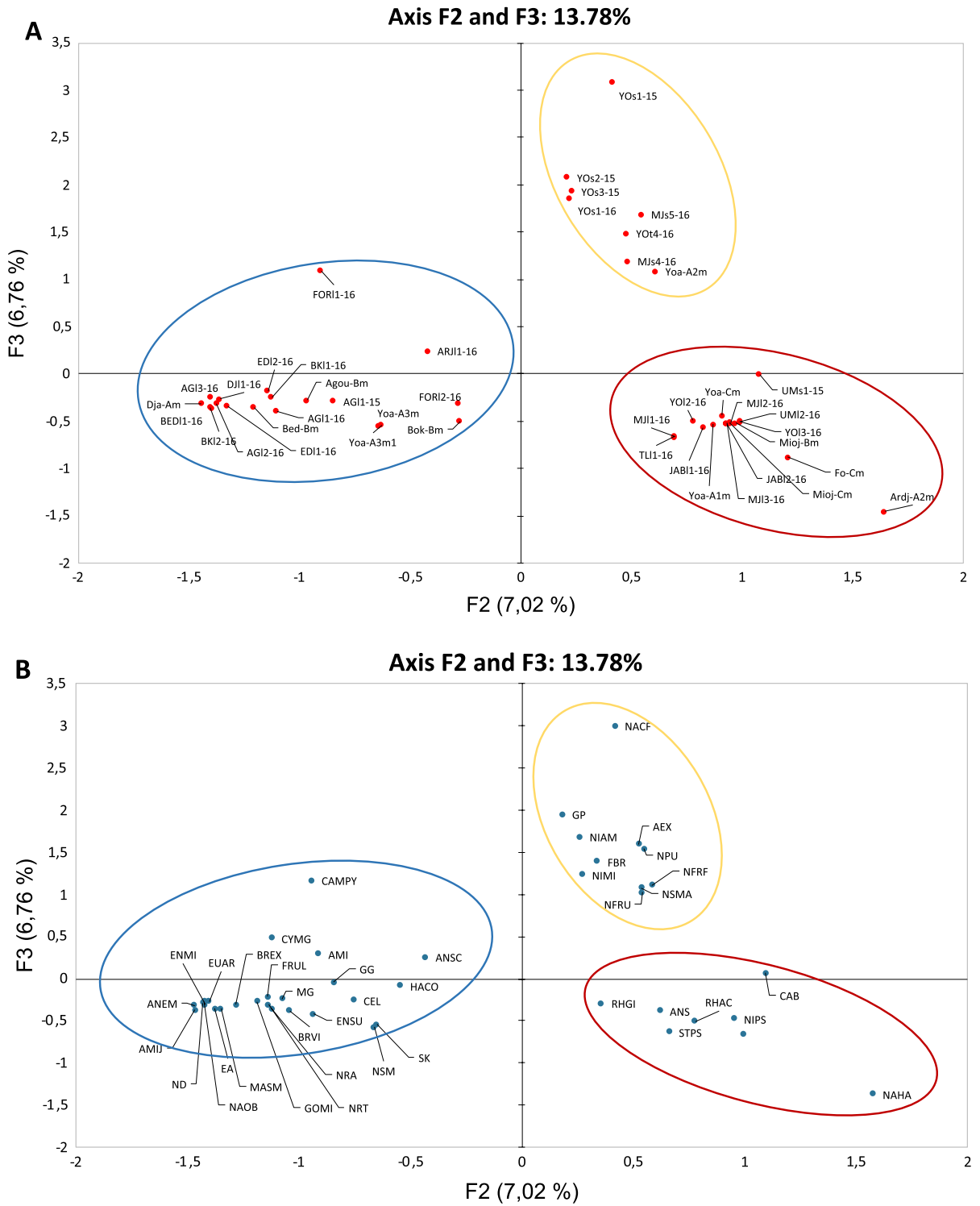


Fig. 4 Factorial plane F2x F3 of CA with **A** the distribution of samples (codes for samples are in Table 1) and **B** the species (codes for species are in ESM Table S1)

parvulum and *Nitzschia pusilla* were also observed in samples YO3-15, YO2-15, YO1-16 and MJ4-16.

Group (b) contains samples collected in the freshwater lakes (AG11-15, AG11-16, AG12-16, AG13-16, Agou-Bm, ED11-16, ED12-16, BED11-16, Bed-Bm, BK11-16, BK12-16, Bok-Bm, Dja-Am, DJ11-16 and ARJ1-16). The latter are found only in Ounianga Serir and each has individual dominant taxa, with the exception of the species *Mastogloia smithii*, *Encyonema minutum* and *Craticula elkab*, which are observed in at least two samples (Fig. 4B). *Mastogloia smithii* is present in four samples: BED11-16, AG12-16, ED11-16 and AG11-16. The species dominates overwhelmingly in samples BED11-16 (91.28%) and AG12-16 (84.26%). In sample ED11-16, it represents 51.38%, and is associated with *Epithemia argus* (25.61%). It represents 13.61% in sample AG11-16, and the diatom flora of this sample is dominated by *Encyonopsis subminuta* (58.31%). Other samples display different species assemblages, for example sample DJA1-16, in which *Encyonema minutum* accounts for 27.67%, followed by *Achnanthydium neomicrocephalum* (26.44%). Sample BK12-16, collected in Lake Bokou, contains *Achnanthydium minutissimum jacksonii*, and was the only sample in which the taxon was found. Sample ARJ1-16 is dominated by *Anomoeoneis sphaerophora costata* (42.35%) and *Craticula elkab* (27.51%). Sample AG13-16 is the only one that contains *Navicula oblonga* (40.92%), and is followed in abundance by *Encyonema minutum* (14.58%). *Aulacoseira granulata* is almost the only species in sample BK11-16 (82.53%). *Ulnaria ulna* and *Achnanthydium minutissimum* account for 36.87% and 13.48%, respectively, in ED12-16. Sample AG11-15 is dominated by the species *Craticula elkab* (50.30%), but *Navicula cryptotenella* is also present (12.88%).

The samples that make up group (c) are mainly from Ounianga Kebir, with the exception of TL1-16, which was collected in central, hypersaline Lake Teli at Ounianga Serir, and Ard-A2m, collected on reeds in Lake Ardjou (Fig. 4A). Samples from the meso-hypersaline lakes are overwhelmingly dominated by a single species. *Nitzschia pusilla* and *Stauraphora ouiangaensis* are the two best-represented taxa in these samples (Fig. 4B). *Nitzschia pusilla* represents a very high percent of the total diatoms in samples YO13-16 (98.48%), MJ13-16 (80.26%), MJ12-16 (86.88%), JAB12-16 (80.06%) and JAB11-16

(45.75%). It is the only species in sample UMI2-16 (100%), and is followed in relative abundance by *Stauraphora ouiangaensis* in samples JAB11-16 (42.71%), JAB12-16 (71.51%) and MJ13-16 (19.01%). *Stauraphora ouiangaensis* represents 97.40% of the diatom assemblage in sample TL11-16 and 97.15% in sample MJ11-16. *Nitzschia pusilla* is also observed (19.37%) in sample YO12-16, which is dominated by *Rhopalodia acuminata* (56.17%). *Craticula elkab* accounts for 60.80% in sample FOR12-16, where it is accompanied by *Nitzschia pusilla* (20.77%). Sample FOR11-16 is the only sample in which *Campylodiscus clypeus* (66.12%) is found, accompanied by *Cyclotella meneghiniana* (19.67%).

Relationships between diatoms and hydrochemical variables

The relationship between the diatom floras and physical and chemical variables in the lakes was investigated using canonical correspondence analysis (CCA). The two first axes of the CCA represent 11% of the total variance (F1: 6.86%; F2: 4.14%) (Fig. 5). On the basis of the correlation of environmental variables with these two axes, the limnological factors that most influence diatom population patterns are log conductivity (LogCond), pH, Na⁺, Mg²⁺ and Ca²⁺. They are followed by RC, Cl⁻, SO₄²⁻, and K⁺, and finally Alk and RA, which are almost uncorrelated with the first two factorial axes.

The variance inflation factor (VIF) parameter shows the extent to which a variable provides unique (or redundant) information in the dataset analysis. The higher the value of the parameter, the more the information that it provides is redundant, as regards other variables. Among the variables well correlated with factorial axes 1 and 2 above, Mg²⁺, Na⁺, and Ca²⁺ show very high VIF values (Table 2), indicating that the information provided by these three variables can be obtained using other environmental variables of interest. LogCond and pH, however, show lower values of VIF, indicating that the information corresponding to these two variables is unique in the dataset, i.e., not covered by other variables in the analysis.

Additionally, in order to determine if conductivity is the most appropriate variable, we conducted analyses of variance partitioning. For all the variables we tested (Cond, LogCond, pH, anion and cation ratios), conductivity expressed in log values showed a higher

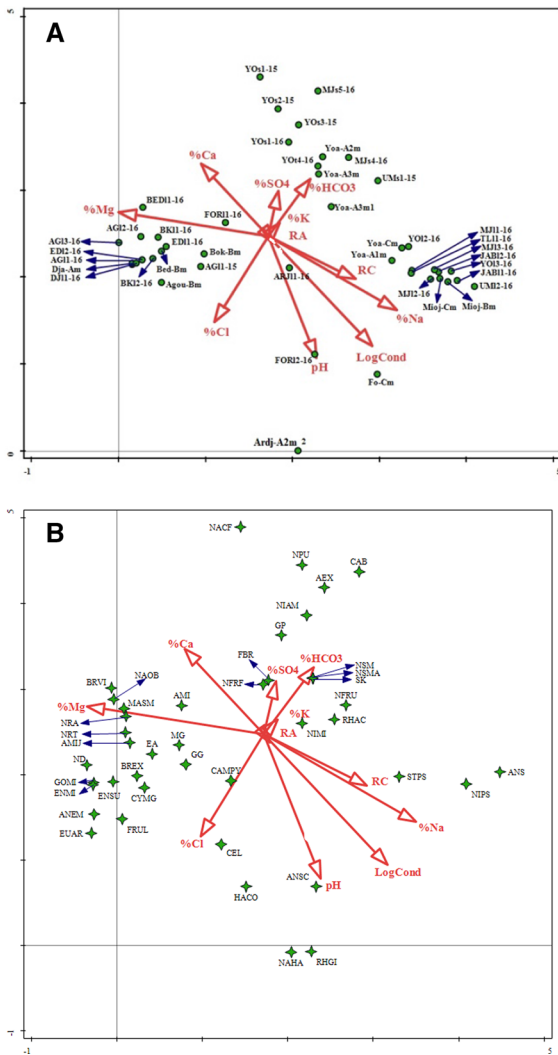


Fig. 5 CCA for 43 samples and 11 environmental variables. (A) Scores for samples and environmental variables (codes for samples are in Table 1). (B) Scores for species (codes for species are in ESM Table S1) and environmental variables. The length of each vector shows its importance in the variance of the data

explained part of the variance than did untransformed conductivity values. Compared to the other main variables (Cond expressed in log values versus pH, versus anion ratio and versus cation ratio), LogCond was always the variable that explained the higher percentage of the variance. When considering LogCond and pH, which are the main diatom-inferred reconstructed variables in the literature, the analyses show that only a minor part of the variance can be explained by the interdependence of these two variables. LogCond and

pH together explain 7.3% of the total variance. Log-Cond and pH account for, respectively, 55.8% and 27.7% of the 7.3% (i.e., 4.1% and 2% of the total variance); interaction between LogCond and pH accounts for only 16.5% of the 7.3% explained variance. We therefore considered conductivity to be the main variable for a diatom-based transfer function, and we investigated it using LogCond values.

The dataset for which the transfer function procedure was implemented was the same as that used for CCA analysis, with 42 diatom taxa in 43 samples. Regression coefficients for the deshinking procedure in both the classical and inverse methods are shown in Table 3. Performance of the transfer functions is reported in Table 4. Figure 6 shows results for Log-Cond and displays diatom-estimated values *versus* measured values for the WA-Tol_cla method, showing the best inference performance. For LogCond inference, using the transfer function method (WA or WA-Tol) and deshinking procedure (‘inverse’ or ‘classical’), the RMSEs display similar values, between 0.57 and 0.59. R^2 is between 0.75 and 0.78 (‘apparent’ R^2 between 0.87 and 0.89) and maximum bias is between 0.57 and 0.71.

Discussion

Diatom distributions in the Ounianga lakes are explained mainly by the conductivity gradient, spanning from freshwater (defined as $<1500 \mu\text{S cm}^{-1}$) to hypersaline (defined as $>60,000 \mu\text{S cm}^{-1}$) conditions, with measured values between 200 and $352,000 \mu\text{S cm}^{-1}$. Compared with other training sets from the African continent (Gasse et al. 1995; Mills and Ryves 2012), our calibration covers the broadest conductivity gradient. Intermediate conductivities, in the range 10^3 – $10^4 \mu\text{S cm}^{-1}$ are less well represented than fresh and hypersaline waters, unlike other modern calibrations (Verschuren 2003; Mills and Ryves 2012). But our calibration dataset includes several samples from lakes with conductivities between 1000 and $3000 \mu\text{S cm}^{-1}$. It also has lakes that span the gradient between 11,000 and $100,000 \mu\text{S cm}^{-1}$, but with some gaps between 3000 and $10,000 \mu\text{S cm}^{-1}$, 11,000 and $69,000 \mu\text{S cm}^{-1}$, 82,000 and $100,000 \mu\text{S cm}^{-1}$ and 130,000 and $352,000 \mu\text{S cm}^{-1}$. However, despite these gaps, our modern calibration set enabled us to develop a diatom-based inference model that covers

Table 2 Results of CCA analysis with LogCond = log (10) conductivity

Parameter	Average	Standard Deviation	Correlation				Variance Inflation Factor (VIF)
			Axis 1	Axis 2	Axis 3	Axis 4	
LgC	3.60	1.04	0.5416	-0.6464	-0.3067	0.0033	15.79
pH	8.37	1.02	0.2576	-0.5767	-0.3662	-0.0347	5.62
Mg ²⁺	13.08	12.22	-0.8879	0.3350	0.1842	-0.0326	526
Ca ²⁺	13.88	16.98	-0.3692	0.4099	0.3779	0.3357	854
Na ⁺	66.38	23.38	0.7456	-0.4453	-0.3540	-0.1931	1820
RC	94.72	223.0126	0.4171	-0.3347	-0.0993	0.0225	2.97
Cl ⁻	34.79	20.65	-0.2644	-0.2536	-0.1070	0.0379	4364
SO ₄ ²⁻	19.34	9.10	0.0770	0.4961	-0.1075	0.5157	845
K ⁺	6.77	3.30	-0.1428	-0.2207	-0.1615	-0.2004	35.6
Alk	45.92	24.22	0.1986	0.0345	0.1340	-0.2266	6079
RA	1.62	2.07	-0.0273	0.0029	-0.0258	-0.2615	5.45

RA anion ratio, RC cation ratio, Alk alkalinity

Table 3 Regression coefficients of the deshrinking procedure in the transfer function

Variable	Regression coefficients				
	Method	Inverse		Classical	
		b0	b1	b0	b1
LogCond	WA	-0.68	1.19	0.96	0.73
	WA-Tol	-0.53	1.17	0.80	0.75

a very broad range along the conductivity gradient, which should be effective for inferring extreme conductivity conditions that might have occurred in these highly sensitive lakes in the past.

Compared with other transfer functions, developed at different sites and at different scales (regional *versus* continental), our inference model for conductivity, with an apparent coefficient of determination (R^2) of 0.89, is similar to the continental-scale transfer function developed for African lakes ($R^2=0.87$, Gasse et al. 1995) and the model for Ugandan crater lakes ($R^2=0.87$, Mills and Ryves 2012). Our model is

also comparable in strength to the conductivity-based transfer functions developed for lakes in the Great Plains of North America ($R^2=0.83$, Fritz et al. 1991), in British Columbia, Canada ($R^2=0.89$, Cumming and Smol 1993) and in Bolivia ($R^2=0.77$, Sylvestre et al. 2001). Our estimated prediction error with the jackknife method is somewhat lower ($R^2_{jack}=0.78$). This prediction error is similar to that of the European Diatom Database Initiative conductivity transfer function ($R^2_{jack}=0.71$, Battarbee et al. 2001) and African semi-hemispheric-scale database ($R^2_{jack}=0.80$, Gasse et al. 1995). It is also similar to the prediction error of the salinity transfer function developed for the lakes of British Columbia ($R^2_{jack}=0.74$, Cumming and Smol 1993).

We then compared the taxa that are represented at >10% in our dataset, with those from the African semi-hemispheric-scale database (Gasse et al. 1995). After harmonization of the taxonomy, we identified only 23 species in common with the 389 species listed in the African semi-hemispheric-scale training set, meaning that with our model we defined

Table 4 Overall performance of the transfer functions

Method	Deshrinking type	Apparent			Jackknife		
		RMSE	R^2	Max. Bias	RMSEP	R^2	Max. Bias
WA_Inv	I	0.37	0.87	0.57	0.57	0.75	0.71
WA_Cla	C	0.40	0.87	0.35	0.59	0.75	0.57
WA-Tol_Inv	I	0.35	0.89	0.51	0.57	0.78	0.69
WA-Tol_Cla	C	0.37	0.89	0.32	0.58	0.78	0.60

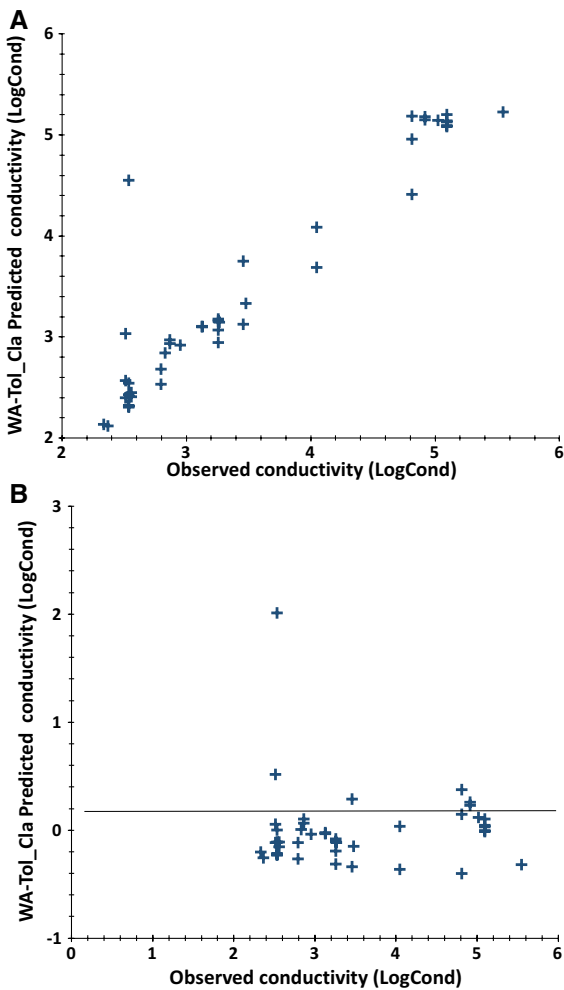


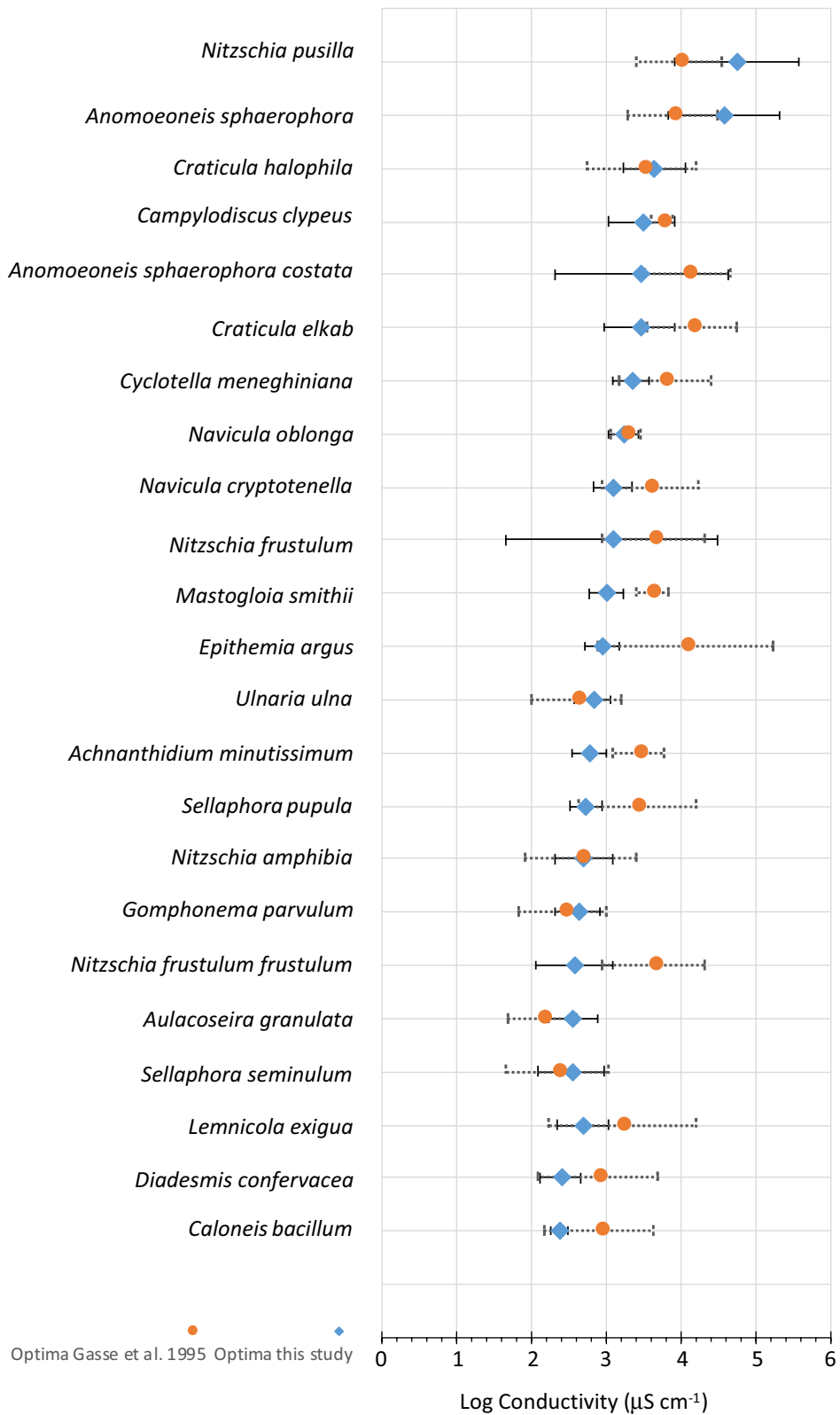
Fig. 6 **A** Diatom-inferred conductivity versus observed conductivity using WA-Tol method, and the inverse deshrinking method and **B** residuals of estimates along the conductivity gradient

new conductivity optima and tolerances for 19 species (Table S1), especially *Staurophora ouniangaensis*, which is a new species, discovered in several lakes of Ounianga (Rirongarti et al. 2022). When we compared both optima and tolerances estimated by the two models (Fig. 7), we found that few species showed good agreement. There are, however, seven species, *Craticula halophila*, *Campylodiscus clypeus*, *Navicula oblonga*, *Ulnaria ulna*, *Nitzschia amphibia*, *Gomphonema parvulum*, and *Sellaphora seminulum* for which the optimum determined in both models is quite similar. For other taxa, the estimated optima were different between models. For most species, the

optimum value was different, but given the tolerance ranges, the two estimated optimum values fell within the range of the error estimates. For other species, however, the estimated optimum and tolerance values are not compatible, despite the errors on the estimates. For instance, that is the case for *Mastogloia smithii* and *Nitzschia frustulum*.

Such inter-model differences were previously encountered when comparing the dataset from Ugandan crater lakes with the African semi-hemispheric-scale one. These differences were attributed to the gradient of conductivity and the size of the training set. For instance, the African dataset covered a larger conductivity gradient than the Ugandan dataset (Mills and Ryves 2012). In our case, our conductivity gradient is much broader (217 to 352,000 $\mu\text{S cm}^{-1}$), than that in the African dataset (40 to 99,060 $\mu\text{S cm}^{-1}$), even if there are some gaps. This enabled us to develop a model that can be used to infer conductivity values more accurately, using diatom species that are common in sediment deposits from lakes in the region, some of which are abundant and/or markers in some sequences or periods, e.g., *Craticula halophila*, *Campylodiscus clypeus* or *Nitzschia amphibia*. We were also able to define the conductivity optima and tolerances of 19 new diatom species, which will be helpful for future reconstructions of past conductivity.

We are aware that the applicability of this model could be restricted because of the low number of diatoms that were selected from the dataset. Because the robustness of application of a transfer function to a fossil dataset depends on the overlap between the modern and the fossil species, our calibration may have limited utility for application to a sediment record. But our calibration includes several species that are widely encountered, sometimes dominating or characterizing the diatom assemblages in African lakes. Moreover, comparison between our dataset and the one developed at the African semi-hemispheric scale also suggests the need to use regional calibration when developing a transfer function for application to fossil diatoms in a specific locality (Sylvestre et al., 2001; Mills and Ryves 2012). For instance, in Lake Yoa, a diatom record that spanned the last 6000 years was analyzed, and a transfer function based on the Africa semi-continental-scale dataset was selected to infer conductivity (Kröpelin et al. 2008). This record displayed a significant increase in conductivity ca. 4200 years ago, viewed as a major



◀**Fig. 7** Weighted average conductivity optima and tolerances for species with a minimum percentage of 10% in the Ounianga lakes dataset, compared with similar species in the African semi-hemispheric-scale database (Gasse et al. 1995)

hydrological event during the Holocene. This event is supported mainly by the occurrence in the assemblage of *Craticula elkab*. Based on our Ounianga calibration-based transfer function, *Craticula elkab* has a lower optimum (3.44 logCond, $\mu\text{S cm}^{-1}$) than in the African continental-scale model (4.14 logCond, $\mu\text{S cm}^{-1}$). This difference does not dramatically alter the results inferred from the Lake Yoa record, but our regional Ounianga lakes diatom-based conductivity model very likely improved the accuracy of the inferred conductivity values.

Conclusions

This study of the modern diatom flora in the lakes of Ounianga revealed large differences in taxa from one lake to another. The diatom flora of each lake reflects the lake's particular physical and chemical conditions, suggesting that the relation between a species and an environmental variable is unimodal. The Ounianga lakes feature large differences in conductivity related to morphological differences (depth, area), hydrology, and aquatic vegetation cover. Each diatom species displays a distinct optimum conductivity value (Ter Braak and Van Dam 1989). Diatom species are distributed according to conductivity and other chemical features of the waters, making it possible to distinguish among freshwater lakes, meso-saline and hyper-saline waters, and springs.

The conductivity transfer function performs well, providing: 1) more appropriate conductivity optima and tolerance values for several diatoms species, than those obtained from previous datasets, and 2) conductivity and tolerance values for some species, never before investigated on the African continent. This new model also suggests that it yields accurate inferences of past conductivity and fills a gap with respect to the study region. It is therefore thought to be a robust 'package,' which can be applied now to relevant fossil diatoms in sediment cores and should yield accurate estimates of past hydrochemical conditions in Saharan lakes.

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