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Research Article

Benthic diatom communities in high altitude lakes: a large scale study in the French Alps

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Abstract – Altitude lakes are weakly impacted by human activities. This makes them choice ecosystems to understand how biological communities are impacted by natural factors. This question was addressed to littoral benthic diatoms, a largely used ecological indicator. We wanted to know if benthic diatoms in lakes are more impacted by local varying factors (altitude, lake depth...) or regional varying factors (geology). The study area takes place in the Northern French Alps. Littoral benthic diatoms of 63 natural lakes situated between 1350 and 2700 m · a.s.l. were sampled. Two categories of communities were observed: one of deep and lower altitude lakes and one of higher altitude and shallower lakes. In each category, communities were characterized and were corresponding to particular lake types: lakes dominated by a particular geology, lakes with a water level fluctuation, turbid lakes,... Communities did not show a spatial structure. We observed that local factors were more important than regional factors. Indeed, the study area displayed a mixed geology even at a local level. On another hand, altitude a local varying factor determines freezing period a determining item of high-altitude lake functioning.

Keywords: Bacillariophyta / high altitude lakes / shoreline / structuring parameters / water framework directive

1 Introduction

Bacillariophyta (diatoms) is a clade of microalgae which is widely distributed through all types of water bodies. Diatoms are a key component of aquatic ecosystems because they are usually the dominating primary producers (Mann and Droop, 1996). Moreover, benthic diatoms are also known as the main element of phytobenthos both in terms of biomass (Stevenson, 1998) and species diversity: more than 1,00,000 species exist on the earth (Mann and Vanormelingen, 2013) and 700 species are commonly found in European freshwater ecosystems (Lange-Bertalot *et al.*, 2013). Diatoms have a short generation time and each species has particular tolerances to organic matter and nutrients (Crossetti *et al.*, 2013; Rimet *et al.*, 2016). These characteristics make them excellent candidates to be ecological indicators. Indeed the first studies demonstrating the effect of pollution on freshwater diatom diversity was over a century ago (Kolkwitz and Marsson, 1908) and 40–50 years after, several authors proposed methodologies based on the taxonomic composition of diatom communities to assess pollution mostly in rivers (*e.g.* Butcher, 1947; Hustedt, 1957; Zelinka and Marvan, 1961). Subsequently, hundreds of studies demonstrated the high sensitivity of this class to anthropogenic pressures (Rimet and Bouchez, 2012a). This convinced water authorities to use benthic diatoms in their legislation to assess the ecological quality of freshwater ecosystems. Indeed, since 1972 in the United States with the Clean Water Act and since 2000 in Europe with the Water Framework Directive, water legislators require to assess the ecological quality of water ecosystems with ecological indicators, among which are diatoms. Many biotic indices, such as the Biological Diatom Index in France (Coste *et al.*, 2009) were developed and are now standardized and routinely applied. More effort has been done to improve the monitoring using benthic diatoms in rivers than in lakes (Cantonati and Lowe, 2014). However, from several years things changed and some authors applied existing river diatoms indices to the littoral zone of lakes (Blanco *et al.*, 2004; Bolla *et al.*, 2010; Cellamare *et al.*, 2011) while others developed new tools based on diatoms communities (Schaumburg *et al.*, 2007; Stenger-Kovács *et al.*, 2007; Marchetto *et al.*, 2013; Bennion *et al.*, 2014) to respond to the demands of lakes assessment. Indeed, whereas phytoplankton is considered as the main ecological indicator on lakes, and usually is used to assess the overall lake quality, littoral diatoms demonstrated their efficiency to assess point source pollution and to be early warning of lake's deterioration (Cantonati and Lowe, 2014; Rimet *et al.*, 2016). Moreover, they can show a better ability to

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assess lake's trophic level than pelagic phytoplankton (Rimet *et al.*, 2015). Therefore, use of diatom indices is a complementary of ecological indicator lakes assessment with phytoplankton.

Lakes are often at the crossroads of multiple societal and economic challenges and most of them are under strong anthropogenic pressure and suffer growing eutrophication (*e.g.* Ostendorp *et al.*, 1995; Millennium Ecosystem Assessment, 2005). High-altitude lakes are among the least impacted lakes largely because they are characterized by an altitude level above 800 meters a.s.l. (Parlement européen *et al.*, 2000) and in such altitudes, human activity is much lesser. Moreover, compared to the other lakes, they can be considered as young and extreme ecosystems (Zaharescu *et al.*, 2016). The elevated topography, the low ions and nutrients contents and the strong climate control make them particular ecosystems where a limited number of species are able to develop (Magnea *et al.*, 2013; Zaharescu *et al.*, 2016). With more than 50,000 high-altitude lakes across Europe (Kernan *et al.*, 2009), a number of studies were conducted to understand the functioning of these lakes (*e.g.* Patrick *et al.*, 1998; Battarbee *et al.*, 2002) and several key results can be highlighted. First, high-altitude lakes have an important patrimonial value due to the small anthropogenic pressure they suffer compared to other lakes. Thus unique plant and animal communities are living around and within these ecosystems (Kernan *et al.*, 2009; Magnea *et al.*, 2013). Second, due to this low impacted character, high-altitude lakes are considered as excellent sensors of environmental changes because of their sensitivity to acid deposition (*e.g.* Jones *et al.*, 1993; Curtis *et al.*, 2009), persistent organic pollutants deposition (Grimalt *et al.*, 2009), trace metals (Camarero *et al.*, 1995, 2009), greenhouse gases and climate change (*e.g.* Beniston *et al.*, 1997). All these global factors affect several chemical and biological characteristics within high-altitude lakes such as species distribution and nutrient cycling (*e.g.* Parker *et al.*, 2008).

Several studies highlighted that natural factors which impact benthic diatoms are minimized because anthropological pressure leads on a homogenization of the communities (*e.g.* Pan *et al.*, 2000; Leira and Sabater, 2005; Tornés *et al.*, 2007). Therefore, because high-altitude lakes are profuse and known to be pristine, these ecosystems appear to be good study sites to analyze the influence of natural parameters on benthic diatoms communities. Moreover, as high-altitude lakes are preserved but endangered ecosystems, applying benthic littoral diatoms to assess anthropogenic pressure is also an objective to take into consideration and which meet the requirements of the natural area managers (National Parks, Conservatory of natural spaces) and the Water Framework Directive. Many studies already demonstrate the influence of natural and/or regional parameters on communities of diatoms such as dominant geology of the catchment area in rivers (Kernan *et al.*, 2009; Rimet, 2009; Soininen, 2004, 2012), the latitudinal gradient (Vyverman *et al.*, 2007) or the climate change in high-altitude lakes (Kernan *et al.*, 2009). Therefore, to respond to the problematic "Are the communities of benthic diatoms in high altitude lakes more structured by local or regional parameters?" this study will focused on two main objectives:

– describe the different communities of benthic diatoms in high-attitude lakes;
– study the main structuring parameters, through regional and local drivers, of these communities. Regional factors include geology, concentrations in calcium, magnesium, sodium, chloride and sulfate and geographical lakes coordinates whereas local parameters are altitude, depth, nutrients, dissolved organic carbon and suspended matter concentrations, pH.

According to the previous studies in particular in rivers (*e.g.* Rimet, 2009; Soininen, 2004), the expected conclusions are that littoral benthic diatom communities in high-altitude lakes will be more structured by regional parameters.

We applied this question to 62 high-altitude lakes situated in the Northern French Alps, with an altitude situated between 1350 and 2700 m · a.s.l. Samplings were carried out once, in summer 2013. Then diatom communities will be explored using a cluster analysis and their structuring parameters will be defined using multivariate analyses.

2 Materials and methods

2.1 Study area and sampling strategy

The study area is situated in the French Alps. This mountain chain is 350 km north-south and is composed by two main areas. First, the Southern Alps are characterized by low mountains and a meteorology close to the Mediterranean climate. Annual precipitations range from 850 to 1000 mm (Meteo France, 2016). Second, the Northern Alps are higher and present wetter climate with annual precipitations ranging from 1200 to 1500 mm (Meteo France, 2016). There are more than six hundred lakes showing diverse typologies (geologies, altitudes, size, etc.) in this mountain chain.

Thirteen mountain massifs in the Northern Alps were sampled. A massif is composed by several mountains and delimited morphologically by valleys. The aim of this study was to study a large range of high-altitude lakes with low anthropogenic pressure. Therefore, 62 natural lakes localized above 1300 m · a.s.l. and which have a surface area higher than 3000 m^2 were sampled (Fig. 1). Reservoirs or lakes of human origin were excluded.

The study area stretches from 46°16' to 45°03' of latitude. Sampled lakes present different characteristics. Approximately 55% of the lakes catchment areas have a siliceous geology whereas 38% have a calcareous geology. 57% of the lakes had one or two refuges in their catchment area. Pastoralism is the dominant activity in 27% of the studied lakes but can also be absent from the catchment area (17.5%). Different limnological, physical and chemical characteristics of lakes are given in Table 1.

2.2 Sampling and laboratory procedures

Benthic diatoms were sampled according to the guidance protocol (King *et al.*, 2006) in summer (July 2013). One sample was collected per lake. The sampling station had to be in light and far away as possible from effluent arrivals, peatlands and refuges. Five stones were collected at 40–50 cm depth and their upper surface was scraped using a tooth brush. The biofilms collected were handled as a composite sample and fixed with 70% ethanol before being treated according to

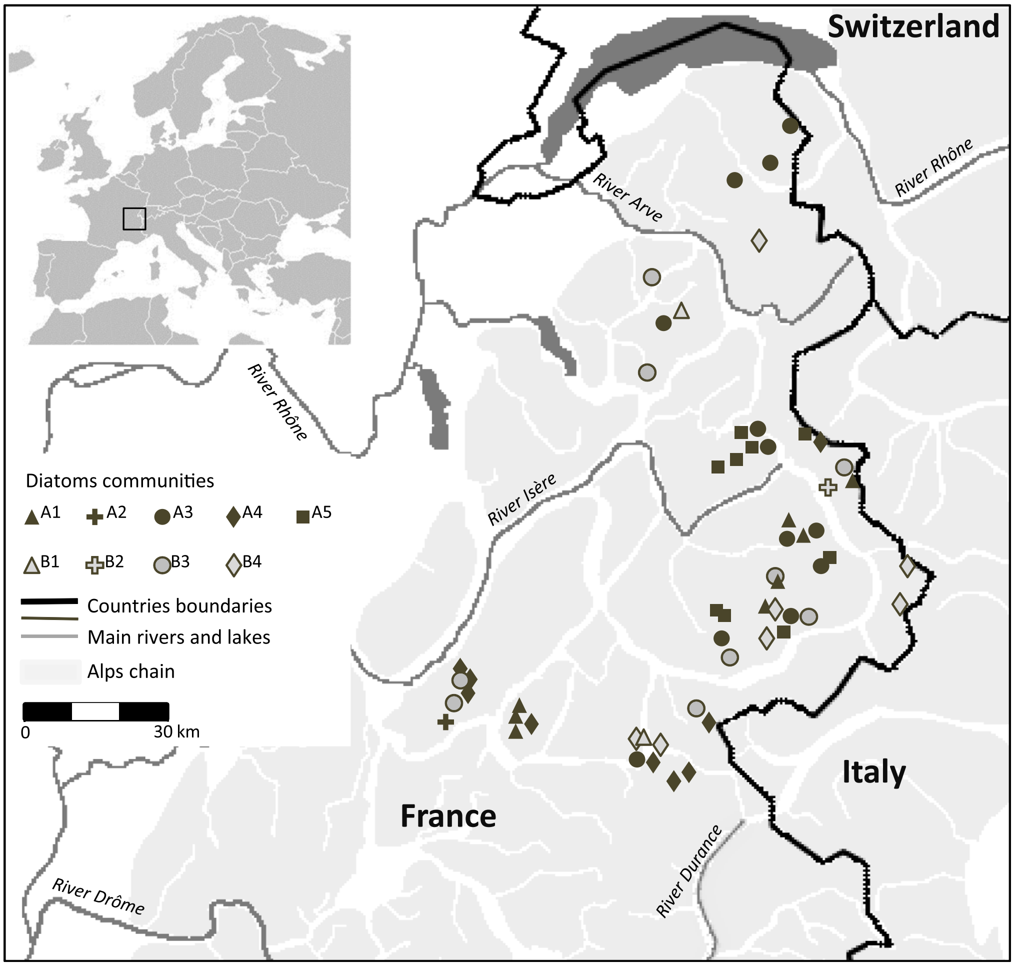

Fig. 1. Location of the study area and of the lakes. The diatom community of each lake is given.

the European standard EN 13946 (Afnor, 2003) using H_2O_2, HCl and Naphrax to assemble permanent slides. Four hundred of frustules per sample were finally counted and identified at the species level according to EN 14407 (Afnor, 2014) using classical European floras (Krammer, 1997a, 1997b; Krammer and Lange-Bertalot, 1997; Krammer, 2000, 2002; Krammer and Lange-Bertalot, 2004; Krammer *et al.*, 2008; Krammer and Lange-Bertalot, 2010). Benthic diatoms and chemical samples were collected at the same time: an integrated sample of water was collected in the middle of the lake with a Van Dorn's bottle. Chemical analyses were carried out following standard procedures (APHA, 1995). Conductivity, pH and temperature were measured in the field with a probe.

Physical and environmental characteristics were also recorded. Altitude, lake size, catchment area size and geology were extracted from maps and from digital terrain models. Maximal depths were found in bibliography.

2.3 Statistical analysis

To define benthic diatoms communities in high-altitude lakes a clustering analysis was carried out. Therefore, main diatoms assemblages composed by groups of lakes with homogeneous taxonomic compositions were determined with TWINSPAN (Hill, 1979). Classifications obtained were tested with MRPP (Mielke *et al.*, 1981) which allowed to choose the best classification thanks to A and p values. A value describes the homogeneity within a group. Then, each group of lakes has been characterized by mean communities of benthic diatoms and ranges of chemical and environmental parameters. Thus, box-plots were created for each parameter and each diatom community. Moreover, for each diatom community, its composition in ecological guilds and in saprobic classes (Van *et al.*, 1994) was defined using the database of Rimet and Bouchez (2012b). Box-plots were drawn for each ecological guild and saprobic class. An Indicator Species Analysis (Dufrêne and Legendre, 1997) was also used to characterize indicator species of each group of lakes. All these analyses were realized with PC-ORD software (McCune and Mefford, 2006).

To determine the main structuring parameters of diatoms communities in high-altitude lakes, CCA were realized on the entire database (biological, chemical and environmental data). Chemical and environmental data were firstly standardized. These analysis were realized with PAST software (Hammer *et al.*, 2015).

3 Results

A total of 326 diatom taxa were identified at the species or sub-species level on 62 diatoms samplings (one sampling per lake). The diatom communities of high-altitude lakes were

Table 1. Summary of mainslimnological, physical and chemical parameters in the sampled high-altitude lakes.

	Average	Standard deviation	Min	Max
Altitude (m)	2290	333	1355	2798
Depth (m)	9.7	6.89	2.1	36.1
Size of the lake (ha)	3.0	2.3	0.3	13.2
Size of the catchment area (ha)	137.6	195.0	2.9	1424.3
pH	7.87	6.95	8.57	0.45
Conductivity ($\mu S \cdot cm^{-1}$ 20°C)	122	135	9	959
Chlorophyll ($mg \cdot m^{-3}$)	3.38	6.64	0.01	29.28
Total P (mgP/L)	0.010	0.109	0.001	0.043
NO_3^- (mgN/L)	0.034	0.029	0.000	0.100
SiO_2 (mg/L)	1.20	0.72	0.08	2.89
Ca^{2+} (mg/L)	17.63	14.87	0.55	58.77

dominated by the genera *Achnanthidium*, *Encyonema*, *Encyonopsis*, *Denticula*, *Staurosirella* and *Navicula*. The most common and abundant species was *Achnanthidium minutissimum* (Kützing) Czarnecki. This species was identified in 62 lakes and its average abundance is 21.8%. Likewise, *Encyonema minutum* (Hilse) Mann was observed in 60 lakes and represented on average 10.2% of the diatom communities in high-altitude lakes. *Encyonopsis subminuta* Krammer & Reichardt and *Denticula tenuis* Kützing were also common and dominant species because they were respectively observed on 50 and 49 lakes with mean averages of 6 and 7% of the frustules observed on these sites. The others main species were *E. ventricosum* (Agardh) Grunow (48 lakes, 4.3%), *Cymbella excisa* Kützing (46 lakes, 2.7%) and *Staurosirella pinnata* (Ehrenberg) Williams & Round (35 lakes, 4%).

3.1 Description of benthic diatom communities

The results of MRPP applied on Twinspan's classifications showed a global increase in the A-value (statistic measuring group homogeneity) as the number of clusters increases. However because of the highly significant A-value ($p < 0.001$) a total of 9 groups of lakes was chosen. These groups gather from 1 to 12 lakes. Figure 2 shows that the final Twinspan's classification. We explained these clusters using biological, chemical, physical and environmental parameters available for this study. Characterization of each group was made thanks to the analysis of mean communities, especially with dominant and indicative species (Tab. 2), but also from box-plots of the ecological guilds, saprobic classes composition (Fig. 3) and of environmental parameters (Fig. 4) and for the 9 diatom assemblages.

The two first communities (A and B) were distinguished by the depth of the lakes. Then, inside community A, lakes are separated according to their trophic level (A1, A4) and their geology (A3, A4 and A5). Inside community B two communities (B1 and B2) were separated because they presented aerophilic and subaerial species and the last two communities (B3 and B4) are characterized by a particular typology. Precise descriptions and references to literature are given in the first section of the discussion.

3.2 Main structuring parameters

A canonical correspondence analysis (CCA) was produced to identify the main structuring parameters of benthic diatom communities. It was applied on all lakes, parameters and species. Figure 5a shows that the main structuring parameters on the first axis are one the positive side lake depth, magnesium and silica concentrations; on the negative side sulfate concentration, depth and altitude. On the second axis, on the positive side the most structuring parameter is lake size and on the negative side calcium concentration. From this first analysis a second graph (Fig. 5b) was realized to compare distribution of each main group of lakes (A and B). This one highlighted a separation between the two clusters along axis 1 (13.45% of inertia). Indeed, group A is positively correlated to axis 1, contrary to group B. The main structuring parameters of this axis are the depth, the silica and magnesium concentrations on the right and the sulfates and suspended matter concentrations with the altitude on the left. Therefore lakes of the group A are deep with high magnesium and silica concentrations whereas lakes of the group B have a higher altitude and higher concentrations in sulfates and suspended matter.

4 Discussion

4.1 Description of the benthic diatom communities

Two main diatom communities were observed: first, diatom communities of deeper lakes with lower altitudes (communities A); secondly those of shallower lakes with higher altitudes (communities B). Both communities can be subdivided into smaller ones which are presented here down.

4.1.1 Diatom communities of deeper lakes (A)

4.1.1.1 Diatom communities of oligotrophic lakes on various geologies (A1)

This diatom community is present in lakes scattered in several mountain chains. These lakes display diverse altitudes, geologies and depths. But based on their low nutrient level they can be considered as ultra-oligotrophic to oligotrophic lakes (Organisation de coopération et de développement économiques, 1982). This community is composed mainly by low-

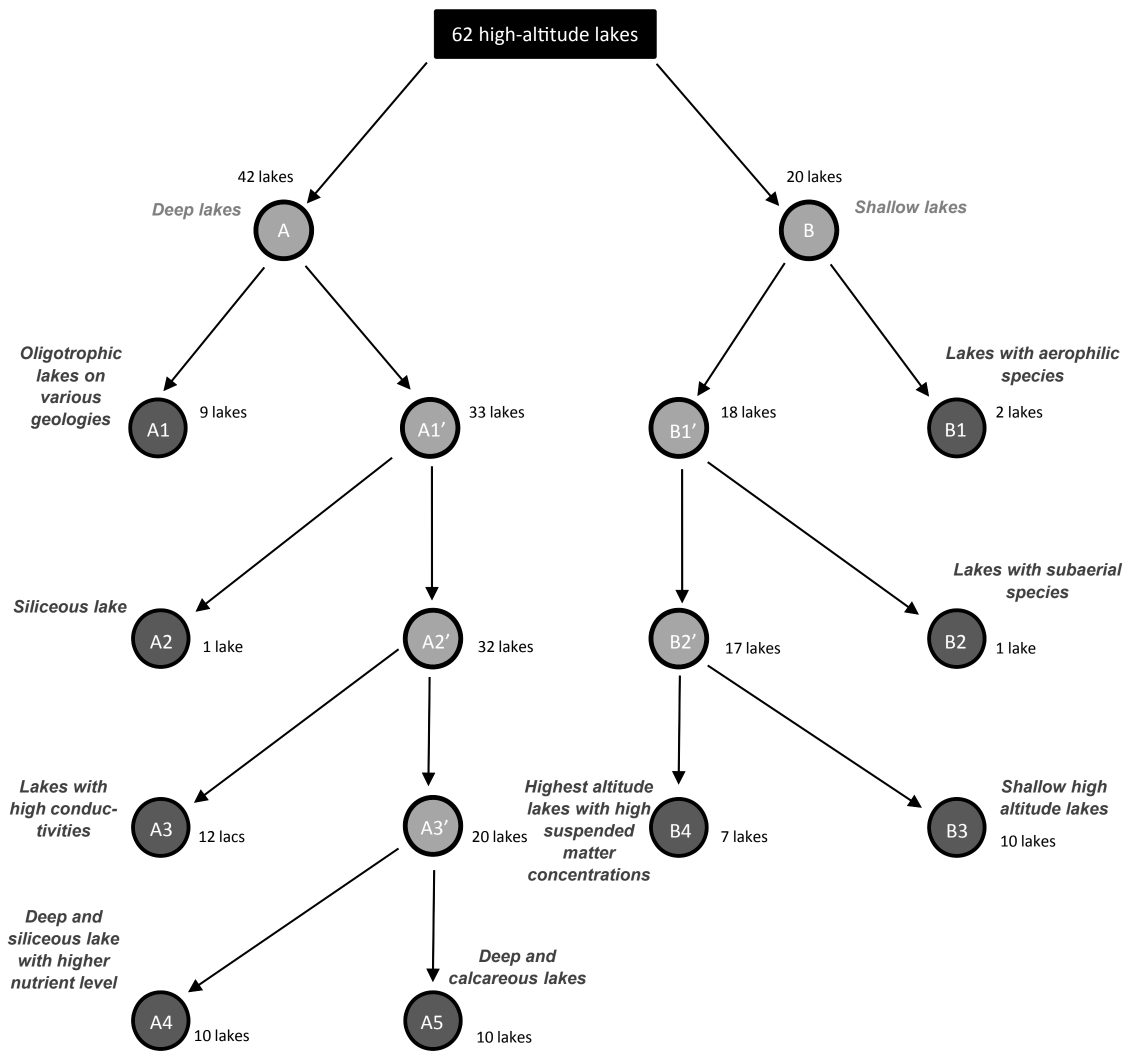

Fig. 2. Groups of samples defined on the basis of their diatom composition. The groups were calculated using a Twin span analysis.

profile (54.7%) and β-mesosaprobic (42.4%) species such as *A. minutissimum* and *E. minuta* (Van *et al.*, 1994). These two species are often observed in oligotrophic lakes (*e.g.* Acs *et al.*, 2003). *A. minutissimum* have a rather wide ecological amplitude (Van *et al.*, 1994; Acs *et al.*, 2003)and is considered as an early colonizer quickly growing when biofilms are scoured (Rimet *et al.*, 2009). *E. minutum* as well as *D. tenuis* were also abundant in this group and are mostly found in ecosystems with low nutrients concentrations (Van *et al.*, 1994; Hofmann *et al.*, 2011). The dominant and indicative taxa of this group are usually observed in calcareous environments: it is the case of *E. minutum* (Rimet *et al.*, 2003; Gomà *et al.*, 2005), *D. tenuis* (Sabater and Roca, 1992), *Brachysira vitrea* (Lange-Bertalot and Moser, 1994) and *Cymbella subleptoceros* (*e.g.* Bahls, 2016).

4.1.1.2 Diatom communities of siliceous lake (A2)

Only one lake, lake Achard (situated in Belledonne's mountain chain) compose this particular diatom community. Its water presented a very low conductivity (37 µS/cm) and is surrounded by a siliceous bedrock. Its community is mainly composed by low-profile (57.1%) diatoms, and its species composition is dominated by *A. subatomoides*, *A. minutissimum* and *Staurosira venter*. *A. subatomoides* is a clear indicator of low conductivities and of siliceous geologies, since it has already been regularly observed in rivers flowing on limestones (Rimet *et al.*, 2004) or granites geologies (Rimet, 2009).

4.1.1.3 Diatom communities of higher conductivities lakes (A3)

This community is present in lakes of a wide variety of mountain chains and presenting a variety of typologies and nutrients levels. Nevertheless, their common characteristic is to have relatively high water conductivities (223 µS/cm on average). The diatom community is dominated by low-profile (46.6%) and β-mesosaprobous (46.6%) diatoms (Van *et al.*, 1994; Rimet and Bouchez, 2012b). Among the dominant species, which are *A. minutissimum*, *E. subminuta*, *Staurosirella pinnata* and *D. tenuis,* two of them are indicators of these relatively high waters conductivities. Indeed, *A. minutissimum* and *D. tenuis* have already been recorded as indicator taxa

Table 2. Dominant species and indicator species for each diatom community. Dominant species are the species with an abundance over 5% and are given in grey. Stars after the abundance are given if the species is a significant indicator species: ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; $^{+}$: $p < 0.1$. Groups A2 and B2 were represented by only one lake therefore indicator species were not possible to calculate for these groups.

Species	Abundance (%)
Group A1	
Achnanthidium minutissimum (Kützing) Czarnecki	28.49
Encyonopsis minuta Krammer & Reichardt	9.86**
Encyonema minutum (Hilse) Mann	9.78
Staurosirella pinnata (Ehrenberg) Williams & Round	6.77
Denticula tenuis Kützing	5.15
Cyclotella comensis Grunow	5.12
Staurosira construens var. binodis (Ehrenberg) Hamilton	2.86*
Nitzschiaper minuta (Grunow) Peragallo	0.66*
Cymbella subleptoceros Krammer	0.16*
Brachysira vitrea (Grunow) Ross	0.11*
Group A2	
Achnanthidium subatomoides (Hustedt) Monnier, Lange-Bertalot & Ector	35.00
Achnanthidium minutissimum (Kützing) Czarnecki	16.67
Staurosira venter (Ehrenberg) Cleve & Moeller	7.14
Psammothidium chlidanos (Hohn&Hellerman) Lange-Bertalot	6.43
Group A3	
Achnanthidium minutissimum (Kützing) Czarnecki	20.67
Encyonopsis subminuta Krammer&Reichardt	10.03+
Staurosirella pinnata (Ehrenberg) Williams & Round	8.74
Denticula tenuis Kützing	6.48
Navicula cryptotenella Lange-Bertalot	2.38*
Nitzschia vacuum Lange-Bertalot	1.96*
Achnanthidium caledonicum (Lange-Bertalot) Lange-Bertalot	1.24+
Group A4	
Achnanthidium minutissimum (Kützing) Czarnecki	28.63
Denticula tenuis Kützing	12.59
Nitzschia costei Tudesque, Rimet & Ector	5.98
*Achnanthidium lineare*Smith	3.08*
Staurosira construens Ehrenberg	2.52+
Achnanthidium daonense (Lange-Bertalot) Lange-BertalotMonnier& Ector	1.08*
Psammothidium levanderi (Hustedt) Czarnecki	0.65**
Rossithidium pusillum (Grunow) Round & Bukhtiyarova	0.32*
Group A5	
Encyonopsis microcephala (Grunow) Krammer	14.45**
Achnanthidium minutissimum (Kützing) Czarnecki	10.93
Denticula tenuis Kützing	7.40
*Encyonopsis subminuta*Krammer&Reichardt	5.53
Delicata delicatula (Kützing) Krammer	5.00*
Encyonopsis moseri Krammer & Lange-Bertalot	4.3+
Encyonema simile Krammer	0.39+
Group B1	
Encyonema minutum (Hilse) Mann	38.72*
Pinnularia borealis Ehrenberg	11.36*
Achnanthidium minutissimum (Kützing) Czarnecki	9.68
Hantzschia amphioxys (Ehrenberg) Grunow	6.68***
Navicular adiosa Kützing	6.18**
*Encyonema caespitosum*Kützing	3.75*
*Cymbella compacta*Østrup	1.38*
Diadesmis contentavar. biceps (Grunow) Hamilton	0.5*

Table 2. (continued).

Species	Abundance (%)
Navicula subalpina Reichardt	0.25**
Caloneis silicula (Ehrenberg) Cleve	0.25*
Group B2	
Achnanthidium minutissimum (Kützing) Czarnecki	38.50
Adlafia muralis (Grunow) Monnier& Ector	17.75
Nitzschia acidoclinata Lange-Bertalot	7.25
*Navicula exilis*Kützing	5.25
Mayamaea permitis (Hustedt) Bruder& Medlin	5.00
Sellaphora minima(Grunow) Mann	5.00
Group B3	
Achnanthidium minutissimum (Kützing) Czarnecki	25.29
Encyonemaminutum (Hilse) Mann	24.65
*Encyonopsis subminuta*Krammer&Reichardt	7.15
Encyonema ventricosum (Agardh) Grunow	6.29
Gomphonema parvulum (Kützing) Kützing	0.42+
Group B4	
Encyonema minutum (Hilse) Mann	21.36
Achnanthidium minutissimum (Kützing) Czarnecki	16.14
Encyonema ventricosum (Agardh) Grunow	15.81*
Nitzschia acidoclinata Lange-Bertalot	5.82*
Navicula exilis Kützing	1.83*
Adlafia muralis (Grunow) Monnier& Ector	1.15*

from mineralized rivers in Spanish mountains headwaters (Tornés *et al.*, 2007). Moreover, *E. subminuta,* which is an indicative species of this community, is usually leaving in calcareous ecosystems (Hofmann *et al.*, 2011).

4.1.1.4 Diatom communities of deep siliceous lakes with higher nutrients levels (A4)

This diatom community is present in lakes of several locations and have in common that they are relatively deep (14 m depth on average) and have among the lowest conductivities recorded in this study (64 µS/cm on average). The geology of their catchments areas is siliceous. Another common feature of these lakes is their relatively elevated nutrient level compared to the other lakes of this study (0.01 mg/l of total phosphorus). The dominant diatoms are mostly low profiles (47%) and β-mesosaprobic (44%) diatoms (Van *et al.*, 1994; Rimet and Bouchez, 2012b). But an uncommon feature compared to the other diatom communities of this study is the presence of *Nitzschia* genus among the dominant taxa: *Nitzschia costei* is usually observed in mesosaprobic and eutrophic rivers of the Loire river basin in western France (Tudesque *et al.*, 2008). Indicative species of this community are *A. lineare*, *A. daonense*, *Psammothidium levanderi* and *Rossithidium pussilum*, they are clearly indicators of low conductivities (Sonneman, 2000; Van de Vijver *et al.*, 2011; Hofmann *et al.*, 2011). Even if *Nitzschia costei* indicates eutrophic waters, the trophic level of these lakes remains modest in an absolute framework, since the majority of the taxa of these lakes are indicators of oligotrophic waters. These results suggest that *N. costei* is probably more ubiquitous that stated in the current literature.

4.1.1.5 Diatom community of deep and calcareous lakes (A5)

This diatom community is present in several lakes scattered in the study area. The common features of these lakes are their important depth and their presence on calcareous bedrocks. This community is dominated by *E. microcephala*, *A minutissimum*, *D. tenuis* and *E. subminuta*. *E. microcephala* is an indicator of karstic (Reichardt, 1997) and pristine waters (Krammer, 1997a; Potapova and Charles, 2007; Van *et al.,* 1994). *E. subminuta* shows relatively similar ecological requirements as it was also observed in low impacted and calcareous environments (Van *et al.*, 1994; Hofmann *et al.*, 2011; Bey and Ector, 2013). Moreover, Sabater and Roca (1992) observed that, *D. tenuis* was abundant in calcareous springs of the Pyrenees. Finally, the indicative specie *Delicata delicatula* is also characteristic of calcareous ecosystems and indicator of very good water quality (Bey and Ector, 2013). Therefore the diatom species of this community clearly reflects calcareous and oligotrophic lakes.

4.1.2 Diatom communities of shallower lakes (B)

4.1.2.1 Diatom communities with aerophilic and subaerial species (B1 and B2)

Diatom community B1 is present in two lakes of different typologies. However, their particularity compared

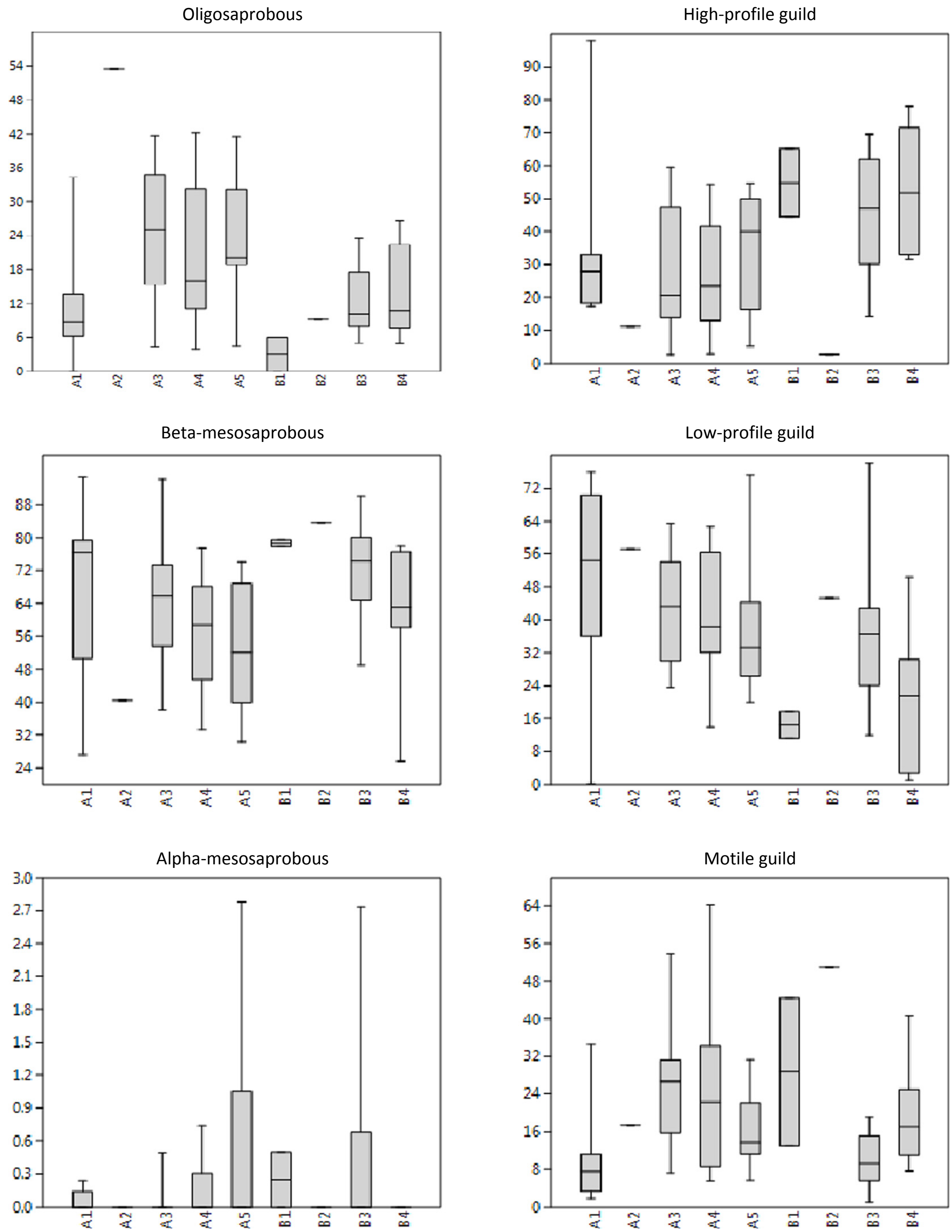

Fig. 3. Box plot of ecological guilds and saprobic classes (Van et al., 1994) abundances (%) in each diatom community. 25th and 75th percent quartiles are drawn using a box, median is shown with a horizontal line inside the box, minimal and maximal values are shown with whiskers.

to all the other lakes is their very special species composition. Indeed, three out of nine of their indicative species are aerophilic. It is the case of *Pinnularia borealis* which is quite common in soils (Ciniglia *et al.*, 2007) and dry environments (Van de Vijver and Beyens, 1999; Sonneman, 2000). *Hantzchia*. *amphioxys* is also a species that easily resists dry periods (*e.g.* Souffreau *et al.*, 2013). And finally *Diadesmis contenta var. biceps* is also aerophilic (*e.g.*Van De Vijver and Beyens, 1999; Lowe et al., 2014). We can assume that the high abundances of aerophilic diatoms can be related to possible fluctuations of the water level drying an important area of the littoral zone, and therefore favouring such diatom species.

A second diatom community, (B2) presents similar ecological features. It has a high abundance of *Adlafia muralis* (17% of the diatom community) which is subaerial species (Van *et al.*, 1994), able to resist to shorter dry periods than species of group B1. As well as group B1, we can assume the abundance of this species is explained by water levels fluctuations.

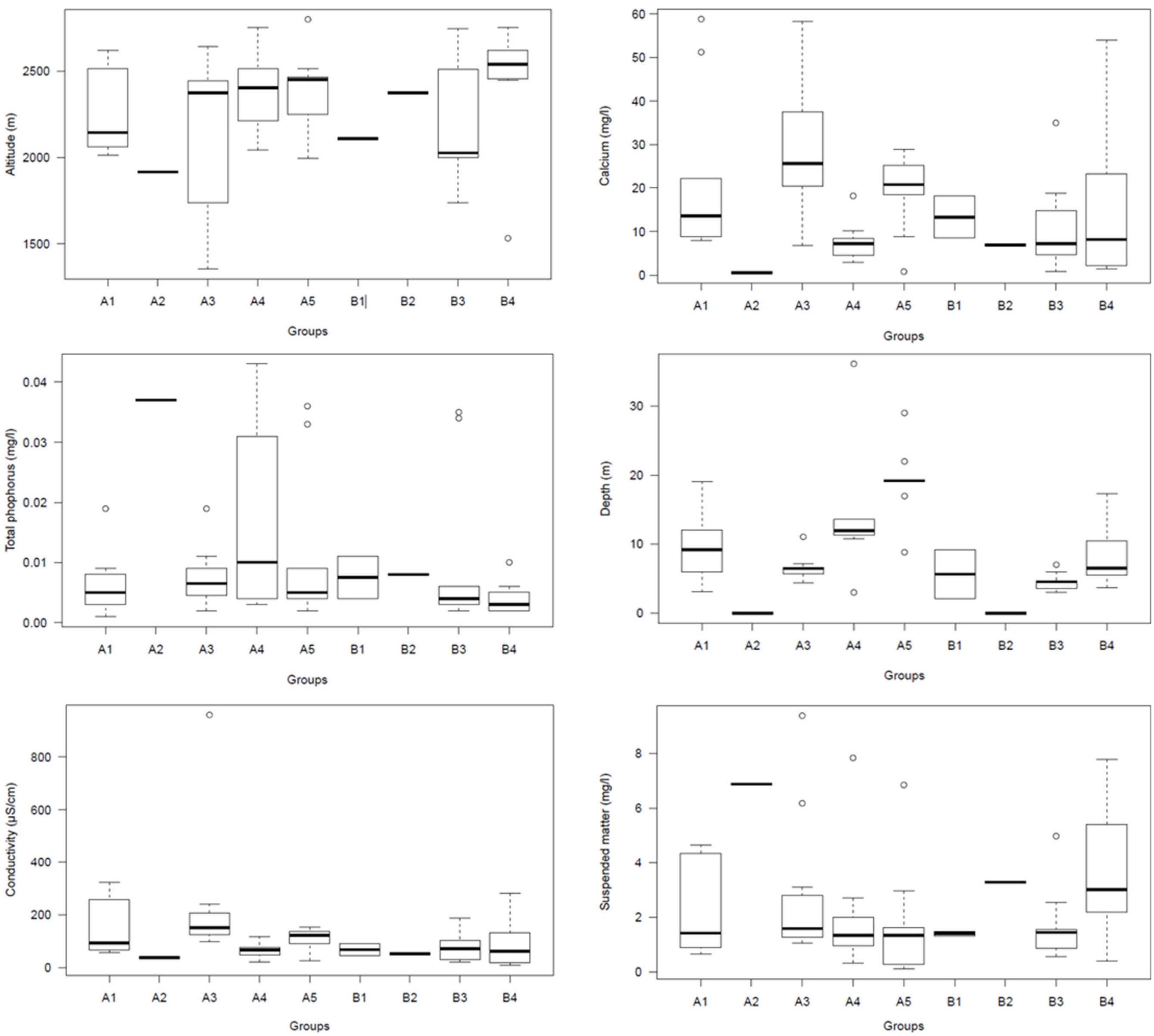

Fig. 4. Box-plot of environmental parameters for the 9 diatom assemblages.

4.1.2.2 Diatom communities of shallow high altitudes lakes (B3)

These diatom communities are present in the shallowest lakes (3.0–7.0 m) of this study (apart lakes of diatom communities A2 and B2). It is composed mostly by low-profile (41.9%) and high-profile species (40.7%). Dominant species are *A. minutissimum*, *E. minutum*, *E. subminuta* and *E. ventricosum*. This cluster has no indicative species.

4.1.2.3 Diatoms communities of the highest altitude lakes with high suspended matter concentrations (B4)

This diatom community is present in the highest altitudes lakes (2371 m on average) which also present the highest suspended matter concentrations (2.63 mg/l on average). These high suspended matter concentrations may explain the presence of two particular indicative species, *Nitzschia acidoclinata* and *Navicula exilis,* which belong to genera known to prefer waters with high suspended matter (Battegazzore *et al.*, 2003). Moreover, these two species are characteristic of slightly acidic waters (Bey and Ector, 2013). The other dominant species (*E. minutum, E. ventricosum, A. minutissimum*) are indicators of oligotrophic waters (*e.g.* Van *et al.*, 1994).

4.2 Local factors impact more diatom communities composition than regional factors

Geology was an important parameter to consider to explain diatom species composition in our study area but its importance was secondary compared to the other parameters such as lake's depth, altitude and suspended matter. We could distinguish communities occurring in lakes with a calcareous watershed (A5) from communities occurring in lakes with a siliceous

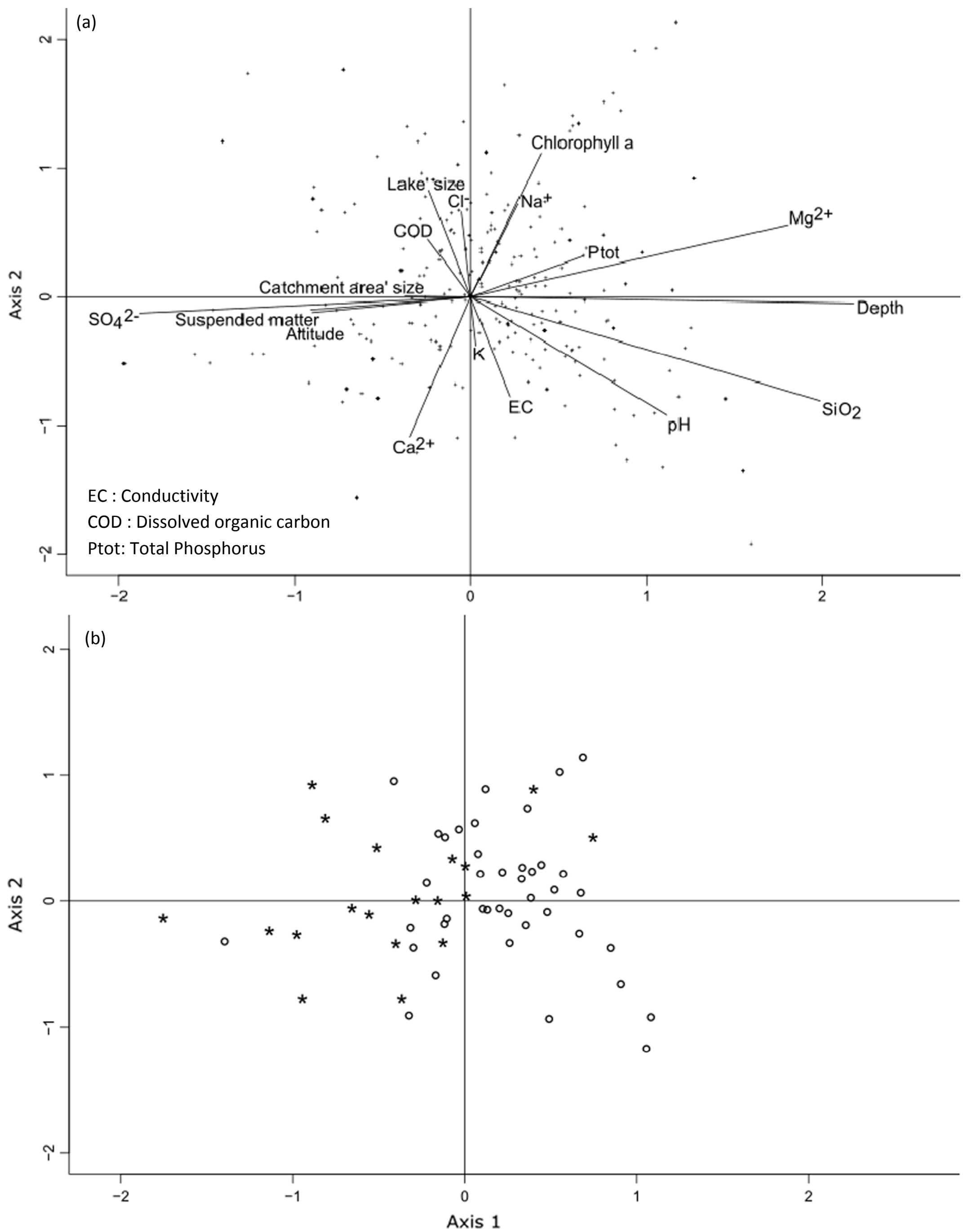

Fig. 5. Ordination diagrams for Canonical Correspondance Analyse (CCA). (a) Species and parameters, axis 1 and 2 respectively explain 13.45 and 10.66% of inertia, (b) lakes and their diatom community belonging: A (°) or B (*).

watershed (A2 and A4). Such discrimination between diatom communities living in contrasted geologies (crystalline *vs.* sedimentary geologies) has already been mentioned several times in rivers from several countries such as U.S.A, France, Luxembourg (*e.g.* Rimet *et al.*, 2004; Tison *et al.*, 2004; Weilhoefer and Pan, 2006; Rimet, 2009). It was also mentioned in high altitude lakes in Europe for sub-fossil diatoms (Kernan *et al.*, 2009) and epilithic diatoms (Marchetto *et al.*, 2009). Geology in rivers is often a main environmental parameter explaining diatom species composition and several authors observed that it is more important to consider than local factors such as pollution level (*e.g.* Rimet *et al.*, 2004; Tison *et al.*, 2004; Rimet, 2009). This was not the case of the lakes we studied and this can probably been explained by the often mixed geologies of the lake's basins we studied. Even if some mountain chains have homogeneous geologies and host diatom communities clearly related these geological substrates, geology of the Alps is often complex with sedimentary and crystalline rocks mixed at a local or regional scale. This situation probably hid and reduced the importance of geology to explain diatom species composition.

The main parameters structuring benthic diatoms communities were lake's depth, altitude and suspended matters concentration. These parameters allowed to distinguished two types of lakes, deeper lakes with lower suspended matter and lower altitudes (communities A) and shallower lakes with higher suspended matter concentrations and higher altitudes (communities B). These factors vary locally. We also observed some communities presenting several aerophilic and subaerial species (B1, B2). Such communities probably occur in lakes which have an important water level fluctuation. Water level fluctuation was already observed as an important structuring factor of littoral diatom communities (Wantzen, 2008). Water level is a feature which also varies locally. Another feature which varies locally is trophic level, which enables to discriminate particular diatom communities in our study area (A4). And finally, the different diatom communities we observed were scattered in our study area and their distribution did not show a clear spatial distribution.

All these results show that local factors are more important to explain diatom communities' composition in the high altitude lakes of French Alps than regional factors. This is in accordance with other authors who also observed that local factors are more important. This is often the case when pollution –a local varying factor- masks the impact of geology in rivers (*e.g.* Tornés *et al.*, 2007). Indeed, pollution is often considered as homogenising species composition (Leira and Sabater, 2005; Pan *et al.*, 1999; Tornés *et al.*, 2007). But pollution was not the overriding parameter in our study area since high altitude lakes are upstream most of human activities. Altitude was one of the most important structuring parameter in our study area. Indeed altitude of a high altitude lake determines its surface freezing duration (*e.g.* Pourriot and Meybeck, 1995), which has an obvious impact on lake biology and therefore on diatom species composition. This factor of primary importance selects only a few species able to survive these extremes habitats as is has already been shown on planktonic diatom of Alpine lakes (Lotter and Bigler, 2000). UV radiations intensity is also related to altitude and also structure littoral communities (Vinebrooke and Leavitt, 1999) and this may impact diatom communities. Similarly, lake's depth was also an important structuring factor in our study area. Shallow lakes are more turbulent and this structure biological communities (*e.g.* Pourriot and Meybeck, 1995). Moreover, diatom of the littoral zone of the lakes are strongly impacted by physical pressures such as wave action (Stevenson and Stoermer, 1981; Hoagland and Peterson, 1990) which again confirms the importance of this locally varying factor.

5 Conclusion

In conclusion, the benthic diatom communities of the high altitude lakes of the French Alps did not show a spatial distribution. The most important structuring factors were varying locally and were altitude, lake's depth and suspended matter. They were not related to geology, which is often considered as an important structuring parameter for river diatoms, but to parameters which were related to physical processes, such as duration of surface water freezing or water turbulence.

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