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# 1 **Planktonic shift with dissolved organic matter**

## 2 **properties: a functional perspective for sentinel lakes**

3

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26 **ABSTRACT**

27 1. Seasonal variations in mountain lakes regulate phytoplankton communities, which are thus  
28 considered as useful indicators mirroring environmental conditions. Climate change is altering  
29 both dissolved organic matter (DOM) properties and phytoplankton dynamics in sentinel  
30 lakes. Here we examined the relationship between dissolved organic matter (DOM) and  
31 planktonic communities to investigate how ecological functions in an oligotrophic lake  
32 change over time. Physical, chemical, and biological data were analyzed during three pre-  
33 defined periods running from complete ice-cover right to the end of the ice-free season to  
34 assess the relationship between DOM, bacteria, and phytoplankton functional phenology.

35 2. The results showed that phytoplankton functional change occurred with dissolved organic  
36 matter variation. Phytoplankton community was dominated by small size autotrophs and  
37 mixotrophic flagellates during the *ice-influenced* period when DOM from sediment and  
38 terrestrial origin dominated the DOM pool of the lake. Phytoplankton diversity and richness  
39 increased during the post-snowmelt *overturn* period when terrestrial DOM dominated the  
40 DOM pool of the lake. Finally, large siliceous autotrophs, competitive under small nitrogen  
41 concentrations and high temperature, dominated almost exclusively the community during the  
42 *late summer* period. Because increasing of phytoplankton biomass, phytoplankton-derived  
43 DOM was dominant during the *late summer* period.

44 3. These phenological changes in phytoplankton community resulted in functional shifts at the  
45 base of the food web: the nature of the relationship between phytoplankton and bacteria  
46 progressively shifted, from strong top-down control exerted by phytoplankton over bacteria  
47 toward predominantly bottom-up control at the end of the ice-free season.

48 4. *Synthesis*. Phenological functional shifts occur rapidly and are related to local processes,  
49 like change in dissolved organic matter properties, nutrient limitation, temperature, and light

50 availability. Phytoplankton functional traits are useful indicators of whole ecosystem  
51 ecological functioning.

52 **KEYWORDS**

53 Mountain lakes; Functional traits; Global change; Trophic interactions; Biogeochemical cycles

54 1. INTRODUCTION

55 In mountain lakes, phenological variations regulate phytoplankton communities, making them  
56 useful indicators mirroring environmental conditions (Kuefner et al., 2021; Oleksy et al., 2020).  
57 Phytoplankton communities during the ice-free season in high-altitude lakes have been widely  
58 described. A large peak of phytoplankton biomass is typically observed in late summer (Pulido-  
59 Villena et al., 2008; Tiberti et al., 2013), usually associated with shifts in community  
60 composition and functional traits. Small unicellular flagellates have been observed in early  
61 summer, followed by a shift toward less edible taxa in late summer, like large mucilaginous  
62 colonies, flagellates (McKnight et al., 1990; Tiberti et al., 2013) or chlorophytes (Pulido-  
63 Villena et al., 2008). However, this successional pattern is not always observed and depends on  
64 the characteristics of the lakes (Jacquemin et al., 2019). Increasing data recorded on  
65 phytoplankton community structure during winter in high-altitude lakes reveals patterns similar  
66 to other seasonally ice-covered lakes (Özkundakci et al., 2016). Phytoplankton taxa show  
67 functional traits that enable them to survive during winter under ice (Bertilsson et al., 2013),  
68 like small size, motility, or mixotrophy (Rue et al., 2020). However, there are gaps in our  
69 knowledge of how phytoplankton shifts occur between ice-covered and ice-free seasons, and  
70 how functional shifts may affect whole lake ecosystem functioning.

71 Dissolved organic matter (DOM) is a very good sensor for mountain lake structure and function  
72 (Aiken, 2014). High-altitude lakes traditionally exhibit an autochthonous DOM fluorescence  
73 signature (Bastidas Navarro et al., 2014; Sommaruga & Augustin, 2006). Nevertheless, DOM  
74 origin can vary at short-term, seasonal, and interannual time scales. For example, allochthonous  
75 DOM can be transferred to lakes during snowmelt and extreme rainfall events at high altitude  
76 (Perga et al., 2018; Sadro et al., 2011). An advancing treeline due to temperature increase, as  
77 well as more frequent extreme precipitation events, may enhance allochthonous inputs in  
78 mountain lakes and their connectivity with their surrounding catchments (Harsch et al., 2009).

79 DOM dynamics strongly affect internal lake processes through direct and indirect  
80 transformations at the base of the food web (Creed et al., 2018). Seasonal variations in DOM  
81 origin and nutrient limitation patterns in high-altitude lakes should lead to temporal variations  
82 in microbial interactions (Jacquemin et al., 2018). Depending on the nutrient limitation, increase  
83 of allochthonous C has been shown to reduce bacterial reliance on phytoplankton-produced  
84 carbon (Jansson et al., 2000), stimulate bacterial biomass, and increase predation over bacteria  
85 by mixotrophs (Bergström, 2009). Experimental DOC and nutrient additions have induced  
86 different interaction between bacterioplankton and phytoplankton in winter, early summer, or  
87 in late summer in a high-altitude lake (Dory et al., 2021; Dory et al., unpublished results). Thus,  
88 a clearer picture is needed of how the phytoplankton-bacterioplankton relationship varies from  
89 the ice-covered to the ice-free season according to DOM dynamics in high-altitude lakes.

90 High-altitude lakes have been identified as sentinels of global change (Moser et al., 2019).  
91 However, their value as sentinels is highly dependent on how well we understand their internal  
92 processes, determined to a large extent by climate seasonality (Catalan, Ventura, et al., 2002).  
93 The functioning of high-altitude lakes is traditionally divided into ice-covered and ice-free  
94 periods, and most studies focus on one period. Based on various lake indicators, however, some  
95 studies track temporal changes on a finer scale to further describe internal lake processes. By  
96 analyzing changes in microbial assemblages, Felip et al. (2002) discriminated between three  
97 periods of winter cover in an alpine high mountain lake. Ecosystem metabolism (Sadro et al.,  
98 2011) and DOM dynamics (Olson et al., 2021) allowed to highlight a snowmelt influence until  
99 late July or after the beginning of August. Tiberti et al. (2013) observed a late summer peak of  
100 phytoplankton biomass in October, slightly behind the physico-chemical variations.

101 We considered three periods ranging from complete ice-cover to the end of the ice-free season  
102 in an alpine lake: (i) the ice-influenced period; (ii) the overturn period; (iii) the late summer  
103 period. The temporal dynamics of dissolved organic matter (DOM) and planktonic

104 communities over these three periods were examined to better understand how lake ecological  
105 functions change over time. We hypothesized that the signature of DOM would be less  
106 influenced by allochthonous inputs and phytoplankton production during the ice-influenced  
107 period, mainly determined by allochthonous inputs during the overturn period, and mainly  
108 determined by primary production during the late summer period. We also anticipated  
109 phytoplankton functional changes according to environmental variations, with more winter-  
110 adapted traits and mixotrophic taxa during the ice-influenced period and more autotrophy  
111 during the ice-free season. Finally, we expected functional shifts at the base of the food web  
112 with a modified balance between heterotrophy and autotrophy, linked to the temporal dynamics  
113 of DOM, bacterioplankton, and phytoplankton communities.

## 114 2. MATERIALS AND METHODS

### 115 2.1. Lake area, sampling, and definition of time periods

116 Samplings were performed in the oligotrophic high-altitude Lake Cordes (Dory et al., 2021a).  
117 The lake was sampled 11 times between February 2020 and July 2021, divided into three  
118 periods. The lake was sampled four times during the ice-influenced period (IIP, from February  
119 to mid-June), four times during the overturn period (OP, from mid-June to late July), and three  
120 times during the late summer period (LSP, from August to October) (**Table A1**). On every date,  
121 samples were collected from the deepest area of the lake. Water was sampled using a Niskin  
122 Bottle 1 m above the bottom and 1 m below the surface. All the samples were realized in  
123 triplicate and then fixed and stored in the field in containers appropriate to the analyses to be  
124 performed in the laboratory. Abiotic parameters of temperature, dissolved oxygen, and turbidity  
125 were monitored using an Exo2 multiparameter probe (YSI, United States) placed 1 m above the  
126 lake bottom.

### 127 2.2. Biotic and abiotic parameters

#### 128 2.2.1. Environmental and climate parameters

129 Water properties of the lake (temperature, dissolved oxygen, and turbidity) were averaged from  
130 continuous data measured by the multiparameter probe. Data were obtained every hour and a  
131 daily average was calculated for each sampling day. Daily precipitations were taken from a  
132 weather station located about 14 km from the lake, and data were collected from the alpine  
133 meteorological observation network (ROMMA, <http://romma.org/>). Average precipitations  
134 were calculated from the 10 days preceding the sampling date.

#### 135 2.2.2. Nutrients (C, N, P, Si)

136 Water samples of 1L for nutrient analysis were filtered through precombusted (4h, 450°C) GF/F  
137 glass filters (Whatman GF/F, 25 mm, 0.7 µm). A first fraction of the filtered water was stored  
138 in 24 ml precombusted (4h, 450°C) glass tubes (Wheaton equipped with Teflon/silicon septa)  
139 and preserved with 25 µL of Sodium Azide solution (1 M NaN<sub>3</sub>) at 4°C for dissolved organic  
140 carbon (DOC) analysis and dissolved organic matter (DOM) fluorescence measurements. DOC  
141 concentrations were measured using a TOC-VCSH analyzer (Shimadzu, TOC-V). A second  
142 filtered fraction was stored in 150 ml HDPE bottles and frozen (-18°C) for analysis of dissolved  
143 inorganic nitrogen (DIN = NH<sub>4</sub><sup>+</sup> + NO<sub>2</sub><sup>-</sup> + NO<sub>3</sub><sup>-</sup>), soluble reactive phosphorus (SRP = PO<sub>4</sub><sup>3-</sup>),  
144 and Silica (Si). DIN, SRP, and Si were measured by ion chromatography (Metrohm, 930  
145 Compact IC Flex).

#### 146 2.2.3. C:N ratio and C isotopic analyses

147 C:N ratios and analyses of carbon stable isotope (δ<sup>13</sup>C) in particulate organic matter (POM)  
148 were performed from June 2020 to September 2020 and in May 2021. Water samples were  
149 filtered (0.7 – 20 µm) to concentrate the finest fraction of the seston, consisting mainly of  
150 phytoplankton. Filters were then dried at 60°C and decarbonated by acid-fuming (HCl 37%)  
151 for analysis. Samples were ground (RETSCH Mixer Mill MM 400), then between 0.2 and 0.6  
152 mg of homogeneous samples were weighed into tin capsules (three capsules per sample). C and



153 N abundances and  $\delta^{13}\text{C}$  ratios were analyzed using an Elemental analyzer (EA, Flash HT plus  
154 - Thermo Scientific) equipped with an autosampler configured with a combustion reactor for  
155 carbon and nitrogen analyses. The elemental analyzer is connected to an isotope ratio mass  
156 spectrometer (IrMS "Delta V Advantage", Thermo Scientific). Organic carbon and total  
157 nitrogen contents were determined from the signal of the TCD detector in the Elemental  
158 Analyzer. The C and N values obtained were used to calculate the C:N ratio of the suspended  
159 particulate organic matter (POM) in the water sample. C:N values were measured from June  
160 2020 to September 2020 and in March and May 2021.  $\delta^{13}\text{C}$  (‰) values were expressed relative  
161 to the international reference (Vienna-Pee Dee Belemnite, V-PDB) using the equation 1 and  
162 0.011237 for  $R_{\text{standard}}$  :

$$163 \quad \delta^{13}\text{C} (\text{‰}) = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \quad (1)$$

164 The  $\delta^{13}\text{C}$  determination was calibrated by a two-point method using the international standard  
165 NBS-22 and a laboratory standard for urea.

#### 166 2.2.4. DOM extractions

167 Leachates of four sources of organic matter were used to characterize the fluorescence signature  
168 of dissolved organic matter in Lake Cordes. The soil and alpine grass were collected randomly  
169 in the watershed on each sample date. When present, common macrophyte species were  
170 collected and cleaned by repeated rinsing in distilled water. Sediment samples were taken at  
171 each sample date with an Ekman grab. All samples were freeze-dried, ground, and sifted  
172 through a 2 mm mesh sieve. The samples were extracted with Milli-Q water (solid to water  
173 ratio, w/v = 0.1), the suspensions were placed at 4°C and stirred manually within 24 h. The  
174 suspensions were then centrifuged (10 000 rpm, 20 min), filtered (pre-combusted GF/F), and  
175 subsequently stored at 4 °C until analysis.

176 2.2.5. Absorbance and fluorescence measurements

177 Leachates and natural water samples were analyzed for UV-vis spectra using a  
178 Spectrophotometer V-550 (Jasco) with 10-cm Suprasil quartz cells. Water was scanned between  
179 230 and 800 nm using a 1000 nm.min<sup>-1</sup> scan rate and 0.5 nm resolution. Milli-Q water was used  
180 as a blank and subtracted from each sample. Fluorescence measurements were performed using  
181 a spectrofluorometer (F4500, Hitachi, Santa Clara, California, USA) equipped with a 450W  
182 xenon lamp. The spectra were acquired in the scan ranges of 200–600 nm for emission and  
183 excitation, with both slits fixed at 5 nm using 1 cm quartz Suprasil cell. The scan speed was set  
184 at 2400 nm.min<sup>-1</sup>, and the detector voltage was 700 V. Fluorescence intensity was normalized  
185 to Raman units (R.U.) using the daily-measured Raman peak of Mili-Q water ( $\lambda_{ex} = 350$  nm,  
186  $\lambda_{em} = 371$ – $428$  nm). The collected EEMs were analyzed using parallel factor analysis  
187 (PARAFAC), to identify the different components of the FDOM pool. PARAFAC was  
188 conducted on the EEM dataset using Progmee software (Redon, 2018) in Matlab language.  
189 PARAFAC was applied to the complete dataset containing all the EEMs (leachates and water  
190 samples of DOM). Three fluorescence indexes were used to characterize the FDOM: the  
191 humification index (HIX), the freshness index (BIX), and the fluorescence index (FI). The HIX  
192 is calculated as the sum of emissions ranging between 435 and 480 nm, divided by the sum of  
193 emissions ranging between 300 and 345 nm, at an excitation intensity of 255 nm, corrected  
194 according to the procedure of Ohno (2002). The BIX is the ratio of emission intensity at 380  
195 nm divided by maximum emission intensity between 420 and 435 nm, at an excitation intensity  
196 of 310 nm. The BIX value reflects the contribution of recent (autochthonous) organic matter to  
197 the organic matter pool. Low ratios are interpreted as a low contribution of autochthonous  
198 organic matter, while high ratios correlate with a strong contribution of recent autochthonous  
199 organic matter (Gabor et al., 2014). Finally, the FI is the ratio of emission intensity between  
200 470 and 520 nm, at an excitation intensity of 370 nm (Cory & McKnight, 2005). The

201 fluorescence index indicates whether the DOM precursor material is more microbial in nature  
202 (FI ~ 1.8) or is of terrestrial origin (FI ~ 1.2).

#### 203 2.2.6. Phytoplankton analyses

204 Phytoplankton samples were fixed with a formaldehyde solution (5%) and stored in 250 ml  
205 HDPE bottles. Phytoplankton counts were performed according to the Utermöhl (1958)  
206 method, at 40-fold magnification under an inverted microscope (Olympus IX 70).  
207 Phytoplankton samples were identified at genus level and species level when possible, using  
208 appropriate taxonomic guides. Phytoplankton biovolume was estimated by shape assimilation  
209 to known geometric forms and direct measurement of the main cell dimensions. Then the  
210 biovolume was converted into biomass using the particular carbon content defined for each  
211 class by Wetzel & Likens (2000). Phytoplankton taxa were classified in four groups: (i)  
212 taxonomic groups (**TAX**) based on their main phylogenetic affiliations; (ii) protist functional  
213 groups (**PFG**) based on their nutrient acquisition, *i.e.* photoautotrophs lacking phagotrophy  
214 capacity (**PA**) and constitutive mixotrophs (**CM**) (Mitra et al., 2016); (iii) morphology-based  
215 functional groups (**MBFG**) based on their morphological traits (Kruk et al., 2010); and (iv)  
216 functional groups (**FG**) based on their morphology and physiology and on the similarity of their  
217 ecological characteristics (Padisák et al., 2009; Reynolds et al., 2002). Phytoplankton diversity  
218 was characterized according to two indexes: the Species richness index (S) measures the total  
219 number of phytoplankton species in each sample, and the Shannon index (H') takes into account  
220 both the richness and evenness of the species present in each sample. Ciliate abundances were  
221 also estimated via the Utermöhl method.

#### 222 2.2.7. Picoplankton

223 Water samples (1.5 ml) were filtered (20 µm) and analyzed for picoplankton analyses by flow  
224 cytometry. Samples were fixed with glutaraldehyde (0.25% final concentration) and stored at

225 –80°C until flow cytometry analysis. Picoplankton was characterized and enumerated using an  
226 Accuri C6 flow cytometer equipped with a blue laser (488 nm) and using BD Accuri CFlow  
227 Plus Analysis software (BD-Biosciences). Non-fluorescent polystyrene microspheres (Flow  
228 Cytometry Size Calibration Kit, Thermo Fisher Scientific) were used as a size standard. For  
229 picocyanobacteria, 500 µl of sample were run at fast speed (66 µl/min). Picocyanobacteria  
230 (PCY) were identified by their small size (FSC < 2 µm), low complexity (SSC), and  
231 fluorescence (emissions in the orange and red wavelength ranges, respectively 585 ± 20 and  
232 >670 nm). Flow cytometer analysis distinguished between two groups of picocyanobacteria:  
233 cells with high orange fluorescence were classified as phycoerythrin-rich picocyanobacteria  
234 (PE-Pcy); cells with low orange and high dark red fluorescence were classified as  
235 phycocyanine-rich picocyanobacteria (PC-Pcy). For heterotrophic prokaryotes (HP), samples  
236 were stained with 1:10,000 (vol/vol) SYBR® Green II and incubated 20 min in darkness. 50 µl  
237 of stained samples were run at medium speed (35 µl/min). HP were identified by their small  
238 size (low FSC), low complexity (low SSC), high green fluorescence (530 ± 15 nm), and lack  
239 of red (> 670 nm) fluorescence. Picoplankton data were acquired and analyzed using BD Accuri  
240 CFlow Plus Analysis software (BD-Biosciences). Abundances were transformed into carbon  
241 content based on the literature. Cell abundance (cells/ml) of HP was converted to biomass (µg  
242 C/L) using 20 fg C/cell as constant conversion factor (Linacre et al., 2015). A conversion factor  
243 of 112 fg C/cell was used for picocyanobacteria (Linacre et al., 2015).

### 244 **2.3. Statistical analyses**

245 One-way ANOVA tests followed by pairwise comparisons were used to test the effect of period  
246 on the various abiotic and biological variables measured, and to test differences in fluorescence  
247 characteristics between the four leachates of organic matter sources. Non-metric  
248 multidimensional scaling (NMDS) analysis was performed on a Bray-Curtis distance matrix to  
249 visualize the differences in taxonomic structure of the phytoplankton community between

250 periods. To test the hypothesis that the taxonomic distribution of the phytoplankton community  
251 was structured by period, a multivariate permutation analysis of variance (permanova) was used  
252 with 999 permutations ( $p = 0.05$ ) with the adonis function in R. A multivariate homogeneity  
253 analysis of group dispersion ( $\beta$  diversity) was used to assess the homogeneity of phytoplankton  
254 assemblages within a group of samples (betadisper function). Canonical Correspondence  
255 Analysis (CCA) was performed to explore the distribution of the different phytoplankton  
256 taxonomical groups in relation to the measured explanatory variables. The significance of the  
257 phytoplankton composition variance explained by the selected abiotic variables was assessed  
258 by permutation tests. All analyses were performed with R 3.6.3 (R Core Team, 2018).

259

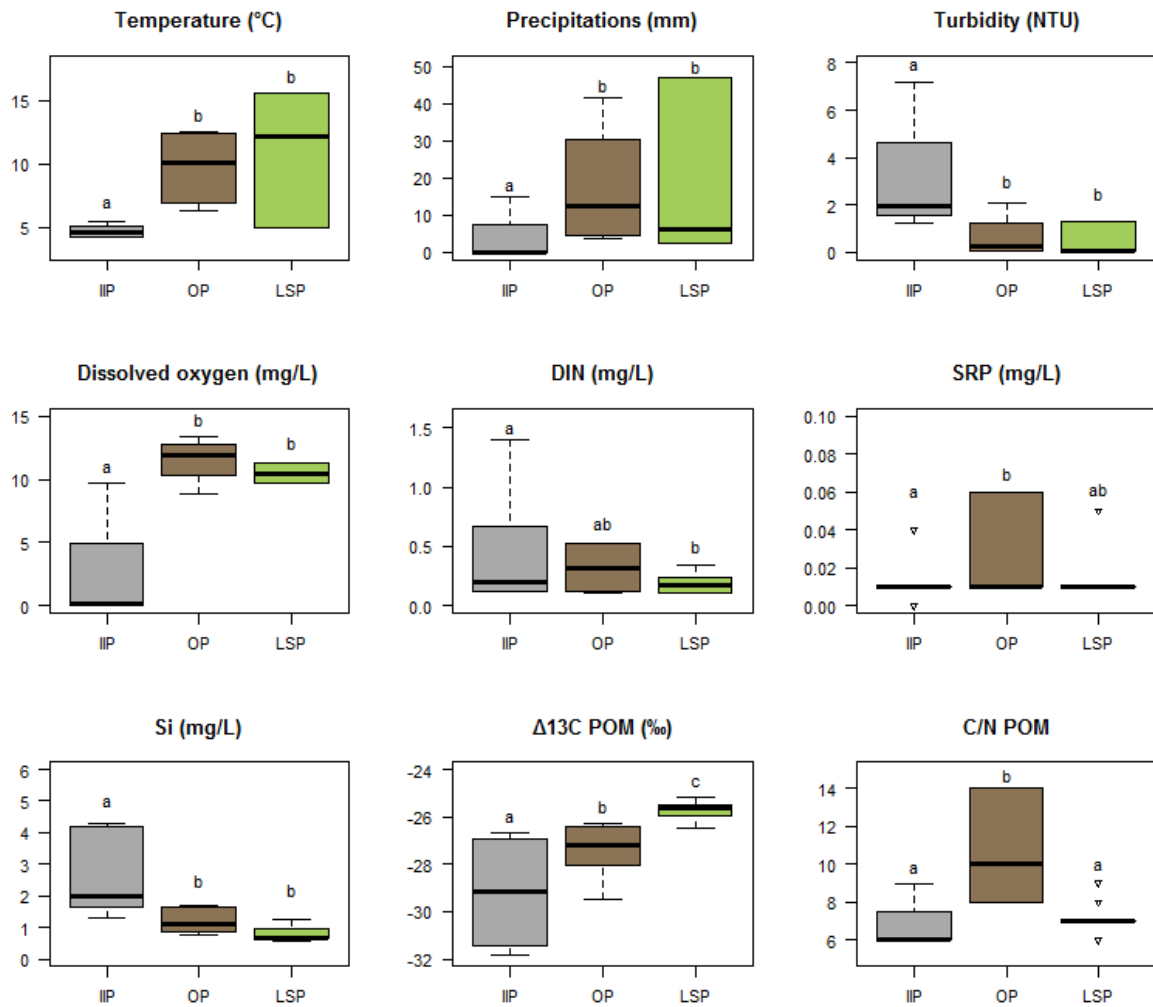
260 3. RESULTS

261 **3.1. Abiotic and climate parameters**

262 The ice-influenced period (IIP) was characterized by significantly lower concentrations of  
263 dissolved oxygen, temperature, and precipitations (**Figure 1**). Turbidity was significantly  
264 greater during this period, but highly variable. SRP concentrations were low during the ice-  
265 influenced period, whereas silica and DIN concentrations were high and highly variable.  
266 Ammonium was the dominant N source of the DIN pool during IIP ( $73 \pm 13\%$ , data not  
267 showed). Particulate organic matter (POM) showed the most negative  $\delta^{13}\text{C}$  values and low C:N  
268 values.

269 During the overturn period (OP), many abiotic parameters significantly increased, such as  
270 dissolved oxygen, temperature, precipitations, and SRP concentrations. The  $\delta^{13}\text{C}$  values and  
271 C:N of POM also significantly increased during OP, whereas turbidity and silica concentrations  
272 were significantly lower than during IIP. While there was no significant change in DIN  
273 concentrations, they were less variable. Nevertheless, within the DIN pool, nitrite became  
274 dominant over ammonium during OP ( $88 \pm 7\%$ , data not showed).

275 The late summer period (LSP) did not significantly differ from OP for any abiotic parameters  
276 except  $\delta^{13}\text{C}_{\text{POM}}$  which showed significantly higher values, and C:N of POM. However, LSP  
277 was significantly different from IIP for all parameters except SRP concentrations and C:N of  
278 POM. This period was characterized by higher variability in temperature and precipitations.

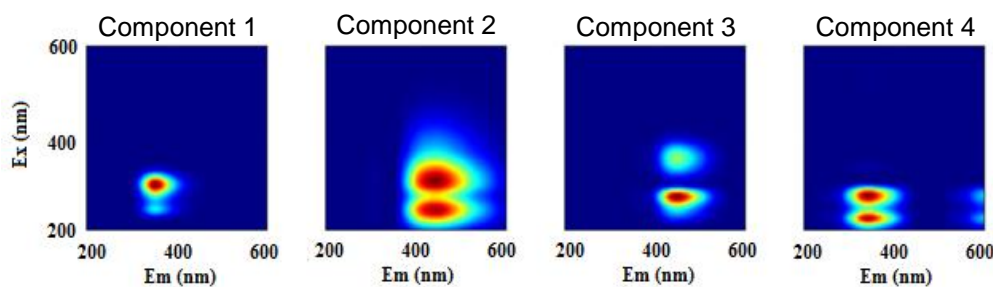


**Figure 1:** Abiotic and climate parameters measured in the three defined functional periods in Lake Cordes. DIN: dissolved inorganic nitrogen; SRP: soluble reactive phosphorus; Si: silica; POM: particulate organic matter.

280 **3.2. Characterization and dynamics of DOM**

281 3.2.1. *Identification of the components by PARAFAC modeling*

282 PARAFAC analysis of the EEM spectra of leachates and water samples identified four  
283 fluorescent components (C1, C2, C3, and C4) (**Figure 2**). C1 and C4 are known to be non-  
284 humic compounds: C1 (Ex/Em = 300/350 nm) is linked to soluble microbial byproduct-like  
285 material (Chen et al., 2003), while C4 (Ex/Em = 230-270/350 nm) is often linked to simple  
286 aromatic proteins such as tyrosine. Conversely, C2 and C3 are considered humic-like  
287 compounds: C2 (Ex/Em = 250-310/450 nm) is referred to as a combined component constituted  
288 by humic acid-like and fulvic acid-like materials. C3 (Ex/Em = 270(360)/460 nm) has been  
289 associated with humic acid-like organics (Murphy et al., 2008).



**Figure 2:** PARAFAC model output showing fluorescence signatures of the four fluorescent components identified in the 4 leachates and in water samples.

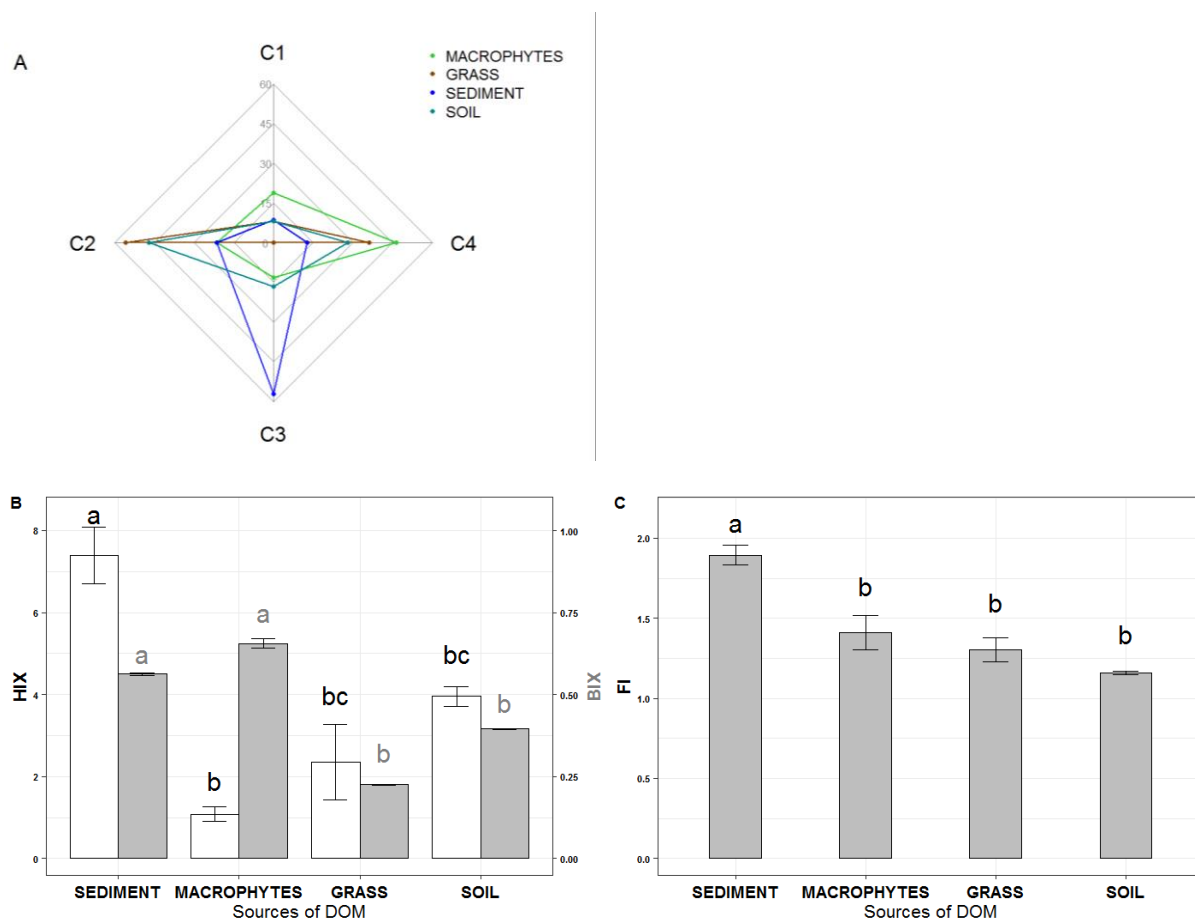
290

291 3.2.2. *Fluorescence signature of the sources of DOM*

292 Regarding the “internal” sources, the macrophytes leachate fluorescence response was mainly  
293 dominated by C4, while the sediment leachate fluorescence response was mainly dominated by  
294 C3 (**Figure 3A**). Regarding the “external” sources, the soil and the grass leachate fluorescence  
295 were mainly dominated by C2 and C4.



296 HIX values varied significantly between sources (Anova,  $F = 14.9$ ,  $p\text{-value} < 0.001$ ), with a  
 297 greater predominance of humic compounds in the sediment and soil leachates than in the  
 298 macrophytes and grass leachates (**Figure 3B**). BIX values were significantly higher in the two  
 299 internal sources than in the two external sources (Anova,  $F = 17.9$ ,  $p\text{-value} < 0.001$ ). Finally, FI  
 300 values were significantly higher in the sediment leachate ( $FI = 1.89 \pm 0.2$ ) than in the other  
 301 sources, and were lowest in the soil leachate ( $FI = 1.16 \pm 0.04$ ) (Anova,  $F = 42.6$ ,  $p\text{-}$   
 302  $\text{value} < 0.001$ ) (**Figure 3C**).



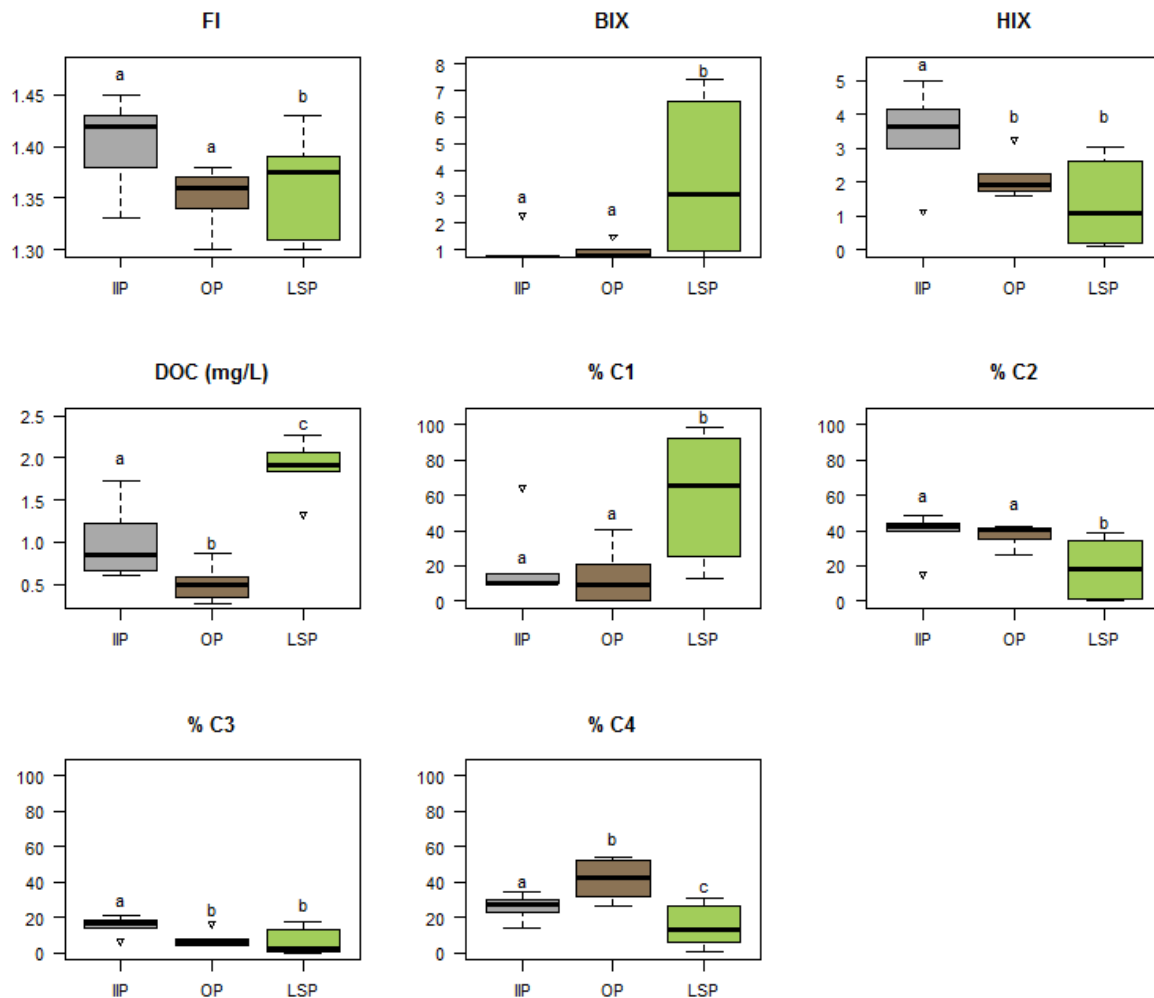
**Figure 3:** (A) Relative contribution of the four components for the four leachates of dissolved organic matter (DOM) sources; (B) Humification index (HIX) in white and freshness index (BIX) in grey of the four leachates of DOM sources; (C) Fluorescence index of the four leachates of DOM sources.

303

304

305        3.2.3. *Dynamic signature of lake DOM*

306        During the ice-influenced period (IIP), significantly higher values for FI, HIX, and the  
307        proportion of C3 were observed than during the two other periods (**Figure 4**). The proportion  
308        of C2 was also high. This period was also characterized by moderate but variable DOC  
309        concentrations and a moderate proportion of C4. The overturn period (OP) was characterized  
310        by significantly lower HIX and FI values than during IIP, while BIX values did not differ  
311        significantly, remaining low. Measured DOC concentrations were low. OP was characterized  
312        by a high proportion of C2 and C4 and a low proportion of C1. Finally, during the late summer  
313        period (LSP), BIX values were significantly higher than during the two other periods,  
314        associated with low but variable values of FI and HIX. DOC concentrations and C1 proportion  
315        were higher in LSP, while the proportions of C2, C3 and C4 were low. It is noteworthy that,  
316        the late summer period was characterized by higher variability in all parameters except DOC.

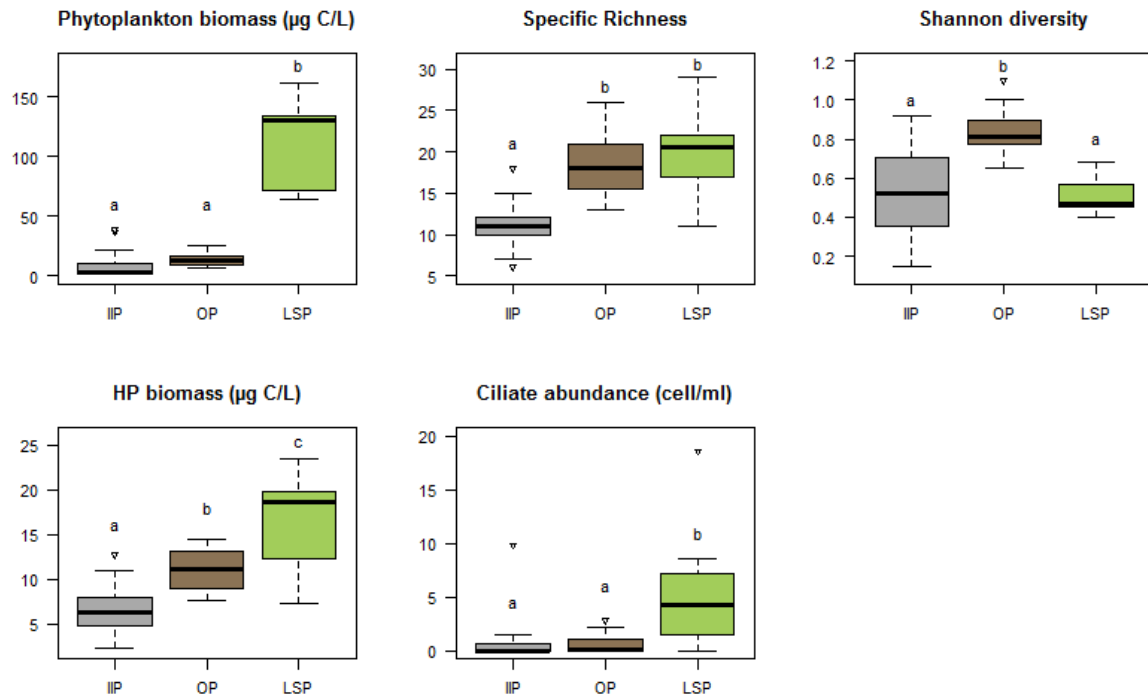


**Figure 4:** DOM characteristics measured in the three defined periods in Lake Cordes. DOC: dissolved organic carbon.

317

### 318 3.3. Planktonic community dynamics

319 Phytoplankton biomass was low during the ice-influenced period (IIP) and the overturn period  
 320 (OP), increasing significantly during the late summer period (LSP) (**Figure 5**). While specific  
 321 richness increased progressively from IIP to LSP, the Shannon diversity index was significantly  
 322 higher in OP than during the two other periods. HP biomass increased progressively over the  
 323 three periods. Ciliate abundance was low during IIP and OP, then significantly increased during  
 324 LSP.

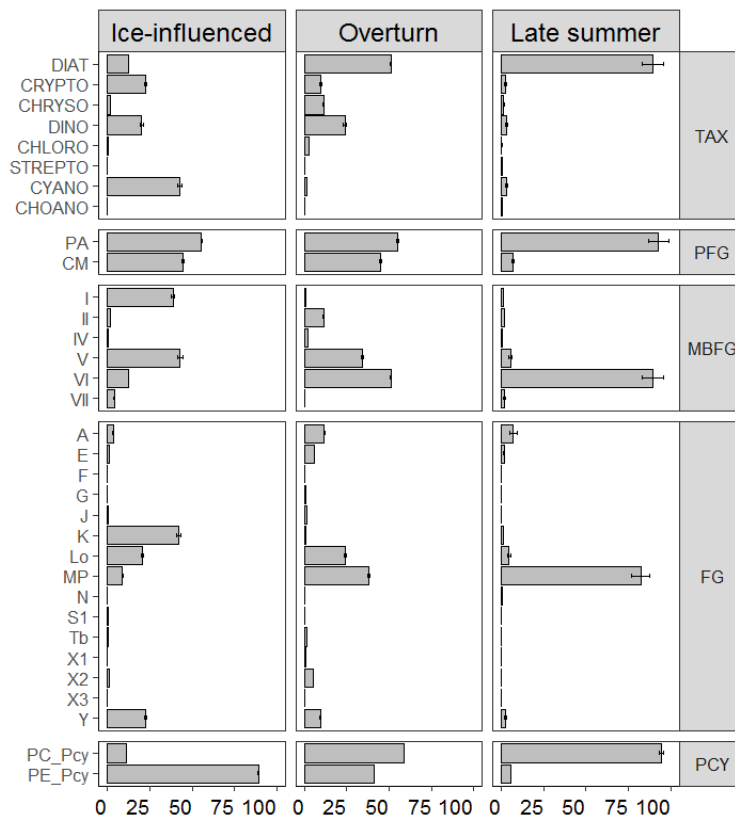


**Figure 5:** Biological parameters measured in the three defined periods in Lake Cordes. HP: heterotrophic prokaryotes.

325

326 Concerning taxonomical and functional changes in phytoplankton assemblages, a significant  
 327 shift in phytoplankton community structure was observed over the three periods (**Figure A1**,  
 328 Adonis,  $F = 29.362$ ,  $r^2 = 0.57$ ,  $p\text{-value} < 0.001$ ). Cyanobacteria dominated the other  
 329 phytoplankton groups during IIP (**Figure 6**), which also showed a high proportion of  
 330 cryptophytes, dinoflagellates, and phycoerythrin-rich picocyanobacteria (PE\_Pcy). A relatively  
 331 high proportion of constitutive mixotrophs was found during IIP (45%), as well as MBFG  
 332 groups I (small cells with high surface/volume ratio) and V (flagellates of medium to large size)  
 333 and FG groups K (shallow, nutrient-rich water column) and Y (small, enriched lakes, lentic  
 334 ecosystems with low grazer pressure). OP was characterized by an increased proportion of  
 335 diatoms (51%), which became dominant over the other phytoplankton groups. Dominance by  
 336 the PE\_rich PCy was replaced by that of the phycocyanin-rich picocyanobacteria (PC\_Pcy).  
 337 The relative proportion of mixotrophs remained high (45%). Among the mixotrophic taxa,

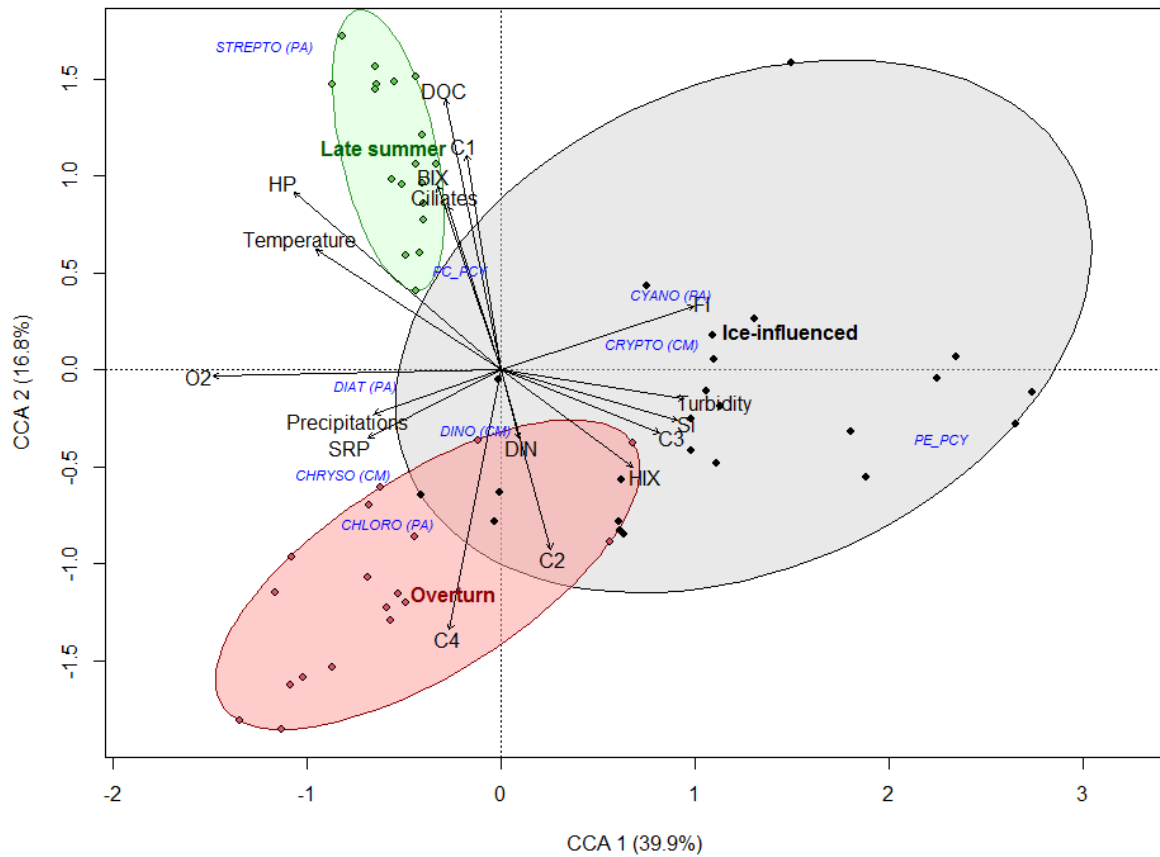
338 while the proportion of dinoflagellates remained the same as during IIP, an increase in the  
 339 proportion of chrysophytes was observed together with a decrease in the proportion of  
 340 cryptophytes. The proportion of MBFG groups II (small siliceous flagellates) and VI (non-  
 341 flagellated with siliceous exoskeletons) increased, as did FG groups A (clear, deep, often well-  
 342 mixed lakes), Lo (all lentic ecosystems), and MP (all types of lakes, or frequently stirred up,  
 343 inorganically turbid shallow lakes). During LSP, the phytoplankton assemblage was mainly  
 344 composed of diatoms (89%), corresponding to the high proportion of MBFG group VI and FG  
 345 group MP. PC\_Pcy dominated the pool of picocyanobacteria in LSP.



**Figure 6:** Phytoplankton composition in each period (error bars correspond to standard error). DIAT = diatoms; CRYPTO = cryptophytes; CHRYSO = chrysophytes; DINO = dinoflagellates; CHLORO = chlorophytes; STREPTO = Streptophytes; CYANO = cyanobacteria; CHOANO = choanoflagellates; PA = photoautotrophic phytoplankton; CM = constitutive mixotrophs; PE\_Pcy = phycoerythrin-rich picocyanobacteria; PC\_Pcy = phycocyanin-rich picocyanobacteria.

### 347        **3.4. Links between microbial plankton and dissolved organic matter**

348        CCA was conducted with phytoplankton taxonomical groups as response variables and abiotic  
349        parameters, and HP biomass and ciliate abundance as explanatory variables (**Figure 7**). The  
350        constrained variables explained 87% of inertia, and the eigenvalues for the first and second  
351        sorting axes were 0.178 and 0.075, respectively. Dissolved oxygen, HP biomass, FI,  
352        temperature, and turbidity showed far higher correlation coefficients with the first axis (-0.87,  
353        -0.63, 0.58, -0.56, and 0.55, respectively), suggesting that these explanatory variables played a  
354        predominant role in affecting the taxonomic composition of the phytoplankton community.  
355        PE\_PCY, cyanobacteria and cryptophytes were associated with higher silica concentrations,  
356        higher proportions of C3, higher HIX values, higher turbidity, but lower dissolved oxygen  
357        concentrations during the ice-influenced period. The second axis discriminated between  
358        overturn and late summer periods, and DOC concentrations and C1 proportions were  
359        particularly high and positively correlated with the late summer period. Both OP and LSP were  
360        characterized by an increase in diatoms, while chrysophytes and chlorophytes were particularly  
361        prevalent during OP.



**Figure 7:** CCA performed on the taxonomic phytoplankton groups (and their corresponding PFG classification) and picophytoplankton groups (PCY) in relation to explanatory variables. DOC: dissolved organic carbon; HP: heterotrophic prokaryotes; O<sub>2</sub>: dissolved oxygen; SRP: soluble reactive phosphorus; DIN: dissolved inorganic nitrogen; Si: silica; CYANO: cyanobacteria; CRYPTO: cryptophytes; DINO: dinoflagellates; CHLORO: chlorophytes; CHRYSO: chrysophytes; DIAT: diatoms; STREPTO: Streptophytes; PC\_PCY: phycocyanin-rich picocyanobacteria; PE\_PCY: phycoerythrin-rich picocyanobacteria.

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363

## 364 4. DISCUSSION

### 365 4.1. Variation in DOM origin

366 We characterized the fluorescence signature of four sources of DOM to better understand DOM  
367 dynamics in Lake Cordes. All the DOM sources exhibited a specific fluorescent signature and,  
368 interestingly, none of the four sources of DOM exhibited a C1-dominated signature. Our  
369 findings demonstrate that the origin of DOM varied greatly over the three periods in Lake  
370 Cordes (**Figure 8**). The ice-influenced period exhibited the highest FI values (1.41). In previous  
371 studies in high-altitude lakes, FI values of 1.44 were considered to be low and to reflect a more  
372 allochthonous DOM pool (Miller et al., 2009; Rose et al., 2015). However, the associated high  
373 HIX values (3.43) and low BIX values (0.96) suggest a refractory and humic DOM linked to a  
374 microbial precursor material (Du et al., 2016; Ohno, 2002). The low C:N values observed for  
375 POM confirm a more autochthonous origin for DOM during the ice-influenced period.  
376 Moreover, the ice-influenced period showed the highest proportion of C3, indicating a higher  
377 contribution of the sediment to the DOM pool than during the two other periods. However,  
378 allochthonous inputs of DOM also occurred during the ice-influenced period, as suggested by  
379 the highly variable C:N values of POM and the relatively high proportion of C2 and C4. Similar  
380 results were previously observed during winter in a subarctic clear-water lake (Karlsson et al.,  
381 2008), where sediment organic carbon was the dominant carbon source for respiration under  
382 the ice, but both allochthonous and autochthonous carbon contributed to DIC accumulation in  
383 the lake. In our study, such allochthonous inputs likely started at the end of the ice-influenced  
384 period, when the snowmelt occurred.

385 During the overturn period, DOM showed the lowest FI (1.35) and BIX (0.90) values and  
386 moderate HIX (2.12) values, suggesting a more refractory, terrestrial origin for DOM than  
387 during the ice-influenced period. The C:N values of POM and the contribution of C2 and C4 to  
388 FDOM were highest during the overturn period, confirming the hypothesis of a higher



389 contribution of the DOM pool originating from the catchment area. Despite the predominant  
390 soil signature of the DOM during the overturn period, however, low DOC concentrations were  
391 measured in the water column. It is therefore possible that DOC inflows occurred earlier, at the  
392 end of the ice-influenced period when the snow and ice started to melt. Indeed, DOC can rapidly  
393 be degraded after allochthonous DOM inputs (Catalán et al., 2013). These low DOC  
394 concentrations may also be explained by low DOC content in the allochthonous DOM  
395 transferred to the lakes (Queimaliños et al., 2019) and a strong dilution effect during snowmelt  
396 or rain events involving shorter water residence (Anderson & Stedmon, 2007).

397 During the late summer period of our study, C1 was predominant in DOM. This component  
398 was not associated with a specific fluorescence signature of the four leachate sources of DOM  
399 but was associated with higher DOC concentrations and higher phytoplankton biomass.  
400 Moreover, DOM showed low but highly variable HIX values (1.35) and high BIX values (3.65),  
401 suggesting a high contribution of fresh, autochthonous DOM. However, FI values were also  
402 low (1.36) thus not indicative of organic material derived from algae and bacteria. Like the  
403 other fluorescence indexes, FI was highly variable during the late summer period, and  
404 particularly low at the October sampling. Heavy precipitations occurred during October,  
405 possibly driving allochthonous inputs into the lake and modifying the autochthonous signature  
406 of the DOM. Thus, despite a variable signature, our results suggest that DOM mainly originated  
407 from phytoplankton development in the water column during the late summer period. These  
408 findings are consistent with other studies in mountain lakes showing a higher contribution of  
409 phytoplankton to the DOM pool at the end of the ice-free period (Sadro & Melack, 2012;  
410 Sommaruga & Augustin, 2006).

#### 411 **4.2. Phytoplankton functional changes**

412 Our results highlight the high sensitivity to environmental variations of phytoplankton  
413 assemblages, whose structure and composition changed according to shifts in lake functioning

414 **(Figure 8)**. During the ice-influenced period, phytoplankton biomass was low and the  
415 assemblage was dominated by small autotrophs with a high surface/volume ratio, and by large  
416 mixotrophic flagellates. Mixotrophs represented 45% of the phytoplankton assemblage, mainly  
417 cryptophytes (*Cryptomonas sp.*) and dinoflagellates (*Katodinium sp.*, *Peridinium umbonatum*,  
418 *Gymnodinium sp.*). These results confirm that mixotrophic strategy and motility are critical for  
419 phytoplankton survival under ice (Özkundakci et al., 2016). The autotrophic fraction was  
420 mainly composed of small cyanobacteria (*Synechococcus sp.* and *Gomphosphaeria sp.*). This  
421 group is known to be cold-tolerant (Jungblut & Vincent, 2017) and has already been observed  
422 under ice in oligotrophic lakes (Bullerjahn et al., 2020). In addition, the pool of  
423 picocyanobacteria was dominated by phycoerythrin-rich picocyanobacteria (PE\_Pcy) during  
424 the ice-influenced period. Picocyanobacteria seems to be well adapted to low levels of light and  
425 low nutrient concentrations (Callieri et al., 2007; Stomp et al., 2007). Because PE\_Pcy use  
426 phycoerythrin for harvesting the prevailing green wavelengths, they are well-adapted to poor  
427 under-ice light conditions (Jungblut & Vincent, 2017).

428 The overturn period was characterized by a similar phytoplankton biomass but changes in  
429 species composition, with more taxa associated with well-mixed systems. Species richness  
430 substantially increased, and diversity was at a peak. Changes in phytoplankton community  
431 structure have previously been observed after snowmelt as a consequence of meltwater inputs  
432 in oligotrophic lakes (Williams et al., 2016), and episodic nutrient enrichments can increase  
433 species richness (Zufiaurre et al., 2021). The increased richness and diversity observed during  
434 the overturn period was therefore likely the result of nutrient inputs occurring during snowmelt.  
435 The proportion of mixotrophs remained the same as in the ice-influenced period and  
436 dinoflagellates remained dominant, but small chrysophytes (*Dinobryon divergens*, *Kephyrion*  
437 *spirale*) prevailed over cryptophytes during the overturn period. This replacement is not  
438 surprising: chrysophytes, especially *Dinobryon*, are known to be obligatory phototrophs

439 (Princiotta et al., 2016) and to form resting stages to withstand adverse environmental  
440 conditions (Özkundakci et al., 2016). Changes in light spectral composition have been shown  
441 to change dominance patterns between cryptophytes and chrysophytes in shallow North  
442 Patagonian lakes (Gerea et al., 2017). Here, in the autotrophic fraction of the phytoplankton  
443 assemblage, diatoms (*Cyclotella comensis* and *Fragilaria nanana*) replaced the small  
444 cyanobacteria. These two species are widely used as an indicator of physico-chemical changes  
445 (Cantonati et al., 2021), especially increased water temperatures in alpine lakes (Catalan, Pla,  
446 et al., 2002; Sochuliaková et al., 2018). In addition, the PE:PC picocyanobacteria changed  
447 during the overturn, and PC\_Pcy became dominant over PE\_Pcy. This result clearly indicates  
448 a modification of the underwater light spectrum, and consequently the pigment composition of  
449 picocyanobacteria (Bastidas Navarro et al., 2009). Our results suggest that the drastic changes  
450 in temperature, nutrients, and light availability after snowmelt lie behind the changes in  
451 phytoplankton community that we observed.

452 Phytoplankton biomass greatly increased during the late summer period, when the  
453 phytoplankton assemblage was almost exclusively composed of less edible, large diatoms  
454 (mainly *Fragilaria nanana*). While previous studies report that *Fragilaria nanana* prefers  
455 nutrient-enriched waters (Cantonati et al., 2019), this species has also been shown to tolerate  
456 very small concentrations of nitrogen (Van Dam et al., 1994). Strong diatom development has  
457 already been observed in high-altitude lakes in summer, when thermal stability is higher (Tolotti  
458 et al., 2007). It appears that the diatoms in our study were more competitive than the other  
459 phytoplankton genera during the late summer period, despite the theoretically successful  
460 mixotrophic strategy under limiting nutrients and warmer temperatures (Bhutiani et al., 2009).

461 Overall, we observed a major functional change in phytoplankton assemblages over the three  
462 periods. Heterotrophy stood out during the ice-influenced period, with the mixotrophy strategy  
463 playing a significant role in the community. Then, mixotrophy was progressively overtaken by

464 autotrophy, becoming negligible during the late summer period next to both the quantity of  
465 autotrophic biomass and the proportion of autotrophs in the phytoplankton assemblage.

### 466 **4.3. Functional shifts at the base of the food web**

467 Bacterial biomass showed the lower values during the ice-influenced period, then progressively  
468 increased until the last summer period. Despite the low biomass during the ice-influenced  
469 period, the observed hypoxia as well as the high proportion of ammonium in the DIN pool  
470 indicate that microbial respiration did occur during this period. Anaerobic metabolism of active  
471 psychrophilic bacteria certainly occurred, as it was previously demonstrated in during winter in  
472 ice-covered lakes (Bullerjahn et al., 2020; Margesin & Miteva, 2011; Bertilsson et al., 2013),  
473 and during the ice-free season in deep high-altitude lakes (Llorens-Marès et al., 2020).

474 Regardless of bacterial respiration, dissolved organic matter properties varied over time and  
475 may explain the observed variation in bacterial biomass. The refractory DOM may have  
476 insufficiently fueled bacteria during the ice-influenced period, as DOM's overall bioavailability  
477 typically declines over time when isolated from fresh inputs (Del Giorgio & Davis, 2003). The  
478 increase in bacterial biomass during the overturn period was associated to inputs of terrestrial  
479 DOM, which could constitute a valuable source of energy and/or inorganic nutrients for  
480 bacteria, stimulating more biomass production than respiration (Guillemette et al., 2016). The  
481 bacterial biomass continued to increase until the end of the late summer period, during which  
482 the high phytoplankton biomass constituted a highly available C source for bacterioplankton.  
483 However, temporal trends of bacterial biomass may also result from bacterial interaction with  
484 phytoplankton. The high abundance of large phytoflagellates during the ice-influenced period  
485 suggests high predation pressure by mixotrophs during this period. Then predation pressure  
486 progressively decreased with the observed change in phytoplankton community composition:

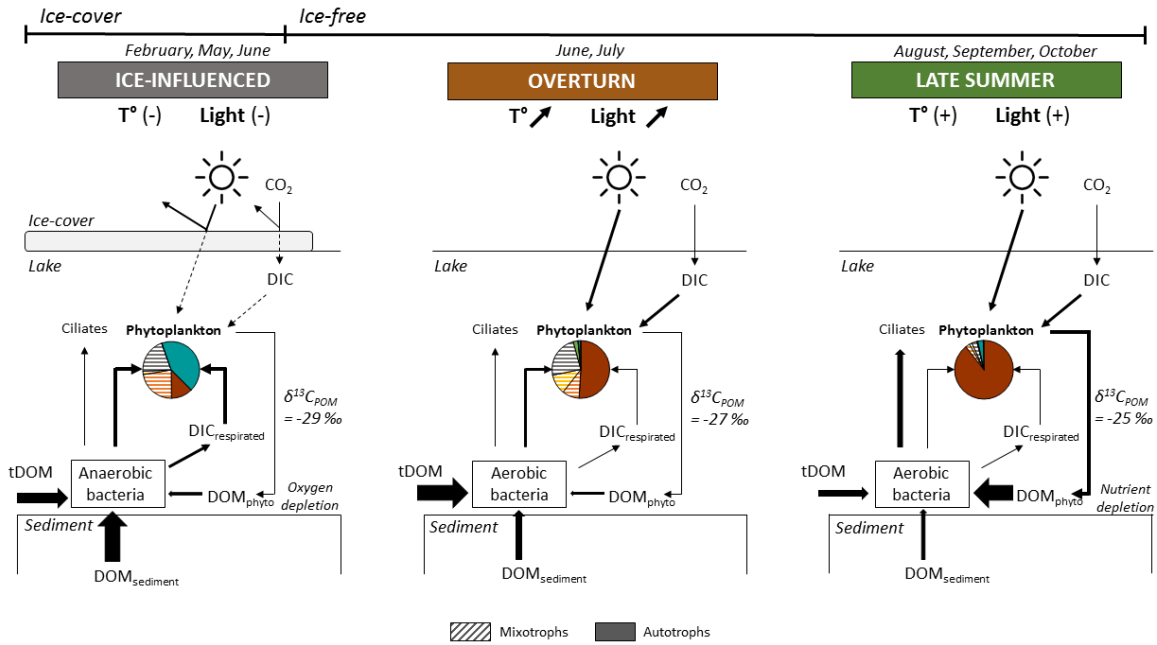
487 some large cryptophytes were replaced by small siliceous chrysophytes during the overturn  
488 period. In taxa such as *Dinobryon*, phagotrophy appears to be more a complementary nutritive  
489 strategy when light is limiting (Saad et al., 2016), and therefore enhanced light availability  
490 during the overturn period may have promoted photosynthesis rather than phagotrophy. Finally,  
491 autotrophs largely dominated the phytoplankton community during the late summer period,  
492 removing the top-down control over bacteria. Our results confirmed that, together with temporal  
493 variation in temperature, oxygen, and nutrient concentrations (Zhou et al., 2020), shifts in DOM  
494 properties and phytoplankton community exerted a key role in bacterioplankton regulation.

495 Thus, our result showed that phytoplankton control over bacteria changed over time, from a  
496 predominantly top-down control exerted by mixotrophs toward a bottom-up control as source  
497 of DOM. By occupying the niche of microheterotrophs and preventing the development of  
498 heterotrophic nanoflagellates and ciliates, mixotrophs are known to reduce the number of  
499 trophic levels, acting as a bypass of C flux toward the grazing chain (Medina-Sánchez et al.,  
500 2004; Ward & Follows, 2016). Indeed, we found low ciliate abundance during the ice-  
501 influenced period but higher ciliate abundance during the late summer period. These results  
502 also suggest a possibly top-down control of ciliates on heterotrophic nanoflagellates, which in  
503 turn allowed an increase in bacterial biomass (Haraguchi et al., 2018).

504 The progressively increase of the  $\delta^{13}\text{C}_{\text{POM}}$  confirmed our previous assumptions on shifts  
505 occurring at the base of the food web. During the ice-influenced period,  $\delta^{13}\text{C}_{\text{POM}}$  ranged  
506 between -31.80 ‰ at the bottom and -26.70 ‰ at the surface. These low values may confirm  
507 (i) the use of isotopically light DIC from anaerobic respiration for phytoplankton  
508 photosynthesis, which might contribute to  $\delta^{13}\text{C}_{\text{POM}}$  depletion at the bottom (Cole et al., 2002);  
509 (ii) the ingestion of anaerobic bacterial prey by mixotrophs, as anaerobic bacteria usually  
510 exhibit further depletion in  $\delta^{13}\text{C}$  (Grey, 2016). The increase in  $\delta^{13}\text{C}_{\text{POM}}$  during the overturn  
511 period could result from multiple processes, like increase inputs of allochthonous DOM (Hou

512 et al., 2013), higher CO<sub>2</sub> uptake rates resulting from greater phytoplankton growth (Gu et al.,  
513 2006), or change in phytoplankton taxonomic composition (Golubkov et al., 2020; Trochine et  
514 al., 2015). In our study, phytoplankton biomass did not increase during the overturn, but both  
515 inputs of allochthonous DOM and change in phytoplankton composition with more efficient  
516 photosynthesis occurred. Finally, in late summer, the higher  $\delta^{13}\text{C}_{\text{POM}}$  values corroborated the  
517 higher CO<sub>2</sub> uptake rates associated with greater autotrophic phytoplankton growth (Gu et al.,  
518 2006), although precipitation events at the end of this period may also contribute to higher  
519 values of  $\delta^{13}\text{C}_{\text{POM}}$ . Thus, if  $\delta^{13}\text{C}$  values in POM did not allow to determine the part of each  
520 process during the different periods, the result confirmed that the origin of the carbon  
521 transferred in the planktonic food web varied over time.

522 To conclude, in accordance with our last hypothesis, we observed a temporal shift in  
523 phytoplankton – bacterioplankton relationships according to lake functioning patterns (**Figure**  
524 **8**). During the ice-influenced period, mixotrophic taxa exerted a strong top-down control over  
525 bacteria. Then, phytoplankton control progressively shifted to a predominantly bottom-up  
526 control by autotrophs that governed the DOM pool of the lake. Considering our three pre-  
527 defined periods thus brings to light differences in the functioning of this high-altitude lake and  
528 provides new insights into the mechanisms controlling the phytoplankton community. Our  
529 study highlights the need to better assess the trophic processes at work between the planktonic  
530 constituents of the food web. Further studies should be conducted to determine the vulnerability  
531 of high-altitude lakes to the shortened ice-cover and increased connectivity with their  
532 catchments that are predicted.



**Figure 8:** General outline reflecting shifts in phytoplankton control over bacteria in relation to dissolved organic matter properties in the Lake Cordes. tDOM: terrestrial allochthonous DOM; DOM<sub>phyto</sub>: autochthonous DOM derived from phytoplankton; DIC: dissolved inorganic carbon; T°: water temperature.

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542 **Conflict of interests**

543 The authors declare no conflicts of interest.

544



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