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1 **Meroplanktic phytoplankton play a crucial role in responding to peak discharge events in the**
2 **middle lowland section of the Loire River (France)**

3 Alexandrine Pannard¹, Camille Minaudo², Maria Leitao³, Andras Abonyi^{4,5,6}, Florentina Moatar⁷ and
4 Nathalie Gassama⁸

5 1. University of Rennes, UMR 6553 ECOBIO, Rennes, France

6 2. Department of Evolutionary Biology, Ecology and Environmental Sciences, University of Barcelona,
7 Av. Diagonal 643, Barcelona 08028, Spain

8 3. Bi-Eau, 15 rue Lainé-Laroche, Angers, France

9 4. Institute of Aquatic Ecology, Centre for Ecological Research, Karolina street 29, Budapest, Hungary

10 5. MTA-ÖK “Lendület” Momentum Fluvial Ecology Research Group, Karolina street 29, Budapest,
11 Hungary

12 6. WasserCluster Lunz, Dr. Kupelwieser-Prom. 5, Lunz am See, Austria

13 7. INRAE, UR RiverLy - Centre de Lyon-Grenoble Auvergne-Rhône-Alpes, Villeurbanne, France

14 8. University of Tours, E.A. 6293 GéHCO, Tours, France.

15 **Corresponding author:** alexandrine.pannard@univ-rennes.fr

16 **Abstract**

17 Meteorological and hydrological forcings influence phytoplankton at very short time scales. The effect
18 of turbulence, dilution, light and nutrients are highly dynamic. Yet, our knowledge of short-term
19 phytoplankton dynamics associated with discharge disturbances and nutrient inputs remains elusive,
20 especially in large rivers.

21 Based on every three-day monitoring, we studied phytoplankton in the middle Loire River (France)
22 and related to the daily variations in water discharge and the physical and chemical parameters. We
23 focused on summer phytoplankton (2013 and 2014), where dissolved inorganic phosphorus
24 concentration was potentially limiting growth. We identified eight discharge events, which increased
25 suspended matter concentration and decreased chlorophyll-a concentration. The most significant

26 environmental drivers of phytoplankton composition were discharge and water temperature, a
27 sensitive proxy for meteorological forcing at short-time scale.

28 The phytoplankton composition responded to changes in hydrology along with three distinct
29 assemblage types, where even small water discharge increase induced a community response.
30 Meroplanktic algae being able to withstand sedimentation and resuspension could take advantage of
31 hydrological peaks, following the benthic retention hypothesis. Our results suggest that short-term
32 dynamics are crucial to understanding community organisation and functioning in large river plankton,
33 with meroplankton playing a decisive role in maintaining phytoplankton diversity and ecosystem
34 functioning.

35 **Keywords:** large rivers; short-term events; benthic retention hypothesis; Reynolds' phytoplankton
36 functional groups; functional traits

37

38 **Introduction**

39 Large rivers are critical players in the biogeochemical dynamics, exerting control over the transport of
40 organic matter and associated chemical elements along the land-sea continuum. Large spatial and
41 temporal variations occur in hydrology and biogeochemical processes in rivers, which also influence
42 the diversity of aquatic communities (Johnson et al., 1995). Large rivers exceeds the sixth river order
43 (Wehr & Descy, 1998) with extended braided arms towards the lowland river section. Their hydrology
44 is subjected to significant variations in discharge in response to meteorological variations and water
45 flow management. Water discharge also controls connectivity among adjacent pools composed by water
46 bodies with different water quality. The longitudinal component from the headwaters to the lowland
47 reach can be described by a continuous change in environmental conditions, well summarised in the
48 'River Continuum Concept - RCC' (Vannote et al., 1980). The RCC also provides a natural gradient to
49 scale the diversity of aquatic communities. The RCC describes changes in river metabolism, in the type
50 of primary producers and the macro-invertebrates and fishes' community structure, associated with
51 changes in the slope (current velocity), allochthonous inputs, light exposure and water residence time.
52 The large lowland river sections are influenced by upstream processes and aquatic communities, with

53 phytoplankton dominance mainly from the middle river section (Reynolds & Descy, 1996). Temporal
54 fluctuations associated with river discharge should affect the taxonomic and functional diversity of
55 aquatic communities, by connecting benthic and planktic communities, in accordance with the benthic
56 retention hypothesis (Istvánovics & Honti, 2011). This latter suggests that fast-sinking meroplanktic
57 diatoms can take advantage of sedimentation and resuspension if the retention time is sufficiently short
58 and can compensate against light deficient conditions (Istvánovics & Honti, 2011). How this hypothesis
59 applies to other taxonomic groups, such as coccal green algae that may be favoured during summer low
60 flow conditions, remains unclear.

61 Phytoplankton play a crucial role in the ecology and functioning of large rivers, reproducing within river
62 (Wu et al., 2011) and exhibiting a rapid response time to environmental conditions ranging from a few
63 hours to a few days. Phytoplankton biomass and composition are controlled by a set of biotic and abiotic
64 factors, such as flushing rate (Reynolds et al., 1994), turbulence (Bormans et al., 2004), light availability
65 into the water column (linked to atmospheric conditions, turbidity and river depth) (Várbiro et al., 2018),
66 water temperature (Peterson & Stevenson, 1989), nutrient availability (Minaudo et al., 2021),
67 competition for nutrients with macrophytes (Sabater et al., 2008), and grazing by zooplankton (Lair &
68 Reyes-Marchant, 1997). Studies often identify and rank controlling factors at a seasonal time scale,
69 focusing on hydrological forcing with high *versus* low-flow periods, on bottom-up aspects (seasonal
70 changes in resource availability) or, more exceptionally on top-down control (Picard & Lair, 2005).
71 While the seasonal and longitudinal dynamics of phytoplankton have been well studied in large rivers
72 (Reynolds & Descy, 1996; Istvánovics et al., 2010), short-term dynamics associated with discharge
73 forcing, have mainly been neglected. Biological responses, in terms of growth and biomass, are known
74 (Kiss et al., 1996), and are increasingly studied based on high-frequency data (Bowes et al., 2016; Pathak
75 et al., 2021). However, much less has been derived in terms of community responses (Dubelaar et al.,
76 2004).

77 Changes in phytoplankton assemblages result from two key interacting processes (Cloern, 1996; Loreau
78 & Mouquet, 1999; Hiltunen et al., 2006): (1) the allogenic processes (also called larger-scale or regional
79 processes), with physical transport, mixing and water advection, which mix populations of different
80 origins and waters with different chemical compositions; (2) the autogenic processes (also called local

81 processes), with biological processes such as species-dependent growth and losses due to competition,
82 predation or response to abiotic changes. Temporal response to allogenic processes is considered
83 immediate whereas autogenic processes need time to produce a visible response in the ecosystem
84 (Reynolds, 1984; Cloern, 1996; Pannard et al., 2008b).

85 In lakes, it is known that short-term dynamic of phytoplankton is mainly controlled by wind forcing
86 (Carrick et al., 1993; Reynolds, 2006; Winder et al., 2008). Wind-induced mixing controls the physical
87 and chemical environment (resource availability, stratification intensity, deepening on the mixed layer)
88 and the development of species adapted to well-mixed conditions (Pannard et al., 2008a). In temperate
89 lakes, the short-term dynamic nests into the seasonal dynamic, leading to a new community structure
90 without any return to the previous one, because of constantly changing environmental conditions
91 (thermocline depth or temperature, for instance). Such 'resetting events' are more common in tropical
92 lakes (Lewis, 1978).

93 In coastal areas, the short-term dynamic of phytoplankton is also controlled by mixing events with
94 estuarine waters due to windy circumstances, river flow and tidal dynamics (Lohrenz et al., 2003).
95 Mixing events lead to an abrupt change in the total phytoplankton biomass and concentration of
96 dominant species with irregularly high growth rates (Pannard et al., 2008b). Consequently, varying
97 intensity and frequency in physical forcing help maintain high phytoplankton diversity in lakes and
98 coastal waters by mixing populations, suppressing dominance and favouring rare species.

99 Water discharge can swiftly regulate autogenic and allogenic processes in river phytoplankton. An
100 elevation in river discharge can alter environmental conditions such as turbulence and turbidity, while
101 facilitating the connection of neighbouring water bodies with distinct nutrient loads and communities,
102 including the benthic-pelagic interface (Istvánovics & Honti, 2011). During flood events, phytoplankton
103 is enriched by meroplankton, which refers to benthic and epiphytic species that have been resuspended,
104 and species from adjacent aquatic ecosystems reconnected by hydrological forcing. Rojo et al. (1994)
105 have shown that meroplankton can represent a significant fraction of the total phytoplankton biomass
106 (up to 50% of suspended taxa). Benthic and epiphytic taxa observed in phytoplankton should be a good
107 proxy of river discharge peak events. Mixing-induced meroplankton occurrence should increase
108 diversity and at the same time may help maintain rare species.

109 River discharge is a crucial driver of phytoplankton dynamics and should promote diversity maintenance
110 by i) transporting new species from adjacent river pools and benthic areas, ii) diluting the resident
111 community, dampening the competitive exclusion by dominant species and therefore sustaining rare
112 species, iii) changing light by increasing turbidity, thus limiting growth except for shade-adapted
113 species, iv) increasing nutrient availability, either directly through nutrient inputs from the catchment
114 area, or indirectly by reducing the boundary layer around large cells through turbulence (Barton et al.,
115 2014) and by reducing the competition for nutrients when dominant species are suppressed. While
116 nutrient pulses favour fast-growing species, large cells might take advantage of these short-term events,
117 thanks to nutrient storage. Thus, species-specific characteristics (i.e. traits) should primarily reflect the
118 species- and community-level responses to discharge-mediated disturbances.

119 Functional traits are morphological, physiological, or phenological features – measurable at the
120 individual level - affecting fitness (Violle et al., 2007). Measuring mechanistic traits at the individual
121 (and even species) level in natural communities is rather impossible. Morphological traits that reflect
122 mechanistic traits are traditionally used in phytoplankton ecology (Litchman & Klausmeier, 2008), and
123 often result in the use of some key traits, such as cell size and organization. Morphological traits also
124 enable classifying phytoplankton taxa into ecological groups (Salmaso et al., 2015), which can help
125 better relate ecosystem functioning to community diversity (Abonyi et al., 2018a). Grouping species
126 into ecological, often called ‘functional groups’, is increasingly adopted by ecologists (Nock et al.,
127 2016). A frequently used functional approach is the classification *sensu* Reynolds (FG) based on habitat
128 templates (Reynolds et al., 2002), which has been advocated as a trait-based approach (Kruk et al.,
129 2021); although we still need to get a mechanistic understanding to link ecosystem-level processes to
130 community composition based on FGs (Abonyi et al., 2021).

131 At the scale of hydrodynamic events, short and long responses can be expected with a modification in
132 phytoplankton species composition and dominance, and a corresponding alteration in functional trait
133 composition. Short-term dynamics in water discharge should promote larger biodiversity in river
134 phytoplankton, partly explained by meroplankton. A bi-monthly sampling in the Moselle river already
135 demonstrated that diversity and the composition of phytoplankton assemblages are clearly linked to river
136 discharge (Descy, 1993).

137 The Loire River is one of the four largest Atlantic rivers with 200-300 m of width in its lower sections
138 and about 1,012 km of length from its source to the estuarine zone (Moatar et al., 2022). Phytoplankton
139 from the Loire have been widely studied since 1920, but its short-term dynamics have never been shown.
140 Many efforts have been conducted since 1991 to limit anthropogenic phosphorus point sources in the
141 hydrosystem to counteract eutrophication which was reaching some extreme levels in the 1980s with
142 chlorophyll-a concentration often over $250 \mu\text{g L}^{-1}$ (Moatar & Meybeck, 2005; Minaudo et al., 2015).
143 Over time, the phosphorus concentration dropped by a factor of three and the Loire phytoplankton now
144 seem to be highly P-limited in late summer (Oudin et al., 2009; Floury et al., 2012; Minaudo et al., 2015,
145 2018, 2021). Longitudinal changes in functional composition, coinciding with the main hydro-
146 ecoregions, have been highlighted, and associated with regional differences in the N:P and Si:P ratios
147 (Abonyi et al., 2014). The Loire River phytoplankton have three distinct assemblage types, upstream
148 detached benthic pennate diatoms, planktic centric diatoms in the middle section (in accordance with an
149 increase in water residence time) and coccal green algae together with small centric diatoms downstream
150 (in accordance with shallowness and increased light availability) (Abonyi et al., 2012; Descy et al.,
151 2012). The Middle Loire River (465 to 772 river km from the headwaters) combines most of the
152 conditions that may favour both pelagic and benthic growth: high light availability with low water level
153 in summer ($\approx 1\text{m}$), high water temperature (Seyedhashemi et al., 2022) and a river morphology with
154 multiple channels, adjacent pools, and numerous islands, slowing down the flow velocity (Latapie et al.,
155 2014). The Middle Loire receives 40% of the total basin contribution, with very little amount of lateral
156 water inputs, making this section the most representative of the large lowland Loire River. Based on the
157 presence of true planktic species (centric diatoms), one can say that autogenic process dominates from
158 the Middle Loire, which makes it an excellent site to study short-term dynamics. A single station was
159 chosen in the Middle Loire and its short-term temporal dynamics were analysed over two hydrological
160 summers in 2013 and 2014. Based on an every 3-day sampling frequency, the short-term variations in
161 river discharge were related to the variations in both local physical and chemical parameters and
162 phytoplankton assemblages.

163 The objective of this study was (1) to highlight the changes in physical, chemical and biological
164 parameters associated with water discharge increase (even in low amplitude), (2) to identify short-term

165 response of phytoplankton assemblage and characterize key taxa and their traits, (3) to highlight a
166 potential effect of repeated disturbances on phytoplankton assemblage, and (4) to evaluate the role of
167 meroplanktic algae on phytoplankton diversity in connection with the benthic retention hypothesis.
168 Studies combining the monitoring of water quality variables (nutrients, physical and chemical
169 parameters) with community data on phytoplankton at a near-daily scale remain scarce.

170

171 **Method**

172 **Study area and sampling location**

173 The geographical and physical characteristics of the Loire River basin have formerly been described
174 extensively in the literature (Descy et al., 2009; Moatar et al., 2022). The sampling station, located at
175 Cinq-Mars-La-Pile near Tours in France, is considered representative of the Middle-Loire (Minaudo et
176 al., 2015). It covers 40 % ($43.6 \times 10^3 \text{ km}^2$) of the total basin contribution with an annual mean river
177 discharge $\sim 355 \text{ m}^3 \text{ s}^{-1}$. The Loire River does not receive any significant inflow over 272 km upstream
178 before arriving to Cinq-Mars-La-Pile, except some groundwater inputs from the Beauce aquifers under
179 high agricultural pressure (Lalot et al., 2015).

180 **Daily river discharge and physical and chemical data**

181 Daily river discharge (Q) at gauging station was downloaded from the online open national water
182 monitoring database (<http://www.hydro.eaufrance.fr/>). Water temperature, pH, dissolved oxygen and
183 conductivity were monitored hourly by Electricité de France (EDF), upstream of the Avoine nuclear
184 power plant, 20 km downstream from our sampling site. Global solar radiation originated from
185 SAFRAN dataset re-analysis (Quintana-Segui et al., 2008), and were averaged over the previous week
186 to account for prior conditions that might had impacted phytoplankton at a given date (Várbíró et al.,
187 2018).

188 **Sampling design**

189 Water was sampled at the thalweg from a bridge in the main river channel. Total suspended solid
190 concentrations (SM) were measured every day. The following parameters were analyzed on a 3-day
191 frequency basis from November 2011 to October 2014: dissolved and particulate organic carbon (DOC
192 and POC), total and dissolved inorganic phosphorus (TP and DIP), total nitrogen (TN), total dissolved

193 nitrogen (TDN) and nitrates ($N-NO_3^-$), dissolved silicon (DSi), chlorophyll-a and pheopigment
194 concentrations. Filtrations were immediately made on-site with 0.45 μm cellulose acetate membrane
195 filters for chemical parameters and with 0.70 μm glass filter (Whatman GFF) previously burned at
196 500°C during 6 hours for chlorophyll-a and pheopigment. SM was determined by filtration of a precise
197 volume of each water sample through pre-weighed filters and by drying them at 105°C. After filtration,
198 water samples and filters were stored at -80°C in polypropylene tubes after acidification of aliquots for
199 nitrates, DIP and DOC analysis. Tubes and filters were unfrozen the day of the analysis. Dissolved
200 organic carbon, TN and TDN concentrations were measured with a carbon and nitrogen analyzer
201 (Shimadzu TOC-V CSH/CSN with TN unit) according to standard protocols from manufacturer
202 (Shimadzu TOC-VCSH/CSN User Manual). Nitrates concentration was determined by ionic
203 chromatography. Phosphorus was measured by colorimetry after solid digestion (potassium-persulfate
204 digestion) when measuring TP (Grasshoff et al., 1983). Dissolved silicon was measured by colorimetry
205 (Aminot & K  rouel, 2004). For POC analyses, the filters were first treated with HCl 2N to remove
206 carbonates, dried at 60°C for 24 hours and then measured with a C/S analyzer (LECO C-S 200).
207 Chlorophyll-a (Chl-a) and pheopigment were measured by fluorimetry at a wavelength > 665 nm after
208 an excitation step between 340 and 550 nm (Strickland & Parsons, 1972). To estimate living
209 phytoplankton and meroplankton in terms photosynthetic activity, we calculated the particulate organic
210 carbon to chlorophyll-a ratio (POC:chl-a) for each sample. It is used as an indicator for ecological and
211 physiological state of phytoplankton, with low ratio when particulate organic matter is dominated by
212 living phytoplankton and high values when there is a lot of organic dead materials (Bibi et al., 2020).
213 Phytoplankton were collected from April to October, with 12 samples in 2012, 44 in 2013 and 44 in
214 2014. Phytoplankton community composition was only related to hydrology in summers 2013 and 2014,
215 where samples were taken with an even distribution (i.e. every 3 days). Summers 2013 and 2014
216 represented ~20 samples in total for each year. Phytoplankton samples were fixed on-site after sampling
217 with Lugol solution. Phytoplankton species were identified with an inverted microscope according to
218 the Uterm  hl method (Uterm  hl, 1958). Phytoplankton manuals for species identification were Geitler
219 (1930-1932), Huber-Pestalozzi (1955), Fott (1968), Ettl et al. (1978, 1985), Kom  rek and Fott (1983),
220 Sarmach (1985), Popovsk  y and Pfiester (1990), Kom  rek and Anagnostidis (1999, 2005). If centric

221 diatom dominance appeared, we prepared permanent slides following the Comité Européen de
222 Normalisation (2003) standard. Diatoms were identified using Krammer and Lange-Bertalot (1986,
223 1988, 1991a, 1991b, Lange-Bertalot (2001) and Krammer (2002). The phytoplankton concentration was
224 first approximated in cells mL^{-1} , and then expressed as wet-weight biomass (mg L^{-1}) using species-
225 specific biovolumes obtained by geometrical approximation according to (Lund & Talling, 1957; Rott,
226 1981). We converted wet weight biomass into carbon biomass (mgC L^{-1}) based on Eppley et al. (1970).
227 Phytoplankton species were assigned to Reynolds functional groups (RFG) according to Borics et al.
228 (Borics et al., 2007), Padisák et al. (2009), and Abonyi et al. (2021). We quantified the dominance
229 relationships based on the inversed Simpson using the *diversity* function of the ‘vegan’ library in R
230 (Oksanen, 2013).

231 **Identification of hydrological events and associated periods**

232 During monitoring of river discharge, a river flow peak was identified when the daily river flow F
233 increased rapidly over a few days, *i.e.* when the slope dF/dt became positive between two consecutive
234 days. This is noticed as * on Fig. 1. The use of the daily average flow rate allows to smooth the curve,
235 but it is possible to perform a smoothing over a few days if the inter-day variations are too big. Minor
236 peaks (even small as $5 \text{ m}^3 \text{ s}^{-1} \text{ day}^{-1}$) were also identified when a slight increase in flow (even over two
237 days) was coupled with changes in biochemical parameters such as POC:chl-a ratio.

238 To highlight change in phytoplankton assemblage associated with hydrological events, we identified
239 different periods according to their timing before and after peak flow events (Fig. 1). The ‘After’
240 period begins when water discharge start increasing (t^*). ‘Before’ and ‘After’ thus correspond to the
241 increase and the beginning of the decrease in water discharge, respectively. It ends at the end of the
242 recession curve of the river flow at t_2 (Fig. 1). We termed periods outside ‘Before’ and ‘After’
243 ‘Stable’.

244 We then tested if these periods corresponded to distinct phytoplankton assemblages through
245 multivariate analyses, for each year independently. Three assemblages per year were highlighted,
246 called ‘stable’ assemblages (during stable periods), ‘disturbed’ assemblages (from t^* to t_2) and
247 ‘repeatedly disturbed’ assemblages (at least two successive disturbed periods).

248 **Multivariate analysis**

249 About 150 phytoplankton species have been observed with many rare species. To characterize the short-
250 term relationships between environmental variables (explanatory variables) and taxa biomass (response
251 matrix), a canonical correspondence analysis (CCA) (Legendre & Anderson, 1999) has been performed
252 for each year, using ‘ade4’ and ‘vegan’ R libraries (Oksanen, 2013). This method is based on both
253 multiple regression and ordination methods. Prior to these canonical analysis, phytoplankton (biomass)
254 community data were Hellinger-transformed to remove the effects of both rare (many zeros) and
255 dominant taxa (Legendre & Gallagher, 2001). The environmental parameters were centered and scaled
256 and collinearity was checked. The link between explanatory and responses variables was tested through
257 a Monte Carlo permutation test with 999 replications (Blanchet et al., 2008) using CCA. CCA was used
258 to identify characteristic phytoplankton assemblages associated with hydrological forcing and to identify
259 environmental parameters. A taxa contributes to a canonical axis if its variability in relative frequency
260 among samples contributes to the variability of the assemblage.

261 A correspondence analysis (CA) has also been performed on Hellinger-transformed RFG biomass. A
262 discriminant analysis (DA) was performed on the CA with the function *discrimin* to identify RFG
263 associated with ‘stable’, ‘disturbed’ and ‘repeatedly disturbed’ assemblages. Instead of maximizing the
264 total variance carried by axes 1 and 2 as in a classical CA or CCA, the analysis focused on maximizing
265 the explained inter-group variance depending on a discriminating factor. The level of significance of the
266 discriminating factor has been tested by a Monte Carlo permutation test (based on 999 permutations).
267 All analyses were performed with ‘ade4’ library in Rstudio.

268 To link individually taxa and RFG with environmental parameters, a Pearson’s correlation matrix was
269 performed with the R library ‘corrplot’ (Wei & Simko, 2017).

270

271 **Results**

272 **Overall variability of hydrology, physical and chemical parameters and phytoplankton** 273 **assemblage among years**

274 Hydrology was contrasting among studied years, with water discharges ranging from 50 to 1,900 m³ s⁻¹
275 ¹ (Fig. S1), and up to 3,580 m³ s⁻¹ downstream. The winter high-flow periods in 2013 and 2014 were

276 wet, with a seasonal maximum of 1900 and 1400 m³ s⁻¹, respectively. Minimum summer discharge
277 was 110 m³ s⁻¹ in 2013 and 90 m³ s⁻¹ in 2014. Total suspended solids (SM) concentrations ranged
278 between 0.2 and 137 mg L⁻¹. SM was in general higher in winter due to major hydrological events,
279 though it was also relatively high (\approx 50 mg L⁻¹) in summer during hydrological events. Nitrates
280 concentration was highly seasonal and synchronous with discharge. DSi showed the lowest values
281 between April and June with 1.4 and 1.1 mg SiO₂ L⁻¹ in 2013 and 2014, while P-DIP was lowest in
282 July and August, with less than 1 μ g P L⁻¹ (Fig. S1). Chlorophyll-a values indicated some extensive
283 phytoplankton growth periods, with similar maximum values every year near 60 μ g L⁻¹. Centric
284 diatoms systematically dominated the phytoplankton assemblage in spring and then decreased in
285 dominance towards summer, when green algae started to grow (Fig. S1). Phytoplankton at the end of
286 the summer were either dominated by green algae (2012) or diatoms (2013 and 2014).

287 **Physical and chemical parameters in summer 2013**

288 From early July to early September 2013, three discharge peak events with increasing intensity were
289 observed, more than eight days apart (events number 1 to 3, Fig. 2a). SM content increased
290 simultaneously with river discharge, each time with an increasing intensity, consistent with the
291 dynamic of river discharge (Fig. 2b). The third event resulted in a sharp increase in the POC:chl-a
292 ratio of SM in the river, which increased by a factor of 9, whereas this ratio did not fluctuate during
293 the first two events (Fig. 2a). This sharp increase was partly related to the drop of chlorophyll-a
294 concentration in the water (Fig. 2e). Three days after this event, DIP exceeded 40 μ g P L⁻¹ (Fig. 2c).
295 On 19/08/2013, six days after this third discharge event, DIP decreased to near pre-disturbance values
296 (3 μ g P L⁻¹), while chlorophyll-a increased to its pre-disturbance maximum value (44.2 μ g L⁻¹). It is
297 noteworthy that overall, DIP and chlorophyll-a concentration correlated negatively (Pearson's
298 correlation, $r = -0.57$; $p = 0.003$), indicating DIP consumption when phytoplankton biomass was high.
299 DOC increased steadily over 9 days following the third discharge event (Fig. 2d). A slight increase in
300 DOC was also observed on 04/08/2013, following event 2. Phaeopigment concentration remained
301 unchanged by the discharge events.

302 A minor increase of river discharge could also be observed at the end of the period, on 03/09/2013
303 (number 4, Fig. 2a). This event doubled the POC:chl-a ratio of suspended matter in the river and led to

304 a 50% increase in DOC (Fig. 2d). Two ‘stable’ periods (outside the before/after periods) could be
305 identified during the summer 2013.

306 The inverse Simpson index increased during stable hydrology periods, and decreased during peak
307 discharge events (Fig. 2f). The strongest event 3 resulted in the minimum value of the index, with 2.3
308 on 19/08/2013.

309 **Short-term responses of phytoplankton to hydrology in summer 2013**

310 To characterize the changes in assemblages and relate them to physical and chemical parameters
311 (temperature, pH, oxygen, nutrients, discharge, DOC), a CCA was performed on the biovolumes data
312 (Fig. 3). Environmental variables explained 62.7% of the total variance in phytoplankton community.

313 The sampling dates grouped together following the hydrological periods specified above (Fig. 2).

314 While some periods showed overlaps (e.g. Before1, After3 and Stable2), others remained highly
315 separated along with axis 1 and axis 2 (Fig. 3c).

316 Along axis 1 of the CCA the consecutive periods Stable1 and Before2, on the right of the axis,
317 contrasted with the initial assembly (Before1) and the ones after event 3 (After3, Stable2 and After4).

318 After1 and After2 had similar ‘mean’ assemblages, i.e. they were located in the centre of the
319 ordination. Temperature was the most significant variable correlating positively with axis 1 ($r = 0.87$),
320 while nitrates ($r = -0.53$), DIP ($r = -0.41$) and DOC ($r = -0.43$) correlated negatively along with the
321 same gradient (Fig. 3b). Considering the weight of these parameters in the prediction of taxa biomass
322 (i.e. the canonical coefficients of environmental parameters in the CCA), temperature changes had a
323 weight more than twice that of nitrates (-0.17 vs. +0.40) and four times that DIP (-0.09 vs. +0.4).

324 Stable1 and Before2 were characterized by higher water temperatures, but lower concentrations of
325 nitrates, DIP and DOC compared to the other periods. Stable2, Before1, After3 and After4 had higher
326 concentrations and lower water temperature. Along axis 2 of the CCA, After4 was separated from the
327 other periods (Fig. 3c). pH ($r = 0.61$) and temperature ($r = 0.40$), with respective weights of +0.33 and
328 +0.22 were the main variables explaining these differences. After4, which corresponded to the
329 assembly of minor event 4, was thus characterized by lower temperatures and pH.

330 The most important contributing taxa along with the canonical axes could be separated into three
331 assemblages (Fig. 3a). Assemblage A1 (Fig. 3a), which included the initial assemblage, was

332 characterized by a higher biomass of the diatoms *Skeletonema potamos* (Weber) Hasle (14.4% of
 333 contribution to axis 1 and 13.1% to axis 2), centric diatoms (9.0% to axis 1 and 1.6% to axis 2) and
 334 *Nitzschia acicularis* (Kützing) W.M. Smith (4.77% to axis 1), and the green algae *Chlamydomonas* sp.
 335 Ehrenberg (8.0% to axis 1 and 3.7% to axis 2), *Coelastrum microporum* Nägeli (1.2% to axis 1 and
 336 2.0% to axis 2) and *Kirchneriella* spp. (1.8% of axis 2 with *K. contorta* (Schmidle) Bohlin, *K. obesa*
 337 (W. West) Schmidle and *K. irregularis* (GM Smith) Korshikov). Assemblage A2, corresponding to the
 338 Stable1 and Before2 periods, showed higher biomasses of the green algae *Actinastrum hantzschii*
 339 Lagerheim (10.4% to axis1), *Crucigenia lauterbornii* (Schmidle) Schmidle (10.7% to axis 1),
 340 *Treubaria triappendiculata* Bernard (6.6% to axis1), *Golenkinia radiata* Chodat (3.9% to axis1),
 341 *Lobomonas ampla* Pascher (3.6% to axis1), *Dictyosphaerium pulchellum* Wood (4.4% to axis1),
 342 *Oocystis* spp. Nägeli ex A.Braun (2.6% to axis1), and *Didymocystis* spp. (2.7% to axis1 with *D. fina*
 343 Komárek, *D. bicellularis* (Chodat) Komárek and *D. planctonica* Korshikov). Assemblage A3
 344 corresponds to After4, with a higher biomass of the benthic diatom *Diatoma vulgare* Bory (4.1% to
 345 axis 1 and 36.7% to axis 2) and *Scenedesmus* spp.: *S. spp. 3* Meyen with for instance *S. group*
 346 *Scenedesmus sensu stricto sensu* Komárek & Fott (3% to axis 1 and 12.7% to axis 2), *S. spp.1* Meyen
 347 with for instance *S. group Abundantes / Spinosi sensu* Komárek & Fott (7.8% to axis 2),
 348 *Acutodesmus* spp. (Hegewald) Tsarenko (5% to axis 2), *Desmodesmus* spp. (R. Chodat) S.S. An, T.
 349 Friedl & E. Hegewald (4.5% to axis 2) and *S. spp. 2* Meyen with for instance *S. group Armati*
 350 *sensu* Komárek & Fott (2% to axis 2). The benthic cyanobacterium *Merismopedia* spp. also
 351 contributed to axis 2 (1.16% with *M. glauca* (Ehrenberg) Kützing and *M. tenuissima* Lemmermann).
 352 This event-driven short-term succession was also found in the time series of species biomasses (Fig.
 353 4). *S. potamos* (Fig. 4b) and *Chlamydomonas* sp. (Fig. 4c) were positively correlated (Pearson's
 354 correlation, $r = 0.52$; $p = 0.008$), with higher biomasses in before1, after2, after3 and stable2
 355 (assemblage 1). In contrast, *G. radiata* (Fig. 4d) and *A. hantzschii* (Fig. 4e), also correlated with each
 356 other (Pearson's correlation, $r = 0.62$; $p < 0.001$), and were almost only present during stable1 and
 357 Before2 (assemblage A2), i.e. during the period of the lowest discharge fluctuation (Fig. 2a). *D.*
 358 *vulgare* (Fig. 4g) showed an increase in biomass at the end of the period (After4), as do *Scenedesmus*
 359 spp. that are previously punctually present (Fig. 4f).

360 Physical and chemical parameters in summer 2014

361 The 2014 study period began with a long stable period in terms of discharge, followed by four
362 temporally close discharge peak events, with Q successively peaking on 16/07/2014, 27/07/2014,
363 9/08/2014 and 15/08/2014, preventing a return to initial conditions (Fig. 5a). The first discharge event
364 started with a gradual increase on 05/07/2014 ($100 \text{ m}^3 \text{ s}^{-1}$) and accelerated on 10/07/2014 ($210 \text{ m}^3 \text{ s}^{-1}$)
365 to reach a maximum on 16/07/2014 ($402 \text{ m}^3 \text{ s}^{-1}$), corresponding to the highest peak of SM observed
366 over summer 2014 with a concentration of 55 mg L^{-1} (Fig. 5b). The following events 3 and 4 resulted
367 in slight increases in SM. A peak in POC:chl-a was observed on 06/07/2014, mainly due to the
368 decrease in chlorophyll-a concentration, potentially indicating an early effect of the first disturbance
369 (Fig. 5e). We considered this period to be isolated from the initially stable period and referred to as
370 Before1.

371 Event 1 was therefore the major event of summer 2014. It corresponded with a peak of DIP ($37 \mu\text{g P}$
372 L^{-1}), which continued to increase with the following discharge disturbances up to $60 \mu\text{g P L}^{-1}$, reached
373 on 9/08/2014 (Fig. 5c). DOC increased after event 1, with a doubling of its concentration from 2 to 4
374 mg C L^{-1} , and then remained above 3 mg L^{-1} during the subsequent events (Fig. 5d). When data from
375 both 2013 and 2014 were taken into account, river discharge correlated positively with DOC
376 concentration (Pearson's correlation, $r = 0.62$; $p < 0.001$) and SM (Pearson's correlation, $r = 0.71$; $p <$
377 0.001).

378 Chlorophyll-a concentration showed a decreasing trend during the first (Stable) period from 35 to 25
379 $\mu\text{g L}^{-1}$ (Fig. 5e), likely due to depleted phosphorus availability (Fig. 5c). Chlorophyll-a peaked after
380 event 2 ($48 \mu\text{g L}^{-1}$) and then remained under $20 \mu\text{g L}^{-1}$ until the end of the summer. Water discharge
381 events as disturbances decreased chlorophyll-a concentration and increased DIP concentrations.

382 Similarly to 2013, a significant negative correlation between chlorophyll-a and DIP was observed
383 (Pearson's correlation, $r = -0.65$; $p < 0.001$).

384 Diversity of the phytoplankton assemblage, monitored with the inverse Simpson index, was maximal
385 during the stable period (Fig. 5f), despite declining biomass and limiting dissolved inorganic
386 phosphorus concentrations. Diversity gradually increased again at the end of the disturbed period.

387 Seven periods could be delineated based on the variations in physical and chemical parameters
 388 described above (Fig. 5).

389 **Short-term responses of phytoplankton to hydrology in summer 2014**

390 Environmental variables explained 42.6% of variance in the phytoplankton community in 2014 (Fig.
 391 6). pH was removed from the CCA to respect the rule of low collinearity between explanatory
 392 variables. Axis 1 was positively correlated with discharge Q ($r = 0.88$), DIP ($r = 0.78$), DOC ($r =$
 393 0.71), silicon ($r = 0.60$) and SM ($r = 0.55$) and negatively correlated with nitrates ($r = - 0.65$) and DO
 394 ($r = - 0.57$) (Fig. 6b). DOC was the parameter with the highest weight (canonical coefficients), with a
 395 weight of +0.22, followed by nitrates (- 0.19) and DSi (+0.17). Axis 2 was correlated with SM ($r =$
 396 0.59), temperature ($r = 0.45$) and DO ($r = - 0.34$).

397 The CCA performed on the 2014 taxa biomass data separated the Stable period to the left of the
 398 ordination from the other periods, including Before1, the first pre-disturbed period (Fig. 6c). Axis 2,
 399 meanwhile, separated periods chronologically, with After1 at the top right of the ordination, After2,
 400 After3 and Before2 in the middle and After4 at the bottom. The post-disturbance assemblages (After1,
 401 2/3 and 4) were thus located in the periphery, while the two transitional assemblages (Before1 and 2)
 402 were found near the centre of the ordination, indicating an average composition.

403 The phytoplankton taxa contributing the most significantly to the canonical axes clustered around 3
 404 assemblages along axes 1 and 2 (Fig. 6a). Assemblage B1 corresponded to the initial assemblage
 405 (Stable), with a higher biovolume of diversified green algae: *A. hantzschii* (8.4% to axis1), *D.*
 406 *pulchellum* (6.5% to axis 1), *Dictyosphaerium* sp. Nägeli (5.4% to axis 1 and 6% to axis 2), *C.*
 407 *lauterbornii* (5.8% to axis 1 and 3.4% to axis 2), *Micractinium pusillum* Fresenius (6.2% to axis 1),
 408 *Plagioselmis nannoplanctica* (H. Skuja) G. Novarino, I.A.N. Lucas & S. Morrall (3.1% to axis 1), *G.*
 409 *radiata* (2.9% to axis 1 and 2.3% to axis 2), *Actinastrum aciculare* Playfair (2.3% to axis 1 and 4.1%
 410 to axis 2), *Monoraphidium* spp. (2.5% to axis 1 with *M. arcuatum* (Korshikov) Hindák, *M. circinale*
 411 (Nygaard) Nygaard, *M. contortum* (Thuret) Komárková-Legnerová, *M. griffithii* (Berkeley)
 412 Komárková-Legnerová, and *M. tortile* (West & G.S.West) Komárková-Legnerová), *Acutodesmus* spp.
 413 (2.3% to axis 1 and 11.3% to axis 2), *Franceia ovalis* (France) Lemmermann (1.3% to axis 1). Only
 414 one diatom contributed to the assemblage 1, with *N. acicularis* (3.1% to axis 1 and 5.2% to axis 2).

415 Assemblage B2 associated with the period following the first major disturbance (After1) was
 416 characterized by an increase in *Tetraedron* spp. (3.3% to axis 2, with *T. caudatum* (Corda) Hansgirg,
 417 *T. incus* (Teiling) G.M. Smith and *T. minimum* (A.Braun) Hansgirg), small indeterminate flagellates
 418 (1.8% to axis 2), *Acutodesmus* spp. (11.3% to axis 2), and *Scenedesmus* spp. 1 (4.2% to axis 1 and
 419 5.5% to axis 2). This B2 assemblage was also characterized by decreasing biovolumes of the diatom
 420 *N. acicularis* (3.1% to axis 1 and 5.2% to axis 2), and the green algae *Dictyosphaerium subsolitarium*
 421 Van Goor (6.1% to axis 2), *C. microporum* (4.5% to axis 2), *A. aciculare* (2.3% to axis 1 and 4.1% to
 422 axis 2), and *Chroococcus* sp. Nägeli (5.1% to axis 2). Assemblage B3 observed at the end of the
 423 disturbed period (After4) was characterized by a higher biovolume of the benthic cyanobacterium
 424 *Merismopedia* spp. (9.6% to axis 1 and 3.3% to axis 2), the diatom *S. potamos* (25.3% to axis 1 and
 425 5.0% to axis 2) and the green algae *Scenedesmus* spp. 3 (3.1% to axis 1).
 426 This succession with a calm period in terms of river discharge, followed by a period with several
 427 discharge events was observed in the time series of species biovolumes (Fig. 7), with a bell-shaped
 428 curve of colonial green algae during the stable period (Fig. 7a and b). *Tetraedron* spp., a small green
 429 alga, although remaining in low biomass, was only observed during the transition period (Fig. 7c).
 430 Some genera such as *Scenedesmus* also took advantage of this transition period (Fig. 7f). The benthic
 431 cyanobacteria *Merismopedia* spp. and the diatoms *S. potamos* and *N. acicularis* increased temporarily
 432 following the major first disturbance (Fig. 7d, e and g).

433 **Phytoplankton assemblage and functional trait compositions between hydrologically contrasting** 434 **summers**

435 Six characteristic phytoplankton assemblages were identified in 2013 (Fig. 3a) and 2014 (Fig. 6a). We
 436 could group them in pairs based on their location in relation to the river discharge disturbances (Fig.
 437 8): two were in stable condition (A2 and B1 grouped as stable assemblage), two following a strong
 438 disturbance (A1 and B2, grouped as disturbed assemblage) and two after a series of disturbances,
 439 called here 'repeatedly disturbed' assemblage (A3 and B3). Common species could be identified with
 440 at least four green algae during stable conditions (*A. hantzschii*, *D. pulchellum*, *C. lauterbornii*, *G.*
 441 *radiata*) and one benthic cyanobacterium genus in the repeatedly disturbed period (*Merismopedia*
 442 spp.) (Fig. 8). Some diatoms were observed over two periods, such as the needle-shaped species *N.*

443 *acicularis* during stable and disturbed periods, and the flexible filaments of *S. potamos* during
 444 disturbed and repeatedly disturbed periods. Several *Scenedesmus* taxa were observed in the samples,
 445 in particular in the repeatedly disturbed periods, in B1 and B2, but the specificity of the species to a
 446 period was less markable.

447 Three typical assemblages of the Loire River could thus be specified here (Fig. 8):

448 1) The 'stable' assemblage occurred each time in phosphorus-depleted condition, with a diverse
 449 assemblage, but under the dominance of colonial green algae and diatoms. The stable
 450 assembly could be characterized by 16 species: four species have spine-like morphology (n°5
 451 *G. radiata*; n°8 *F. ovalis*; n°12 *M. pusillum* ; n°13 *T. triappendiculata*), six species are
 452 colonial green algae (n°2 *D. pulchellum*; n°3 *Tetrastrum triangulare* (Chodat) Komárek; n°4
 453 *A. hantzschii* and *A. aciculare*; n°11 *Oocystis* spp. ; n°12 *M. pusillum* ; n°14 *Scenedesmus*
 454 spp., *Desmodesmus* spp. and *Acutodesmus* spp. and two are mobile, with two flagella per cell
 455 (n°7 *L. ampla*; n°9 *P. nannoplanctica*). Even if several species were colonial, their size was
 456 rather medium compared to large colonial cyanobacteria or Pennate diatoms. The single
 457 diatom taxon that regularly occurred during the stable phase was the needle-shaped *N.*
 458 *acicularis*. One third of the 'stable' group species belonged to the co-occurring functional
 459 groups **F** and **J**, which correspond to middle and lower sections of large rivers and indicate
 460 low turbulence with enhanced residence time and light availability (Abonyi et al., 2021).
 461 Finally, these 16 taxa observed in stable conditions belonged to only 5 Reynolds FGs (**D**, **F**, **J**,
 462 **X1**, and **X2**).

463 2) The 'disturbed' assemblage contained 10 taxa, observed either during A1 or during B2. Three
 464 species were colonial green algae (n°15 *Kirchneriella* spp., n°14 *Scenedesmus* spp. and n°16
 465 *C. microporum*) and one was mobile, with two flagella per cell (n° 18 *Chlamydomonas*). The
 466 flexible filaments of *S. potamos* (n°19) were also observed. The needle-shaped *N. acicularis*
 467 (n°1) already observed during Stable period showed a contrasting response to disturbance,
 468 with an increase during A1 and a decrease during B2. The group **J** of Reynolds was still the
 469 dominant functional group. The characteristic taxa of the 'disturbed' assemblages also

470 belonged to four Reynolds FGs (**D**, **F**, **J**, **X2**, thus losing **X1** compared with the ‘Stable’
471 assemblage).

472 3) The ‘repeatedly disturbed’ assemblage had only four characteristic taxa, but all representing
473 different Reynolds FGs (still **D** and **J**, with **T_B** and **Lo** more; Fig. 8). The flexible filaments of
474 *S. acicularis* (FG **D**) were still observed. The benthic cyanobacterium *Merismopedia* spp.
475 (n°20), specific of that period, was observed during both A3 and B3 and was the only
476 representative of the group **Lo**. A new benthic diatom was observed, *D. vulgaris* (n°21 ; FG
477 **T_B**). Finally, half of the four species were benthic, half were diatoms and only one a small
478 colonial green (*Scenedesmus* spp., FG **J**).

479 The discriminant analysis (DA) performed on the CA of RFG biomass shows that 19% of total
480 variance of the RFG data was explained by three assemblages’ types (Fig. 9). The DA separated the
481 stable period on the left from the disturbed period on the upper right and the repeatedly disturbed
482 period on the lower right of the plot (Fig. 9). The FG **F** (cov. -0.83 with axis 1; clear epilimnetic
483 habitat) and **X1** (cov. -0.79; shallow mixed layer in enriched conditions) characterized the stable
484 assemblage. The FG **T_B** (cov. 0.55 with axis 1; highly lotic environments, streams and rivulets)
485 characterized both disturbed and repeatedly disturbed assemblages. The FG **D** pointing to the upper
486 right (covariance of 0.55 with axis 1 and 0.32 with axis 2 ; shallow enriched turbid water including
487 rivers) characterized the disturbed assemblage. The FG **Lo** pointing to the lower right (cov. -0.77 with
488 axis 2; summer epilimnion) characterized the repeatedly disturbed period.

489 Most RFG and taxa positively correlated with water temperature and solar radiations, while they
490 negatively correlated with river discharge and DIP, irrespective of life form and taxonomic position
491 (diatoms, benthic taxa or colonial green algae, Fig. 10). Chlorophyceae biomass thus correlated
492 positively with solar radiation (Pearson’s correlation, $r=0.30$; $p<0.01$) and negatively with river
493 discharge (Pearson’s correlation, $r=-0.30$; $p<0.01$). Only the benthic diatom *D. vulgaris* correlated
494 negatively with temperature, and positively with nitrates.

495 Variance partitioning showed that time generally explained a low proportion of total variance in
496 phytoplankton, with less than 5% (except the 22% for *Chlamydomonas* sp. in summer 2013; see **X1** on
497 Fig. S2). DIP concentration explained between 10 and 40% of the variance at both the seasonal and

498 short-term time scale for centric diatoms and *N. acicularis* (codon **D** – see **X3** on Fig. S2). Interestingly,
499 water temperature appeared as the most significant predictor for many taxa if data were pooled, but also
500 when analysed separately (see **X2** on Fig. S2).

501

502 **Discussion**

503 Here, we asked how short-term alterations in water discharge affected the physical and chemical
504 environment and corresponding changes in phytoplankton community composition and diversity in the
505 Middle Loire. In two contrasting summers, our data suggested that hydrological events systematically
506 affected phytoplankton composition, along with three assembly types: a stable assemblage type with
507 many colonial green algae; a disturbed assemblage type that decreased in biomass but benefited from
508 new taxa such as *S. potamos* ; and a repeatedly disturbed assemblage type that benefited from the
509 resuspension of benthic species, temporarily replacing colonial greens. These short and long responses
510 to disturbance allowed for the maintenance of greater taxonomic and functional diversity on a seasonal
511 scale in the Loire River. Taxa richness is mainly driven by green algae and diatoms in accordance with
512 literature (Wehr & Descy, 1998; Wang et al., 2014). This suggests that community dynamics of
513 phytoplankton are predictable in the Middle section of large rivers, if hydrology and hydrology-related
514 parameters are monitored with high resolution.

515 The biogeochemical functioning of large rivers differs strongly between high and low flow, the latter
516 corresponding to a growing period for phytoplankton and so represents strong biological activity.
517 Variations in discharge, e.g. "water flush", can occur over a few hours that dilutes phytoplankton
518 biomass, increases the mortality rate, and changes a full set of environmental conditions (e.g. turbulence,
519 light climate, nutrients availability). However, community dynamics in phytoplankton has rarely been
520 studied at a sub-weekly time scale – but chlorophyll-a (Bowes et al., 2016) and community biomass
521 (Pathak et al., 2021) - in response to river hydrology (Istvánovics & Honti, 2011), in particular at a fine-
522 scale taxonomic and functional levels.

523 Here, we could identify eight water discharge events that have affected the Loire River phytoplankton.

524 Even minor discharge increases modified the physical and chemical parameters with an increase in the

525 POC:chl-a *ratio*, a decrease in phytoplankton biomass, and a change in assemblage structure. Pickett
526 and White (1985) defined disturbance as “any relatively discrete event in time that disrupts ecosystem,
527 community, or population structure, and that changes resources, availability of substratum, or the
528 physical environment”. The hydrological events thus represented disturbances for the phytoplankton,
529 leading to a dilution of the bulk community but with alterations in community composition based on
530 species functional characteristics before, during, and after disturbance. Wang et al. (2014) highlighted
531 distinct assemblages driven by hydrological forcing in a large subtropical river, with after-flood
532 assemblages associated with higher abundance of green algae and tychoplanktic taxa. While
533 disturbances in rivers are generally associated with high floods, which then mobilize nearby sediments,
534 here, we refer to a disturbance as soon as the river discharge increases even slightly, such as a daily
535 increase of $5 \text{ m}^3 \text{ s}^{-1} \text{ day}^{-1}$. Our study highlights that hydrology-related disturbance is not necessarily
536 related to any threshold, rather, the disturbance can even under slight changes in hydrology.

537 The rate of change of the river discharge appears more important than its intensity to constrain the
538 phytoplankton biomass and assemblage in the Loire River. The discharge rate of change with the
539 previous day was overall mainly negative: river discharge decreased compared with the previous day
540 62% of days (all seasons considered), while it increased during 35% of the days or remained stable for
541 3% of the days. When we focused on the period of May to September, river discharge decreased 67%
542 of the days. Hydrological recession thus represents the most common condition in the Middle Loire
543 River in summer.

544 **Short-term changes in physical and chemical parameters**

545 Temperature, solar radiations, nutrients and river discharge have been identified as main drivers of
546 river phytoplankton at the seasonal scale (Descy et al., 2013). We had expected that during summer
547 high temperature influenced less phytoplankton production and assemblages, being already high
548 compared with spring and fall. In summer, mean daily water temperature varies by a few degrees over
549 a few days, following meteorological forcing and high/low pressure events. Water temperature was a
550 stronger predictor for the biomass of individual phytoplankton taxa than solar radiation. Most of the
551 variance in taxa biomass was also explained by water temperature. It is therefore likely that water
552 temperature indirectly affected phytoplankton growth, e.g. jointly with other meteorological

553 conditions such as calm and sunny *versus* disturbed periods. River temperature follows a diurnal cycle
554 and a seasonal cycle, associated with meteorological forcing and depending on the hydrological
555 context. Water temperature is sensitive to air temperature, relative humidity, solar radiation and river
556 width, but also river discharge, upstream temperature (Gu & Li, 2002), and lateral groundwater inputs
557 (Wawrzyniak et al., 2017). More than a controlling factor, water temperature seems to be a good proxy
558 for short-term meteorological and hydrological forcings. Changes in the similarity of pelagic diatoms
559 in a large German river have been successfully linked to the antecedent precipitation index, which
560 considers rainfall and wetness of the basin, and so remobilisation on a wider scale (Wu et al., 2016).
561 At the short time scale, CCA showed that DIP and DOC were associated with discharge peak events
562 for both 2013 and 2014, where suspended matter (SM) also increased nearly simultaneously with
563 discharge peaks. In 2014, SM strongly increased just after the first main disturbance, while next
564 events, despite being higher in intensity, did not lead to higher SM concentration. Remobilization of
565 organic and inorganic particles from the benthos in the Middle Loire seems to depend on the delay
566 between discharge disturbances, with a small remobilization if time for settling of suspended particles
567 from one event to the next is too short.

568 In conjunction with peaks in SM, most of the discharge disturbances resulted in simultaneous drops in
569 chlorophyll-a concentration, likely by dilution. It is known that phytoplankton biomass in large rivers
570 varies inversely with discharge, and is linked to water residence time and hydrology-mediated light
571 availability (Wehr & Descy, 1998; Várbró et al., 2018). However, on our semi-weekly time series, we
572 observe that chlorophyll-a tends to increase rapidly 2-6 days after a discharge event, probably due to
573 both the enrichment by meroplankton and the phytoplankton growth stimulated by the mobilisation of
574 nutrients (Minaudo et al., 2018). The increase of SM in the river recharges phosphorus, by desorption
575 processes from the particulate phase to the dissolved one and diffusion of pore water from the
576 underlying sediment (Reddy et al., 1995). Discharge events in summer also flush DIP-repleted water
577 with direct and diffuse inputs from the upper catchment. Disturbances have, therefore, first a negative
578 impact on the phytoplankton biomass (dilution effect combined with light limitation due to
579 resuspended solids), then a positive impact by recharging the ecosystem in potentially bio-assimilable

580 phosphorus. The response of the assemblages to short-term forcing in P-limited conditions should
581 differ from the response in eutrophic conditions.

582 Short-term nutrients dynamic in summer can be related here to short-term dynamics in phytoplankton
583 and the uptake of nutrients for its biomass. The summer concentration of DIP was lower than $10 \mu\text{g P}$
584 L^{-1} in 50% of the samples, while nitrates concentration, with a minimum concentration of $950 \mu\text{g N L}^{-1}$,
585 was sufficient throughout the year for the growth of phytoplankton. A mean biomass of $60 \mu\text{g L}^{-1}$ (we
586 had 40 to $50 \mu\text{g L}^{-1}$ during this study) indeed requires $\sim 100 \mu\text{g P L}^{-1}$ (Dillon & Rigler, 1974) and 722
587 $\mu\text{g N L}^{-1}$, based on the Redfield ratio. The concentrations of silicon remained also high enough most of
588 the year, with values $>1 \text{ mg SiO}_2 \text{ L}^{-1}$ in 99% of samples. The lack of correlations between DSi or nitrates
589 concentrations with the phytoplankton biomass can be explained by the fact that nutrient uptake by
590 phytoplankton remained low compared to the nutrient stock in the river. On the contrary, concentrations
591 of DIP and chlorophyll-a were negatively correlated. Short-term DIP concentration in the Loire River
592 is thus controlled by phytoplanktic uptake, with maximum DIP concentrations reached when
593 chlorophyll-a concentration is minimal. Descy (2012) also observed concentrations $<10 \mu\text{g P L}^{-1}$ from
594 June to October in the Loire River. The molar N:P ratio calculated on biologically available nutrients
595 (Ptacnik et al., 2010) was always > 64 during that study, clearly above the 16:1 Redfield ratio, also
596 confirming that P was a limiting nutrient for growth, in accordance with literature (Minaudo et al., 2015).

597 Over the last 30 years, the Loire River has indeed undergone changes in its phytoplankton assemblages,
598 with a 90% biomass decrease, which has been related to different factors: P reduction, altered discharge
599 and the invasion of the Asian clam *Corbicula* sp. (Minaudo et al., 2021). Planktic cyanobacteria always
600 remained a minor fraction of the total phytoplankton biomass, irrespective of the study period (Descy et
601 al., 2012; Minaudo et al., 2021).

602 Short-term DOC dynamics were also related to river discharge, with increases of 1 to 5 mg C L^{-1}
603 following discharge disturbances. Most of the total organic carbon (TOC) was in the dissolved form,
604 with DOC representing $\sim 70\%$ of the TOC, in accordance with literature (Peterson et al., 1994) and
605 other stations on the Loire River (Minaudo et al., 2015). The highest DOC concentrations were
606 observed during the main hydrological events, indicating a remobilization of DOC pool during
607 discharge peak events. DOC originates from both terrestrial sources (hydrologically connected soils

608 and wetlands) and local production by phytoplankton, microphytobenthos and the microbial loop.
609 Upstream terrestrial DOC inputs thus fuels a semi-labile pool, more conservative, while local
610 production fuels a labile pool, rapidly lost through photolysis, flocculation, consumption or adsorption
611 (Del Giorgio & Pace, 2008). A higher local production or lower lost processes may explain that DOC
612 concentration generally increases after a discharge disturbance. DOC could thus represent an excellent
613 chemical proxy for river discharge disturbances in the Loire River, and also elsewhere.
614 In recent years, the use of *in situ* high-frequency spectrophotometric and electrode technologies,
615 particularly of chlorophyll fluorescence probes, represents a good opportunity to go further in the
616 study of short-term dynamics with time series data at a scale down to the minute (Wade et al., 2012).
617 Thresholds of environmental drivers can be highlighted, as for water discharge and temperature whose
618 thresholds for cyanobacteria blooms could have been calculated in a eutrophic river (Bowes et al.,
619 2016). The main limitation of new technologies is that nutrients are by now rarely measured at such a
620 fine time scale. Moreover, the simultaneous acquisition of assemblage data remains scarce, although
621 sensor development is progressing. The coupling of high frequency physical and chemical
622 measurements with daily monitoring of species by flow cytometry or sequencing for instance would
623 be a real step forward in the near future to increase our understanding of assembly rules and short-term
624 drivers of river phytoplankton.

625 **Short-term functional changes in phytoplankton in response to hydrological disturbance**

626 The phytoplankton assemblage measured semi-weekly was in agreement with the seasonal succession
627 already described in the Loire River (Abonyi et al., 2012, 2014; Descy et al., 2012) and more generally
628 in large rivers, with a spring bloom of diatoms, followed by small centric diatoms in May-June, and by
629 Chlorophyceae during summer (Descy et al., 2012, 2013). Diatoms represented ~10% of the total
630 biomass in summer, which indicates stable low flow conditions that can trigger the sedimentation of
631 large diatoms. It is known that centric diatoms develop successfully in well-mixed, nutrient-replete
632 and turbid rivers, which are not so different from shallow lakes (Reynolds et al., 1994). Here also,
633 small centric diatoms dominated the community over large diatoms when present. Summer coccal
634 green algae, some with ornamentations and/or mucilage, were typical of the summer highly diverse
635 Chlorophyceae assemblage (Descy et al., 2012). Their dominance has been associated to high light

636 and shallow depth as main environmental drivers (Abonyi et al., 2012). Coccal green algae took
637 advantage of stable periods between disturbances, in accordance with the benthic retention hypothesis
638 (Istvánovics & Honti, 2011). Many species of the planktic genera *Scenedesmus*, *Acutodesmus* and
639 *Desmodesmus* were also observed during all periods from stable to repeatedly disturbed periods. These
640 genera are among the commonest green algae and one of the most diverse genera (John et al., 2002),
641 and have already been observed with high biomass in many rivers elsewhere (Gosselain et al., 1994).
642 Their small size and rapid growth rate make these algae very competitive in rivers and water bodies,
643 allowing a good sustainability of populations in high flushing environments where dilution effects are
644 likely. *Scenedesmus* spp. have already been related to hydrological factors and temperature in a
645 German lowland river (Wu et al. 2011). Also, coccal greens represent a group that is favoured by
646 sedimentation and resuspension during hydrological events (Reynolds & Descy, 1996). In nutrient
647 depleted conditions, small cells are also more competitive for nutrients uptake than large ones at low
648 concentrations, thanks to a higher surface/volume ratio. While these taxa are especially sensitive to
649 grazing by zooplankton, top-down effects remain largely understudied in the Loire River (Lair &
650 Reyes-Marchant, 1997), but also elsewhere.

651 Despite the discharge disturbances, colonial green algae, such as *Kirchneriella* spp. or the coccal *C.*
652 *microporum*, remained an important part of the total biomass. On the contrary, colonial green algae
653 with spine-like ornamentations decreased and raised the question of a counter-selection driven by the
654 turbulent regime. The presence of spines may be useful against grazing and to regulate sinking
655 velocity. Two main strategies against grazing were observed here (Lürding, 2021), the presence of
656 spines and the colonial form, sometimes mucilaginous. Grazing pressure in large river is, however,
657 less important than in lakes, because zooplankton is dominated by small-sized fast growing species
658 because of flushing (Wehr et al., 2015). However, our knowledge on how long-term changes in
659 hydrology with extended low flow conditions and re-oligotrophication affected zooplankton
660 community composition remains largely elusive. Spines and protuberances can also increase the
661 resistance to sedimentation, by increasing fluid drag coefficient, and stabilization of the horizontal
662 position with the highest form resistance (Padisák et al., 2003). Spines can also increase the effects of

663 viscosity at an individual scale like mucilage (Naselli-Flores et al., 2021) and help regulate population
664 density to avoid collapse.

665 *S. potamos*, a filamentous diatom, was also observed in the aftermath of summer discharge
666 disturbances. Cells of *S. potamos* form a chain attached by external tubes organized in one marginal
667 ring, giving flexibility to the filament able to support deformations. The length of the chain depends on
668 river turbulence (Duleba et al., 2014). *S. potamos* is one of the most important species in some
669 eutrophic rivers, with high biomass occurring during the growing season and seems favoured by
670 warmer temperatures and high light availability (Kiss et al., 1994; Abonyi et al., 2018b), including in
671 the Loire River (Descy et al., 2012). It is a warm-stenotherm centric diatom, with a relatively recent
672 dispersion across the World (Duleba et al., 2014), which may make it as a good indicator of late
673 summer warm conditions among planktic river species. Increase in its relative biomass since the last
674 40 years has been observed in the Danube River and was linked to the increase in water temperature
675 (Duleba et al., 2014). This species was also observed by Descy in the Moselle River and related to the
676 stable summer conditions and the minimum discharge (Descy, 1993). This centric diatom has a thin
677 frustule weakly silicified and small chloroplasts. Silicification intensity varies greatly among diatoms
678 and is a strategy against grazing but with a cost on the competition abilities (Assmy et al., 2013;
679 Pančić & Kiørboe, 2018). *S. potamos* is thus competitive for silicon, with an optimal quota two to
680 three times lower than other centric and large diatoms (Descy et al., 2012). Large filament well
681 silicified of *Aulacoseira granulata* (Ehrenberg) Simonsen used to be observed in the Loire River
682 before 1990 when nutrient availability was high, in particular silicon $>7 \text{ mg L}^{-1}$ (Lair & Reyes-
683 Marchant, 1997). Its cell and filament sizes can also change with turbulence in a large river (Wang et
684 al. 2015). High summer temperature, higher turbulence and low DSi requirement may explain the
685 dominance of *S. potamos* following discharge disturbances in the Loire River. Also, while DSi might
686 not be limiting in most of the European rivers, the Si:P ratio has largely been altered due to P decrease
687 and damming, likely affecting phytoplankton (Abonyi et al., 2014; 2018a).

688 The needle-shaped diatom *N. acicularis* maintained its biomass after the discharge disturbances, and
689 regularly increased in biomass. This truly planktic species is very common in the Loire River and can
690 be abundant at high river discharge (Descy et al., 2012). As shown by experiments and numerical

691 simulations, a needle-like shape can lead to aggregation during sedimentation thanks to hydrodynamic
692 interactions at low Reynolds number, independently on fluid shear and Brownian motion, (Botte et al.,
693 2013). This can be a strategy to decrease sedimentation rate for needle-like shape taxa, such as
694 *Pseudo-nitzschia spp.*, which forms chains of needles in stable periods (low Reynolds number), while it
695 becomes individualized in periods of flooding (high Reynolds number) to be more easily driven by
696 turbulent eddies. It would be interesting to make observations of fresh samples of *N. acicularis* in
697 sedimentation to see if this hypothesis is valid for this species. More than minimizing sinking velocity,
698 phytoplankton traits are selected to maximize the entertainability of cells by turbulent eddies (Naselli-
699 Flores et al., 2021). Interestingly, the two main diatoms *N. acicularis* and *S. potamos* belong to both
700 freshwater and marine genera, suggesting a shape that withstands high turbulence as in the sea.
701 *D. vulgaris*, a characteristic benthic diatom which normally forms zig-zag colonies attached to the
702 substrate, increased in biomass during repeated discharge events. Living in various habitats in rivers,
703 such as rock and plants, it predominates in eutrophic water with high conductivity and with pH > 7
704 (Kelly, 2000). This benthic diatom has been observed in high biomass in upstream reaches of the Loire
705 River (Abonyi et al., 2012), but also in the Middle Loire during high flow periods, with other species
706 like *Amphora ovalis* (Kütz.) Kütz. or *Cocconeis placentula* Ehrenberg (Descy et al., 2012). Its
707 presence is, therefore, an excellent indicator of flushing or high discharge events.
708 Benthic cyanobacteria observed following repeated discharge disturbances were *M. tenuissima* and *M.*
709 *glauca*. Both meroplanktic species are often associated with bottom silt and live at the water-sediment
710 interface, even if they can be observed in the water column (John et al., 2002). *M. tenuissima* is also
711 indicative of eutrophic conditions, with bottom reducing conditions (John et al., 2002). Already widely
712 observed in the Loire River, it probably develops in the main river channel on the riverbanks
713 (Minaudo et al., 2021). As for cyanobacteria, warm summer temperature may have promoted this
714 species.
715 Benthic taxa were thus the most responsive group to repeated disturbances, in accordance with their
716 shear-induced resuspension. The presence of benthic diatoms and cyanobacteria with discharge
717 disturbances has already been highlighted in the literature (Rojo et al., 1994; Abonyi et al., 2012).
718 Antecedent discharge disturbance is thus important to consider for the assembly rules of

719 phytoplankton, as well as the role of meroplankton in sustaining diversity. The maintenance of
720 functional richness is needed to sustain ecosystem functions, while high taxonomic richness with
721 functional redundancy increases the insurance of the community against disturbances (Naeem, 2008).
722 Other biotic and abiotic factors than discharge may have controlled phytoplankton assemblage during
723 stable periods, such as spatial heterogeneity. It has been shown that the Loire River has a very high
724 taxonomic diversity, partly explained by its relative shallowness, braided arms and ‘dead zones’
725 occurring in the Middle and Lower river sections (Descy et al., 2012). Spatial heterogeneity in
726 phytoplankton distribution increases as river discharge decreases. Our sampling station, located in the
727 Middle Loire River, has no significant upstream tributaries over 272 km, but many disconnected pools
728 can form under low flows and may represent a potential inoculum of planktic species. Grazing
729 pressure and selectivity may also have controlled phytoplankton assemblage. Small zooplankton
730 probably developed during stable period of summer months, favoured by low discharge and high
731 temperature, especially because we observed traits against grazing. Such zooplankton data would help
732 increase our understanding of the functional traits of green algae. Mussels, such as the Asian clams
733 *Corbicula* spp., are also known to reduce phytoplankton and meroplankton biomasses in the Loire
734 River (Descy et al., 2012). However, feeding selectivity seems to be low in mussels (Boltovskoy et al.,
735 1995; Frau et al., 2016). One can also consider that *Corbicula* spp. grazing should not change on a
736 short-term scale in response to discharge except if the mixing regime shifts from laminar to turbulent.
737 Mixing regime of the water column is indeed essential to bring phytoplankton cells in contact with
738 benthic invertebrates (Smith et al., 1998).

739 With climate change, summer conditions of high temperatures and strong solar radiations are likely to
740 favor benthic primary producers, while phytoplankton may remain limited by phosphorus availability.
741 Severe low water levels, such as those observed in 2022 in the Loire River, will likely enhance benthic
742 growth, on the other hand, likely decrease exchanges between the benthic and planktic compartments.
743 The decrease of meroplankton enrichment, i.e., taxa that can potentially live both sedimented and
744 resuspended, could compromise the biodiversity of the Loire River. Meroplankton should be
745 emphasized along with the benthic retention hypothesis (Istvánovics & Honti, 2011) and points at the

746 importance of hydrological variations in mediating phytoplankton biodiversity, biomass and
747 ecosystem functioning via resuspension.

748 **Conclusion**

749 This study analyzed the impact of short-term discharge disturbances on physical, chemical and
750 biological parameters and on the Loire River phytoplankton assemblage. Suspended matter increased
751 with river discharge, while chlorophyll-a concentration decreased due to the dilution effect. We
752 highlighted three assemblage types along with increasing hydrological forcing: (i) a short community
753 response associated with the dilution and collapse of community dominance, followed by the enrichment
754 of benthic species. Discharge disturbances promoted species with specific adaptations to turbulence,
755 while stable periods in terms of hydrology promoted species with adaptations against sedimentation and
756 grazing. DIP dynamic was directly linked to its consumption by phytoplankton as it correlated
757 negatively with biomass. Even in the short term, temperature remains a key parameter, which was
758 positively correlated to taxa biomass and is likely an excellent proxy for meteorological and hydrological
759 forcings at the short-term scale. In a context of re-oligotrophication and global warming, meroplanktic
760 algae will likely plays a decisive role in maintaining phytoplankton diversity and ecosystem functioning
761 in the Loire River, which may also likely the case in other shallow and large rivers.

762

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773

774 **Author Contributions**

775 FM, CM and NG collected data on physical and chemical parameters; AA and ML collected data on
776 phytoplankton; AP and CM conceptualized the study, and performed the data analyses and statistics.
777 AP, CM, NG and AA wrote the manuscript, with equal contributions from all authors.

778

779 **Data Availability Statement**

780 The data presented in this study will be available as Supplementary materials.

781

782 **Conflicts of Interest**

783 The authors declare no conflict of interest.

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784 **References**

- 785 Abonyi, A., Z. Horváth & R. Ptacnik, 2018a. Functional richness outperforms taxonomic richness in
786 predicting ecosystem functioning in natural phytoplankton communities. *Freshwater Biology* 63: 178–
787 186. <https://doi.org/10.1111/fwb.13051>
- 788 Abonyi, A., É. Ács, A. Hidas, I. Grigorszky, G. Várbíró, G. Borics & K. T. Kiss, 2018b. Functional
789 diversity of phytoplankton highlights long-term gradual regime shift in the middle section of the
790 Danube River due to global warming, human impacts and oligotrophication. *Freshwater Biology* 63:
791 456–472. <https://doi.org/10.1111/fwb.13084>
- 792 Abonyi, A., J.-P. Descy, G. Borics & E. Smeti, 2021. From historical backgrounds towards the
793 functional classification of river phytoplankton sensu Colin S. Reynolds: what future merits the
794 approach may hold? *Hydrobiologia* 848: 131–142. <https://doi.org/10.1007/s10750-020-04300-3>
- 795 Abonyi, A., M. Leitao, A. M. Lançon & J. Padisák, 2012. Phytoplankton functional groups as
796 indicators of human impacts along the River Loire (France). *Phytoplankton responses to human*
797 *impacts at different scales. Hydrobiologia.* 233–249. <https://doi.org/10.1007/s10750-012-1130-0>
- 798 Abonyi, A., M. Leitão, I. Stanković, G. Borics, G. Várbíró & J. Padisák, 2014. A large river (River
799 Loire, France) survey to compare phytoplankton functional approaches: do they display river zones in
800 similar ways? *Ecological Indicators* 46: 11–22. <https://doi.org/10.1016/j.ecolind.2014.05.038>
- 801 Aminot, A. & Kérouel, R., 2004. *Hydrologie des écosystèmes marins: paramètres et analyses.* Editions
802 Quae. Ed. Ifremer. 336 pp.
- 803 Assmy, P., V. Smetacek, M. Montresor, C. Klaas, J. Henjes, V. H. Strass, J. M. Arrieta, U. Bathmann,
804 G. M. Berg, E. Breitbart, B. Cisewski, L. Friedrichs, N. Fuchs, G. J. Herndl, S. Jansen, S. Krägel, S.
805 M. Lataš, I. Peeken, R. Röttgers, R. Scharek, S. E. Schüller, S. Steigenberger, A. Webb, & D. Wolf-
806 Gladrow, 2013. Thick-shelled, grazer-protected diatoms decouple ocean carbon and silicon cycles in
807 the iron-limited Antarctic Circumpolar Current. *Proceedings of the National Academy of Sciences.*
808 <https://doi.org/10.1073/pnas.1309345110>
- 809 Barton, A. D., B. A. Ward, R. G. Williams & M. J. Follows, 2014. The impact of fine-scale turbulence
810 on phytoplankton community structure. *Limnology and Oceanography: Fluids and Environments* 4:
811 34–49. <https://doi.org/10.1215/21573689-2651533>
- 812 Bibi, R., H. Y. Kang, D. Kim, J. Jang, G. K. Kundu, Y. K. Kim & C.-K. Kang, 2020. Dominance of
813 Autochthonous Phytoplankton-Derived Particulate Organic Matter in a Low-Turbidity Temperate
814 Estuarine Embayment, Gwangyang Bay, Korea. *Frontiers in Marine Science* 7: 580260.
815 <https://doi.org/10.3389/fmars.2020.580260>
- 816 Boltovskoy, D., I. Izaguirre & N. Correa, 1995. Feeding selectivity of *Corbicula fluminea* (Bivalvia)
817 on natural phytoplankton. *Hydrobiologia* 312: 171–182.

- 818 Borics, G., G. Várbíró, I. Grigorszky, E. Krasznai, S. Szabó & K. T. Kiss, 2007. A new evaluation
819 technique of potamo-plankton for the assessment of the ecological status of rivers. *Large Rivers*, 17.
820 *Archiv für Hydrobiologie Supplement* 161: 465–486. <https://doi.org/10.1127/lr/17/2007/466>
- 821 Bormans, M., P. W. Ford, L. Fabbro & G. Hancock, 2004. Onset and persistence of cyanobacterial
822 blooms in a large impounded tropical river, Australia. *Marine and Freshwater Research* 55(1): 1-15.
823 <https://doi.org/10.1071/MF03045>
- 824 Botte, V., M. Ribera D'Alcalà & M. Montresor, 2013. Hydrodynamic interactions at low Reynolds
825 number: an overlooked mechanism favouring diatom encounters. *Journal of Plankton Research* 35:
826 914–918. <https://doi.org/10.1093/plankt/fbt033>
- 827 Bowes, M. J., M. Loewenthal, D. S. Read, M. G. Hutchins, C. Prudhomme, L. K. Armstrong, S. A.
828 Harman, H. D. Wickham, E. Gozzard & L. Carvalho, 2016. Identifying multiple stressor controls on
829 phytoplankton dynamics in the River Thames (UK) using high-frequency water quality data. *Science*
830 *of The Total Environment* 569–570: 1489–1499. <https://doi.org/10.1016/j.scitotenv.2016.06.239>
- 831 Carrick, H. J., F. J. Aldridge & C. L. Schelske, 1993. Wind influences phytoplankton biomass and
832 composition in a shallow, productive lake. *Limnology and Oceanography* 38: 1179–1192.
833 <https://doi.org/10.4319/lo.1993.38.6.1179>
- 834 Comité Européen de Normalisation, 2003. Water quality – Guidance standard for the routine sampling
835 and pre-treatment of benthic diatoms from rivers. European Standard: EN 13946:2003.
- 836 Cloern, J. E., 1996. Phytoplankton bloom dynamics in coastal ecosystems: A review with some
837 general lessons from sustained investigation of San Francisco Bay, California. *Reviews of Geophysics*
838 34: 127–168. <https://doi.org/10.1029/96RG00986>
- 839 Del Giorgio, P. A. & M. L. Pace, 2008. Relative independence of organic carbon transport and
840 processing in a large temperate river: The Hudson River as both pipe and reactor. *Limnology and*
841 *Oceanography* 53: 185–197. <https://doi.org/10.4319/lo.2008.53.1.0185>
- 842 Descy, J.-P., 1993. Ecology of the phytoplankton of the River Moselle: effects of disturbances on
843 community structure and diversity. *Hydrobiologia* 249: 111–116.
- 844 Descy, J.-P., M. Leitao, E. Everbecq, J. S. Smitz & J.-F. Deliege, 2012. Phytoplankton of the River
845 Loire, France: a biodiversity and modelling study. *Journal of Plankton Research* 34: 120–135.
846 <https://doi.org/10.1093/plankt/fbr085>
- 847 Descy, J.-P., K. Patrick, E. Everbecq, G. Verniers, P. Usseglio-Polatera, P. Gérard, L. Viroux, J. Beisel
848 & J. Smitz, 2009. Continental atlantic rivers. *Rivers of Europe*. EAWAG/ETH, Switzerland. Elsevier,
849 London 151199.
- 850 Descy, J.-P., C. S. Reynolds & J. Padisák, 2013. Phytoplankton in turbid environments: rivers and

- 851 shallow lakes. Springer Science & Business Media. <https://doi.org/10.1007/978-94-017-2670-2>
- 852 Dillon, P. J. & F. Rigler, 1974. The phosphorus-chlorophyll relationship in lakes 1, 2. *Limnology and*
853 *oceanography* 19: 767–773. <https://doi.org/10.4319/lo.1974.19.5.0767>
- 854 Dubelaar, G. B. J., P. J. F. Geerders & R. R. Jonker, 2004. High frequency monitoring reveals
855 phytoplankton dynamics. *Journal of Environmental Monitoring* 6: 946-952.
856 <https://doi.org/10.1039/B409350J>
- 857 Duleba, M., L. Ector, Z. Horváth, K. T. Kiss, L. F. Molnár, Z. Pohner, Z. Szilagy, B. Toth, C. F. Vad,
858 G. Várbíró & É. Ács, 2014. Biogeography and phylogenetic position of a warm-stenotherm centric
859 diatom, *Skeletonema potamos* (CI Weber) Hasle and its long-term dynamics in the River Danube.
860 *Protist* 165: 715–729. <https://doi.org/10.1016/j.protis.2014.08.001>
- 861 Eppley, R. W., F. M. H. Reid & J. D. H. Strickland, 1970. The Ecology of the Plankton Off La Jolla,
862 California, In the period April through September, 1967, Part III, Estimates of Phytoplankton Crop
863 Size, Growth Rate, And Primary Production. ISBN: 0-520-09362-3
- 864 Ettl, H., J. Gerloff & H. Hegnig, 1978. Xanthophyceae vol 1. Gustav Fischer Verlag, Stuttgart, 530 pp.
- 865 Ettl, H., J. Gerloff & H. Hegnig, 1985. Chrysophyceae und Haptophyceae. Gustav Fischer Verlag,
866 Stuttgart, 515 pp.
- 867 Flourey, M., C. Delattre, S. J. Ormerod & Y. Souchon, 2012. Global versus local change effects on a
868 large European river. *Science of the Total Environment* 441: 220–229.
869 <https://doi.org/10.1016/j.scitotenv.2012.09.051>
- 870 Fott, B., 1968. Cryptophyceae, Chloromonadophyceae, Dinophyceae, vol 3. E. Schweizerbart'sche
871 Verlagsbuchhandlung (Nägele u. Obermiller), Stuttgart, 322 pp.
- 872 Frau, D., F. R. Molina & G. Mayora, 2016. Feeding selectivity of the invasive mussel *Limnoperna*
873 *fortunei* (Dunker, 1857) on a natural phytoplankton assemblage: what really matters? *Limnology* 17:
874 47–57. <https://doi.org/10.1007/s10201-015-0459-2>
- 875 Geitler, L., 1930-1932. Cyanophyceae von Europa. Koeltz Scientific Books, Koenigstein, 1196 pp.
- 876 Gosselain, V., J.-P. Descy & E. Everbecq, 1994. The phytoplankton community of the River Meuse,
877 Belgium: seasonal dynamics (year 1992) and the possible incidence of zooplankton grazing.
878 *Hydrobiologia* 289: 179–191.
- 879 Grasshoff K, Ehrhardt M & K. Kremling, 1983. *Methods of Seawater Analysis*. 2nd ed. Verlag
880 Chemie, Weinheim, Germany.
- 881 Gu, R. R. & Y. Li, 2002. River temperature sensitivity to hydraulic and meteorological parameters.
882 *Journal of Environmental Management* 66: 43–56. <https://doi.org/10.1006/jema.2002.0565>

- 883 Hiltunen, T., J. Laakso & V. Kaitala, 2006. Interactions between environmental variability and
884 immigration rate control patterns of species diversity. *Ecological Modelling* 194: 125–131.
885 <https://doi.org/10.1016/j.ecolmodel.2005.10.010>
- 886 Huber-Pestalozzi, G., 1955. *Euglenophyceen*, vol 4. E. Schweizerbart'sche Verlagsbuchhandlung
887 (Nägele u. Obermiller), Stuttgart, 606 pp.
- 888 Istvánovics, V. & M. Honti, 2011. Phytoplankton growth in three rivers: The role of meroplankton and
889 the benthic retention hypothesis. *Limnology and Oceanography* 56: 1439–1452.
890 <https://doi.org/10.4319/lo.2011.56.4.1439>
- 891 Istvánovics, V., M. Honti, L. Vörös & Z. Kozma, 2010. Phytoplankton dynamics in relation to
892 connectivity, flow dynamics and resource availability—the case of a large, lowland river, the
893 Hungarian Tisza. *Hydrobiologia* 637: 121–141. <https://doi.org/10.1007/s10750-009-9991-6>
- 894 John, D. M., B. A. Whitton, & A. J. Brook, 2002. *The freshwater algal flora of the British Isles: An*
895 *identification guide to freshwater and terrestrial algae*, University Press, Cambridge. pp. 878.
- 896 Johnson, B. L., W. B. Richardson & T. J. Naimo, 1995. Past, present, and future concepts in large
897 river ecology. *BioScience* 45: 134–141. <https://doi.org/10.2307/1312552>
- 898 Kelly, M., 2000. Identification of common benthic diatoms in rivers. *Field Studies Council* 9.4: 118
899 pages.
- 900 Kiss, K. T., É. Ács & A. Kovács, 1994. Ecological observations on *Skeletonema potamos* (Weber)
901 Hasle in the River Danube, near Budapest (1991–92, daily investigations). In Descy, J.-P., C. S.
902 Reynolds & J. Padišák (eds), *Phytoplankton in turbid environments: rivers and shallow lakes* Springer,
903 Dordrecht, Netherlands: 163–170.
- 904 Kiss, K. T., A. Schmidt & É. Ács, 1996. Sampling strategies for phytoplankton investigations in a
905 large river (River Danube, Hungary). *STUDIA Studentenförderungs GmbH*. ISBN 0395000902.
- 906
- 907 Komárek, J. & B. Fott, 1983. *Chlorophyceae*, vol 7, *Chlorococcales*. E. Schweizerbart'sche
908 Verlagsbuchhandlung (Nägele u. Obermiller), Stuttgart, 1044 pp.
- 909 Komárek, J. & K. Anagnostidis, 1999. *Cyanoprokaryota*, vol 1, *Chroococcales*. Gustav Fischer
910 Verlag, Stuttgart, 548 pp.
- 911 Komárek, J. & K. Anagnostidis, 2005. *Cyanoprokaryota*, vol 2, *Oscillatoriales*. Gustav Fischer Verlag,
912 Stuttgart, 759 pp.
- 913
- 914 Krammer, K., 2002. *Cymbella*. In Lange-Bertalot, H. (ed) *Diatoms of Europe*. A.R.G. Gantner Verlag

- 915 K. G., Königstein, 586 pp.
- 916 Krammer, K. & H. Lange-Bertalot, 1986. Bacillariophyceae. 1. Teil: Naviculaceae. Gustav Fischer
917 Verlag, Stuttgart, Stuttgart.
- 918 Krammer, K. & H. Lange-Bertalot, 1988. Bacillariophyceae. 2. Teil: Bacillariaceae, Epithemiaceae,
919 Surirellaceae. Gustav Fischer Verlag, Stuttgart, Stuttgart.
- 920 Krammer, K. & H. Lange-Bertalot, 1991a. Bacillariophyceae. 3. Teil: Centrales, Fragilariaceae,
921 Eunotiaceae. Stuttgart.
- 922 Krammer, K. & H. Lange-Bertalot, 1991b. Bacillariophyceae. 4. Teil: Achnantheaceae. Kritische
923 Ergänzungen zu *Navicula* (Lineolatae) und *Gomphonema*. Gustav Fischer Verlag, Stuttgart, Stuttgart.
- 924 Kruk, C., M. Devercelli & V. L. Huszar, 2021. Reynolds Functional Groups: a trait-based pathway
925 from patterns to predictions. *Hydrobiologia* 848: 113–129. [https://doi.org/10.1007/s10750-020-04340-](https://doi.org/10.1007/s10750-020-04340-9)
926 9
- 927 Lair, N. & P. Reyes-Marchant, 1997. The potamoplankton of the Middle Loire and the role of
928 the 'moving littoral' in downstream transfer of algae and rotifers. *Hydrobiologia* 356: 33–52.
- 929 Lalot, E., F. Curie, V. Wawrzyniak, F. Baratelli, S. Schomburgk, N. Flipo, H. Piegay & F. Moatar,
930 2015. Quantification of the contribution of the Beauce groundwater aquifer to the discharge of the
931 Loire River using thermal infrared satellite imaging. *Hydrology and Earth System Sciences* 19: 4479–
932 4492. <https://doi.org/10.5194/hess-19-4479-2015>
- 933 Lange-Bertalot, H., 2001. *Navicula sensu stricto*: 10 genera separated from *Navicula sensu lato*
934 *Frustulia*. In Lange-Bertalot, H. (ed) *Diatoms of Europe*. vol 2. A. R. G. Gantner Verlag K. G.,
935 Königstein, 526 pp.
- 936 Latapie, A., B. Camenen, S. Rodrigues, A. Paquier, J. P. Bouchard & F. Moatar, 2014. Assessing
937 channel response of a long river influenced by human disturbance. *Catena* 121: 1–12.
938 <https://doi.org/10.1016/j.catena.2014.04.017>
- 939 Legendre, P. & M. J. Anderson, 1999. Distance-based redundancy analysis: testing multispecies
940 responses in multifactorial ecological experiments. *Ecological Monographs* 69: 1–24.
941 [https://doi.org/10.1890/0012-9615\(1999\)069\[0001:DBRATM\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2)
- 942 Legendre, P. & E. Gallagher, 2001. Ecologically meaningful transformations for ordination of species
943 data. *Oecologia* 129: 271–280. <https://doi.org/10.1007/s004420100716>
- 944 Lewis, W. M., Jr, 1978. Dynamics and succession of the phytoplankton in a tropical lake: Lake Lanao,
945 Philippines. *The Journal of Ecology* 849–880. <https://doi.org/10.2307/2259300>
- 946 Litchman, E. & C. A. Klausmeier, 2008. Trait-Based Community Ecology of Phytoplankton. *Annual*
947 *Review of Ecology, Evolution, and Systematics* 39: 615–639

- 948 <https://doi.org/10.1146/annurev.ecolsys.39.110707.173>
- 949 Lohrenz, S. E., C. L. Carroll, A. D. Weidemann & M. Tuel, 2003. Variations in phytoplankton
950 pigments, size structure and community composition related to wind forcing and water mass properties
951 on the North Carolina inner shelf. *Continental Shelf Research* 23: 1447–1464.
952 [https://doi.org/10.1016/S0278-4343\(03\)00131-6](https://doi.org/10.1016/S0278-4343(03)00131-6)
- 953 Loreau, M. & N. Mouquet, 1999. Immigration and the maintenance of local species diversity. *The*
954 *American Naturalist* 154: 427–440. <https://doi.org/10.1086/303252>
- 955 Lund, J. W. G. & J. F. Talling, 1957. Botanical limnological methods with special reference to the
956 algae. *The Botanical Review* 23: 489–583.
- 957 Lürling, M., 2021. Grazing resistance in phytoplankton. *Hydrobiologia* 848: 237–249.
958 <https://doi.org/10.1007/s10750-020-04370-3>
- 959 Minaudo, C., A. Abonyi, M. Leitão, A. M. Lançon, M. Floury, J.-P. Descy & F. Moatar, 2021. Long-
960 term impacts of nutrient control, climate change, and invasive clams on phytoplankton and
961 cyanobacteria biomass in a large temperate river. *Science of The Total Environment* 756: 144074.
962 <https://doi.org/10.1016/j.scitotenv.2020.144074>
- 963 Minaudo, C., F. Curie, Y. Jullian, N. Gassama & F. Moatar, 2018. QUAL-NET, a high temporal-
964 resolution eutrophication model for large hydrographic networks. *Biogeosciences* 15: 2251–2269.
965 <https://doi.org/10.5194/bg-15-2251-2018>
- 966 Minaudo, C., M. Meybeck, F. Moatar, N. Gassama & F. Curie, 2015. Eutrophication mitigation in
967 rivers: 30 years of trends in spatial and seasonal patterns of biogeochemistry of the Loire River (1980–
968 2012). *Biogeosciences* 12: 2549–2563. <https://doi.org/10.5194/bg-12-2549-2015>
- 969 Moatar, F., J.-P. Descy, S. Rodrigues, Y. Souchon, M. Floury, C. Grosbois, C. Minaudo, M. Leitao, K.
970 M. Wantzen & F. Bertrand, 2022. The Loire River basin Rivers of Europe. p. 245–271. In K. Tockner,
971 C. Zarfl, and C. Robinson [eds]. *Rivers of Europe*. Elsevier. <https://doi.org/10.1016/B978-0-08-102612-0.00007-9>
- 972
- 973 Moatar, F. & M. Meybeck, 2005. Compared performances of different algorithms for estimating
974 annual nutrient loads discharged by the eutrophic River Loire. *Hydrological Processes* 19: 429–444.
975 <https://doi.org/10.1002/hyp.5541>
- 976 Naeem, S., 2008. Species Redundancy and Ecosystem Reliability. *Conservation Biology* 12: 39–45.
977 <https://doi.org/10.1111/j.1523-1739.1998.96379.x>
- 978 Naselli-Flores, L., T. Zohary & J. Padisák, 2021. Life in suspension and its impact on phytoplankton
979 morphology: an homage to Colin S. Reynolds. *Hydrobiologia* 848: 7–30.
980 <http://dx.doi.org/10.1007/s10750-020-04217-x>

- 981 Nock, C. A., R. J. Vogt & B. E. Beisner, 2016. *Functional Traits* In John Wiley & Sons, Ltd (ed), eLS.
 982 Wiley: 1–8. <https://doi.org/10.1002/9780470015902.a0026282>
- 983 Oksanen, J., 2013. *Multivariate Analysis of Ecological Communities in R: vegan tutorial*. R package
 984 version 1–43.
- 985 Oudin, L. C., N. Lair, M. Leitão, P. Reyes-Marchant, J.-F. Mignot, P. Steinbach, T. Vigneron, J.-P.
 986 Berton, M. Bacchi, J. E. Roché & J.-P. Descy, 2009. *Rivers of Europe* (Eds Tockner K. & C.T.
 987 Robinson). British Library, London.
- 988 Padisák, J., L. O. Crossetti & L. Naselli-Flores, 2009. Use and misuse in the application of the
 989 phytoplankton functional classification: a critical review with updates. *Hydrobiologia* 621: 1–19.
 990 <https://doi.org/10.1007/s10750-008-9645-0>
- 991 Padisák, J., E. Soróczki-Pintér & Z. Reznér, 2003. Sinking properties of some phytoplankton shapes
 992 and the relation of form resistance to morphological diversity of plankton—an experimental study.
 993 *Hydrobiologia* 500: 243-257. <https://doi.org/10.1007/978-94-007-1084-9>
- 994 Pančić, M. & T. Kiørboe, 2018. Phytoplankton defence mechanisms: traits and trade-offs. *Biological*
 995 *Reviews* 93: 1269–1303. <https://doi.org/10.1111/brv.12395>
- 996 Pannard, A., M. Bormans & Y. Lagadeuc, 2008a. Phytoplankton species turnover controlled by
 997 physical forcing at different time scales. *Canadian Journal of Fisheries and Aquatic Sciences* 65: 47–
 998 60. <https://doi.org/10.1139/F07-149>
- 999 Pannard, A., P. Clauquin, C. Klein, B. Le Roy & B. Véron, 2008b. Short-term variability of the
 1000 phytoplankton community in coastal ecosystem in response to physical and chemical conditions'
 1001 changes. *Estuarine, Coastal and Shelf Science* 80: 212–224. <https://doi.org/10.1016/j.ecss.2008.08.008>
- 1002 Pathak, D., M. Hutchins, L. Brown, M. Loewenthal, P. Scarlett, L. Armstrong, D. Nicholls, M. Bowes
 1003 & F. Edwards, 2021. Hourly Prediction of Phytoplankton Biomass and Its Environmental Controls in
 1004 Lowland Rivers. *Water Resources Research* 57: 1-20. <https://doi.org/10.1029/2020WR028773>
- 1005 Peterson, B., B. Fry, M. Hullar, S. Saupe & R. Wright, 1994. The distribution and stable carbon
 1006 isotopic composition of dissolved organic carbon in estuaries. *Estuaries* 17: 111–121.
- 1007 Peterson, C. G. & R. J. Stevenson, 1989. Seasonality in river phytoplankton: multivariate analyses of
 1008 data from the Ohio River and six Kentucky tributaries. *Hydrobiologia* 182: 99–114.
- 1009 Picard, V. & N. Lair, 2005. Spatio-temporal investigations on the planktonic organisms of the Middle
 1010 Loire (France), during the low water period: biodiversity and community dynamics. *Hydrobiologia*
 1011 551: 69–86. <https://doi.org/10.1007/s10750-005-4451-4>
- 1012 Pickett, S. & P.S.White, 1985. *The ecology of natural disturbance and patch dynamics*, Pickett, STA
 1013 and PS White (Ed.). *the Ecology of Natural Disturbance and Patch Dynamics*. Orlando, Fla, USA.

- 1014 Popovský, J. & L. A. Pfister, 1990. *Dinophyceae (Dinoflagellida)*. Gustav Fischer Verlag, Stuttgart,
1015 272 pp.
- 1016 Ptacnik, R., T. Andersen & T. Tamminen, 2010. Performance of the Redfield Ratio and a Family of
1017 Nutrient Limitation Indicators as Thresholds for Phytoplankton N vs. P Limitation. *Ecosystems* 13:
1018 1201–1214. <https://doi.org/10.1007/s10021-010-9380-z>
- 1019 Reddy, K. R., O. A. Diaz, L. J. Scinto & M. Agami, 1995. Phosphorus dynamics in selected wetlands
1020 and streams of the Lake Okeechobee Basin. *Ecological Engineering* 5(2-3): 183-207.
1021 [https://doi.org/10.1016/0925-8574\(95\)00024-0](https://doi.org/10.1016/0925-8574(95)00024-0)
- 1022 Reynolds, C. S., 1984. Phytoplankton periodicity: the interactions of form, function and environmental
1023 variability. *Freshwater Biology* 14: 111–142.
- 1024 Reynolds, C. S., 2006. *The ecology of phytoplankton*. Cambridge University Press.
- 1025 Reynolds, C. S. & J.-P. Descy, 1996. The production, biomass and structure of phytoplankton in large
1026 rivers. *Large Rivers. Archiv für Hydrobiologie Supplement* 10 (1–4): 161–187.
1027 <https://doi.org/10.1127/lr/10/1996/161>
- 1028 Reynolds, C. S., J.-P. Descy & J. Padisák, 1994. Are phytoplankton dynamics in rivers so different
1029 from those in shallow lakes? *Hydrobiologia* 289: 1–7.
- 1030 Rojo, C., M. A. Cobelas & M. Arauzo, 1994. An elementary, structural analysis of river
1031 phytoplankton. *Hydrobiologia* 289: 43–55.
- 1032 Rott, E., 1981. Some results from phytoplankton counting intercalibrations. *Schweizerische Zeitschrift*
1033 *für Hydrologie* 43: 34–62. <https://doi.org/10.1007/BF02502471>
- 1034 Sabater, S., J. Artigas, C. Durán, M. Pardos, A. M. Romaní, E. Tornés & I. Ylla, 2008. Longitudinal
1035 development of chlorophyll and phytoplankton assemblages in a regulated large river (the Ebro River).
1036 *Science of The Total Environment* 404: 196–206. <https://doi.org/10.1016/j.scitotenv.2008.06.013>
- 1037 Salmaso, N., L. Naselli-Flores & J. Padisák, 2015. Functional classifications and their application in
1038 phytoplankton ecology. *Freshwater Biology* 60: 603–619. <https://doi.org/10.1111/fwb.12520>
- 1039 Seyedhashemi, H., J.-P. Vidal, J. S. Diamond, D. Thiéry, C. Monteil, F. Hendrickx, A. Maire & F.
1040 Moatar, 2022. Regional, multi-decadal analysis on the Loire River basin reveals that stream
1041 temperature increases faster than air temperature. *Hydrology and Earth System Sciences* 26: 2583–
1042 2603. <https://doi.org/10.5194/hess-26-2583-2022>
- 1043 Smith, T. E., R. J. Stevenson, N. F. Caraco & J. J. Cole, 1998. Changes in phytoplankton community
1044 structure during the zebra mussel (*Dreissena polymorpha*) invasion of the Hudson River (New York).
1045 *Journal of Plankton Research* 20: 1567–1579.
- 1046 Starmach, K., 1985. *Chrysophyceae und Haptophyceae*. Gustav Fischer Verlag, Stuttgart, 515 pp.

- 1047 Strickland JDH & T.R. Parsons, 1972. A Practical Handbook of Seawater Analysis (2nd ed.). Fisheries
1048 Research Board of Canada, Ottawa, Bulletin 167. <https://doi.org/10.1086/406210>
- 1049 Utermöhl, H., 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. Mitteilungen
1050 Internationale Ver- einigung Fuer Theoretische Und Angewandte Limnologie 9: 1–38.
- 1051 Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river
1052 continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130–137.
- 1053 Várbíró, G., J. Padišák, Z. Nagy-László, A. Abonyi, I. Stanković, M. Gligora Udovič, V. B-Béres &
1054 G. Borics, 2018. How length of light exposure shapes the development of riverine algal biomass in
1055 temperate rivers? *Hydrobiologia* 809: 53–63. <https://doi.org/10.1007/s10750-017-3447-1>
- 1056 Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel & E. Garnier, 2007. Let the
1057 concept of trait be functional! *Oikos* 116: 882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>
- 1058 Wade, A. J., E. J. Palmer-Felgate, S. J. Halliday, R. A. Skeffington, M. Loewenthal, H. P. Jarvie, M. J.
1059 Bowes, G. M. Greenway, S. J. Haswell, I. M. Bell, E. Joly, A. Fallatah, C. Neal, R. J. Williams, E.
1060 Gozzard & J. R. Newman, 2012. Hydrochemical processes in lowland rivers: insights from in situ,
1061 high-resolution monitoring. *Hydrology and Earth System Sciences* 16: 4323–4342.
1062 <https://doi.org/10.5194/hess-16-4323-2012>
- 1063 Wang, C., Li, X., Lai, Z., Li, Y., Dauta, A. & S. Lek, 2014. Patterning and predicting phytoplankton
1064 assemblages in a large subtropical river. *Fundamental and Applied Limnology* 185: 263-279.
1065 <https://doi.org/10.1127/fal/2014/0684>
- 1066 Wang, C., Baehr, C., Lai, Z., Gao, Y., Lek, S. & X. Li, 2015. Exploring temporal trend of
1067 morphological variability of a dominant diatom in response to environmental factors in a large
1068 subtropical river. *Ecological Informatics* 29: 96-106. <https://doi.org/10.1016/j.ecoinf.2014.11.002>
- 1069 Wawrzyniak, V., P. Allemand, S. Bailly, J. Lejot & H. Piégay, 2017. Coupling LiDAR and thermal
1070 imagery to model the effects of riparian vegetation shade and groundwater inputs on summer river
1071 temperature. *Science of The Total Environment* 592: 616–626.
1072 <https://doi.org/10.1016/j.scitotenv.2017.03.019>
- 1073 Wehr, J. D. & J.-P. Descy, 1998. Use of phytoplankton in large river management. *Journal of*
1074 *Phycology* 34: 741–749.
- 1075 Wehr, J. D., R. G. Sheath & J. P. Kociolek, 2015. *Freshwater algae of North America: ecology and*
1076 *classification*. Elsevier.
- 1077 Wei, T. & V. Simko, 2017. R package “corrplot”: Visualization of a Correlation Matrix (Version
1078 0.84). Available from <https://github.com/taiyun/corrplot>.
- 1079 Winder, M., J. E. Reuter & S. G. Schladow, 2008. Temporal organization of phytoplankton

- 1080 communities linked to physical forcing. *Oecologia* 156: 179–192. <https://doi.org/10.1007/s00442-008->
1081 0964-7
- 1082 Wu, N., B. Schmalz & N. Fohrer, 2011. Distribution of phytoplankton in a German lowland river in
1083 relation to environmental factors. *Journal of Plankton Research* 33: 807-820.
1084 <https://doi.org/10.1093/plankt/fbq139>
- 1085 Wu, N., Faber, C., Sun, X., Qu, Y., Wang, C., Ivetic, S., Riis, T., Ulrich, U. & N. Fohrer, 2016.
1086 Importance of sampling frequency when collecting diatoms. *Scientific reports* 6(1): 36950.
1087 <https://doi.org/10.1038/srep36950>

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1088 **FIGURE CAPTIONS**

1089 **Figure 1.** Identification of hydrological events and associated periods. An increase in the slope dF/dt
 1090 between two consecutive days highlights the beginning of a disturbance and is noticed t^* . The
 1091 ‘Before’ period corresponds to the seven days preceding t^* and begins on day t_1 ($t_1 = t^* - 7\text{days}$). The
 1092 ‘After’ period corresponds to the disturbed period, extending from day t^* to the return to stable
 1093 conditions on day t_2 .

1094 **Figure 2.** Time series in summer 2013 (a) of the river flow Q and the ratio particulate organic carbon :
 1095 chlorophyll-a (POC:Chl-a), with the same y-axis scale, (b) of concentration in suspended matter, (c) of
 1096 dissolved inorganic phosphorus (DIP) concentration, (d) of dissolved organic carbon concentration, (e)
 1097 of chlorophyll-a and pheopigments concentrations, and (f) of the inverse Simpson’s index. Vertical red
 1098 dotted line shows the main disturbances with their numbering. Periods identified are shown at the top
 1099 of the figure.

1100 **Figure 3.** CCA performed on phytoplankton assemblages from 2013 explained by environmental
 1101 parameters ($p=0.001$). (a) Plot of the taxa. Only taxa contributing to at least 1% to canonical axis are
 1102 shown. (b) Plot of the environmental parameters (Q: water discharge; SM: suspended matter; Nitrates:
 1103 nitrates concentration; DSi: DSi concentration; DIP: dissolved inorganic phosphorus concentration;
 1104 Temperature; DOC: dissolved organic carbon concentration; pH; DO: Dissolved Oxygen). (c) Plot of
 1105 the sampling dates, grouped afterwards according to the period (Bef1: before 1; Bef2: before 2; Aft1:
 1106 After 1; Aft2: After 2; Aft3: After 3; Aft4: After 4; Stable 1; Stable 2) See Fig. 2 for periods’ details.
 1107 Scale of x and y axes is given by d value at the top right for each plot.

1108 **Figure 4.** Time series of phytoplankton taxa biovolumes in mg C L^{-1} during summer 2013, with (a)
 1109 *Nitzschia acicularis*, (b) *Skeletonema potamos*, (c) *Chlamydomonas sp.*, (d) *Golenkinia radiata*, (e)
 1110 *Actinastrum hantzschii*, (f) *Scenedesmus spp.* 3 and (g) *Diatoma vulgaris*. Periods identified are shown
 1111 at the top of the figure.

1112 **Figure 5.** Time series in summer 2014 (a) of the river flow Q and the ratio particulate organic carbon :
 1113 chlorophyll-a (POC:Chl-a), with the same y-axis scale, (b) of concentration in suspended matter, (c) of
 1114 dissolved inorganic phosphorus (DIP) concentration, (d) of dissolved organic carbon concentration, (e)
 1115 of chlorophyll-a and pheopigments concentrations, and (f) of the inverse Simpson’s index. Vertical red

1116 dotted line shows the main disturbances with their numbering. Periods identified are shown at the top
 1117 of the figure.

1118 **Figure 6.** CCA performed on phytoplankton assemblages from 2014 explained by environmental
 1119 parameters ($p=0.029$). (a) Plot of the taxa. Only taxa contributing to at least 1% to canonical axis are
 1120 shown. (b) Plot of the environmental parameters (Q: water discharge; SM: suspended matter; Nitrates:
 1121 nitrates concentration; DSi: DSi concentration; DIP: dissolved inorganic phosphorus concentration;
 1122 Temperature; DOC: dissolved organic carbon concentration; DO: Dissolved Oxygen). (c) Plot of the
 1123 sampling dates, grouped afterwards according to the period (Bef1: before 1; Bef2: before 2; Aft1:
 1124 After 1; Aft2: After 2; Aft3: After 3; Aft4: After 4; Stable) See Fig. 2 for periods' detail. Scale of x
 1125 and y axes is given by d value at the top right for each plot.

1126 **Figure 7.** Time series of phytoplankton taxa biovolumes in mg C L^{-1} during summer 2014, with (a)
 1127 *Monoraphidium* spp., (b) *Kirchneriella* spp., (c) *Tetraedron* spp., (d) *Skeletonema potamos*, (e)
 1128 *Merismopedia* spp., (f) *Acutodesmus* spp. and (g) *Nitzschia acicularis*. Periods identified are shown at
 1129 the top of the figure.

1130 **Figure 8.** Illustration of species representative of the three periods, showing their morphometry and
 1131 traits: stable assemblages with A2 and B1; disturbed assemblage with A1 and B2; repeatedly disturbed
 1132 assemblage with A3 and B3. RFG are indicated near each draw. Taxa framed with a dotted blue line
 1133 are observed at least over two periods. Taxa framed in a red line are observed in the same period both
 1134 years. 1. *Nitzschia acicularis* (Kützing) W.M.Smith and *N. dissipata* (Kützing) Grunow; 2.
 1135 *Dictyosphaerium pulchellum* Wood; 3. *Tetrastrum triangulare* (Chodat) Komárek ; 4. *Actinastrum*
 1136 *hantzschii* Lagerheim; 5. *Golenkinia radiata* Chodat; 6. *Monoraphidium contortum* (Thuret)
 1137 Komárková-Legnerová; 7. *Lobomonas ampla* Pascher; 8. *Franceia ovalis* (France) Lemmermann; 9.
 1138 *Plagioselmis nannoplanctica* (H. Skuja) G. Novarino, I.A.N. Lucas & S. Morrall; 10. *Didymocystis*
 1139 *planctonica* Korshikov; 11. *Oocystis lacustris* Chodat; 12. *Micractinium pusillum* Fresenius; 13.
 1140 *Treubaria planctonica* (G.M.Smith) Korshikov; 14. *Scenedesmus* spp. Meyen (with for
 1141 example *Scenedesmus* group *Armati sensu* Komárek & Fott), *Acutodesmus* spp. (Hegewald) Tsarenko
 1142 and *Desmodesmus* spp. (R.Chodat) S.S.An, T.Friedl & E.Hegewald ; 15. *Kirchneriella lunaris*
 1143 (Kirchner) Möbius; 16. *Coelastrum microporum* Nägeli; 17. *Tetraedron minimum* (A.Braun)

1144 Hansgirg; 18. *Chlamydomonas* sp. Ehrenberg; 19. *Skeletonema potamos* (Weber) Hasle; 20.
 1145 *Merismopedia tenuissima* Lemmermann; 21. *Diatoma vulgare* Bory.

1146 **Figure 9.** (a) Plot of the two axes of the discriminant Analysis (DA) performed on phytoplankton
 1147 RFG. The discriminant factor is one of the three assemblages (stable, repeated, repeatedly disturbed)
 1148 and each sample is attached to the gravity center of the group it belongs to. (b) Correlation circle plot
 1149 showing the phytoplankton RFG. Scale of x and y axes is given by d value at the top right for each
 1150 plot.

1151 **Figure 10.** Pearson's correlation matrix between log₁₀-transformed RFG and taxa and environmental
 1152 parameters: Q river discharge, T° daily mean water temperature, DO daily mean dissolved oxygen,
 1153 daily mean pH, Cd daily mean conductivity, SM suspended matter, Ry solar radiations, Nitr. Nitrates,
 1154 DIP, DSi and COD concentrations. Significativity of the Pearson's correlation is shown: *means
 1155 $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$. Colored ellipses indicate the positive (blue) or negative (red)
 1156 correlations.

1157 **Figure S1.** Time series of environmental and biological parameters at the station Cinq-Mars-La-Pile.
 1158 Q: water discharge; SM: suspended matter; Nitrates: nitrates concentration; TP: total phosphorus
 1159 concentration; DSi: silicate concentration; POC: particulate organic carbon; Temp.: temperature;
 1160 radiation: solar radiation; Chl-a: total pigment concentration; DIP: dissolved inorganic phosphorus
 1161 concentration; DOC: dissolved organic carbon concentration; Phy biom: phytoplankton biomass
 1162 calculated from cell counts and grouped by class; Tot biom: total phytoplankton biomass calculated
 1163 from cell counts; Turnover: turnover rate per day.

1164 **Figure S2.** Variance partitioning of taxa biomass depending on time with julian day (X1), water
 1165 temperature (X2) and dissolved inorganic phosphorus (X3), performed with the function *varpart* of the
 1166 package *vegan*. The analysis was performed on all data, on summer 2013 and on summer 2014.

1167

Figure 1.

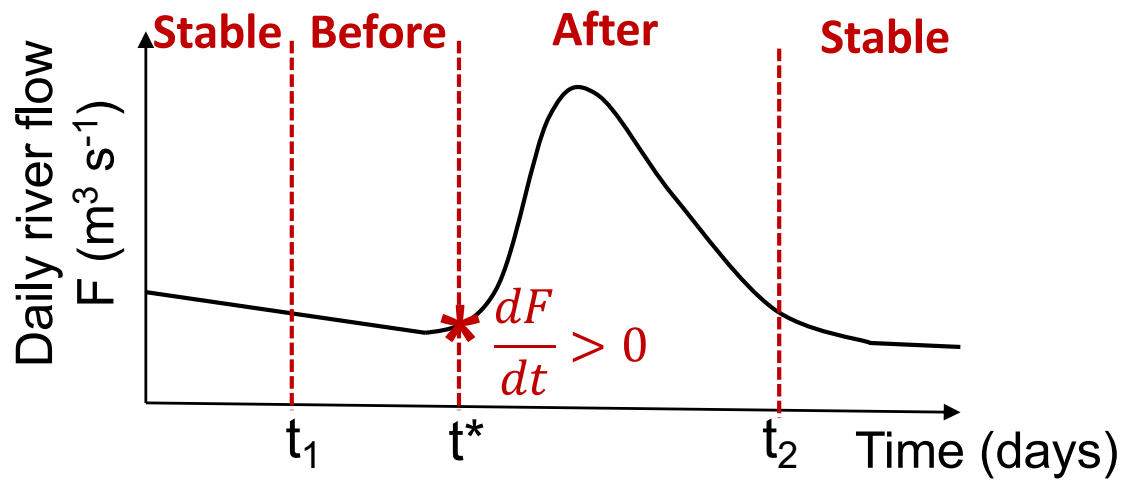


Figure 2.

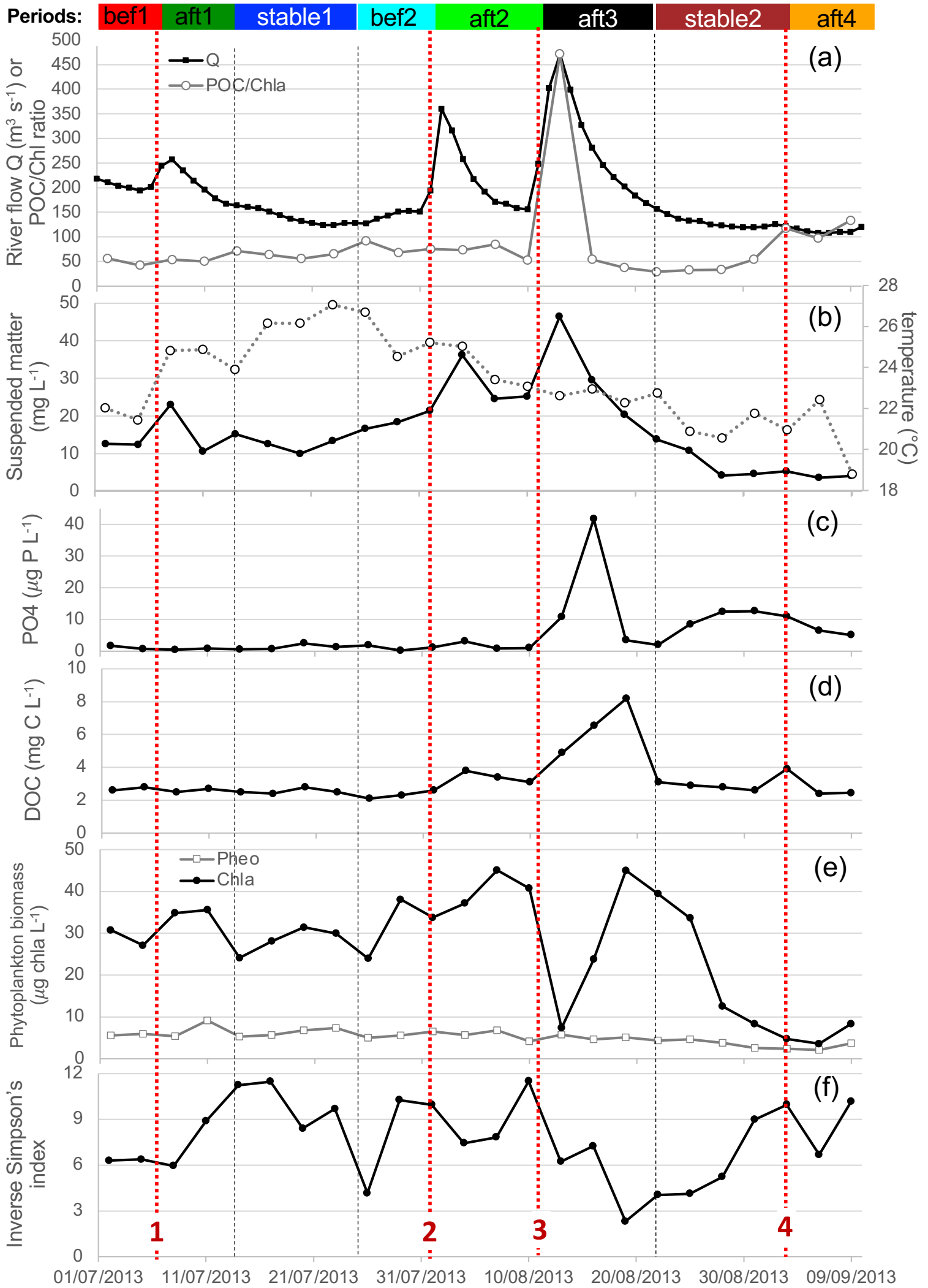
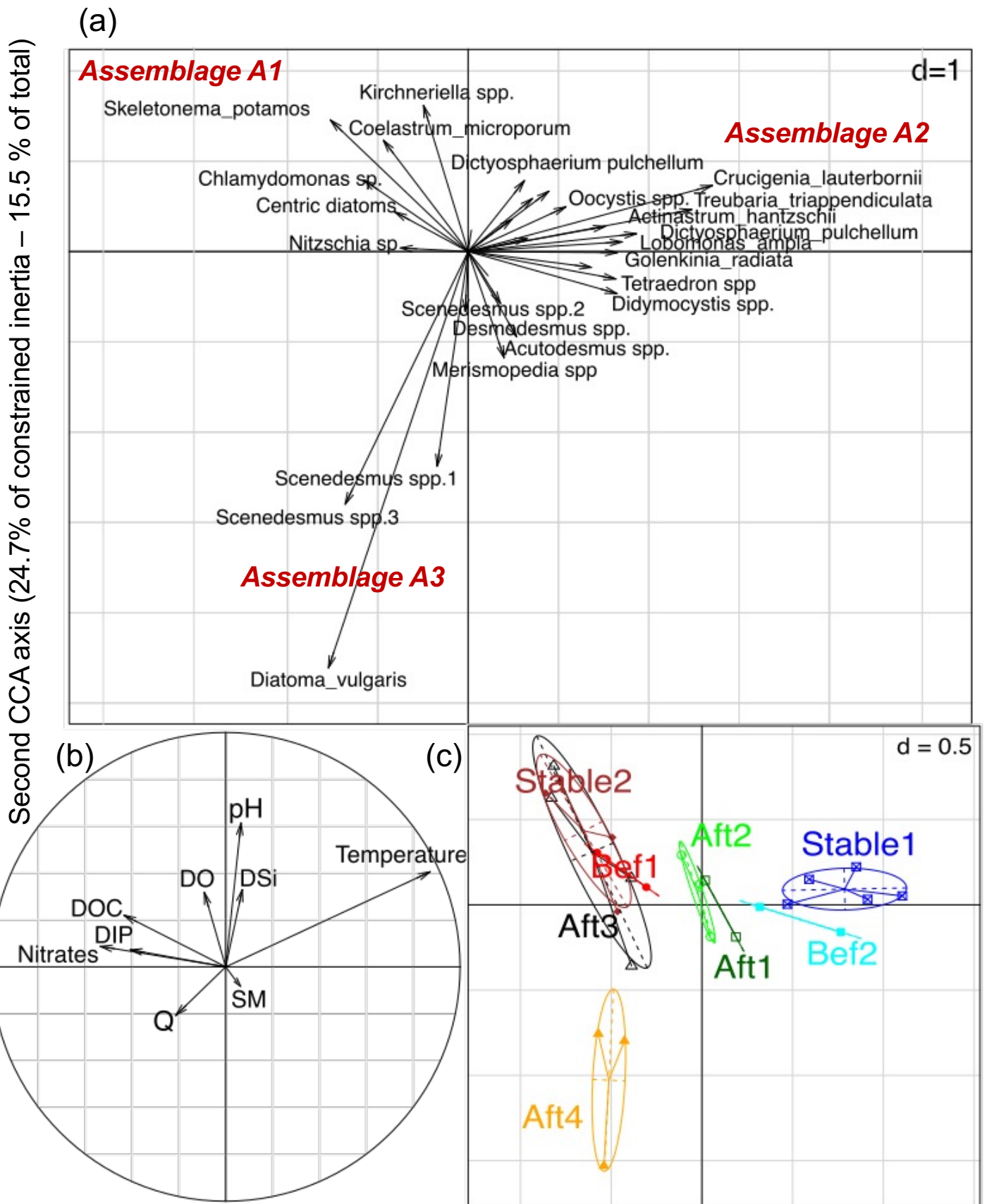


Figure 3.



Second CCA axis (24.7% of constrained inertia – 15.5 % of total)

First CCA axis (38.8 % of constrained inertia – 24.3% of total variance)

Figure 4.

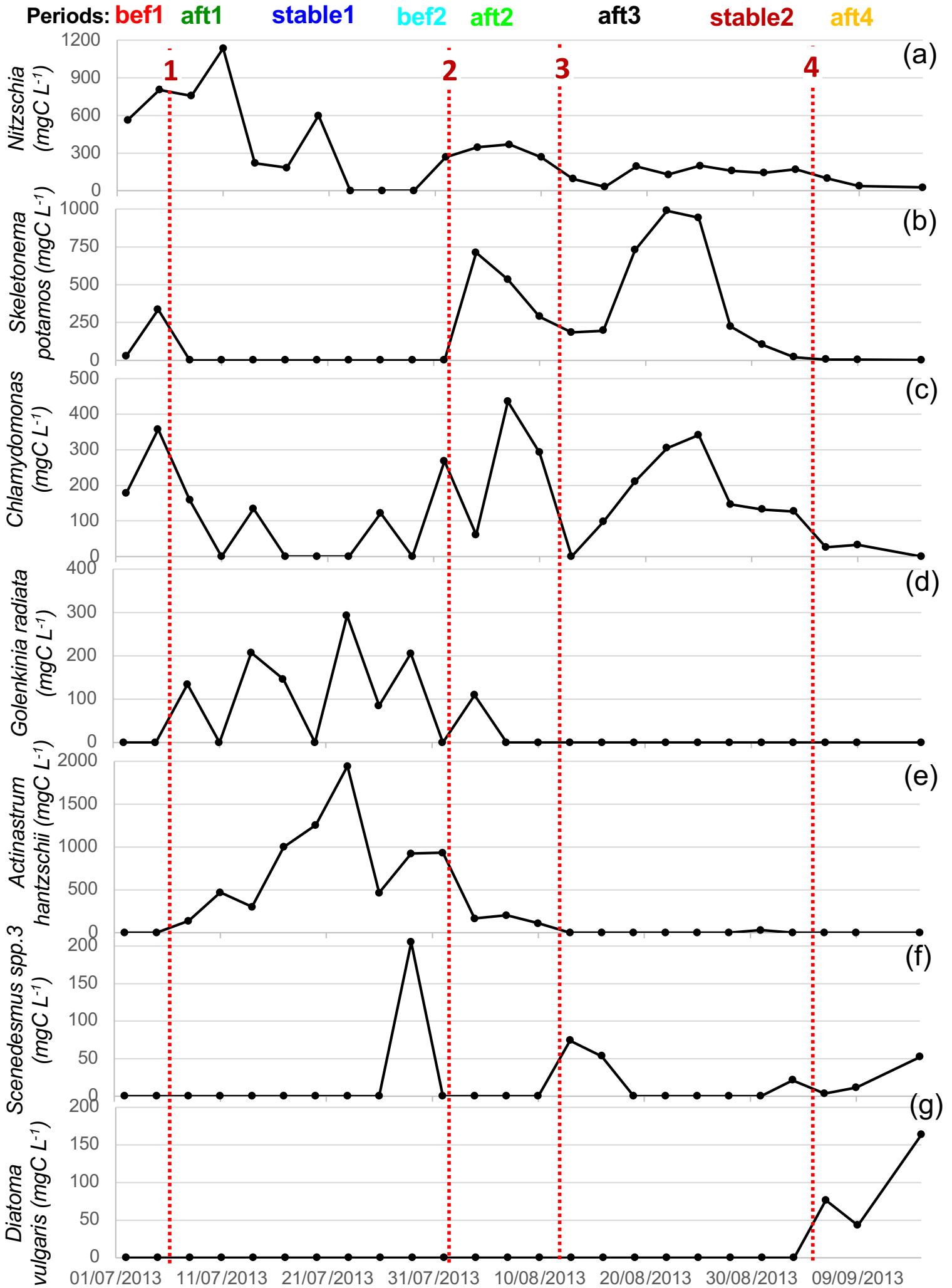


Figure 5.

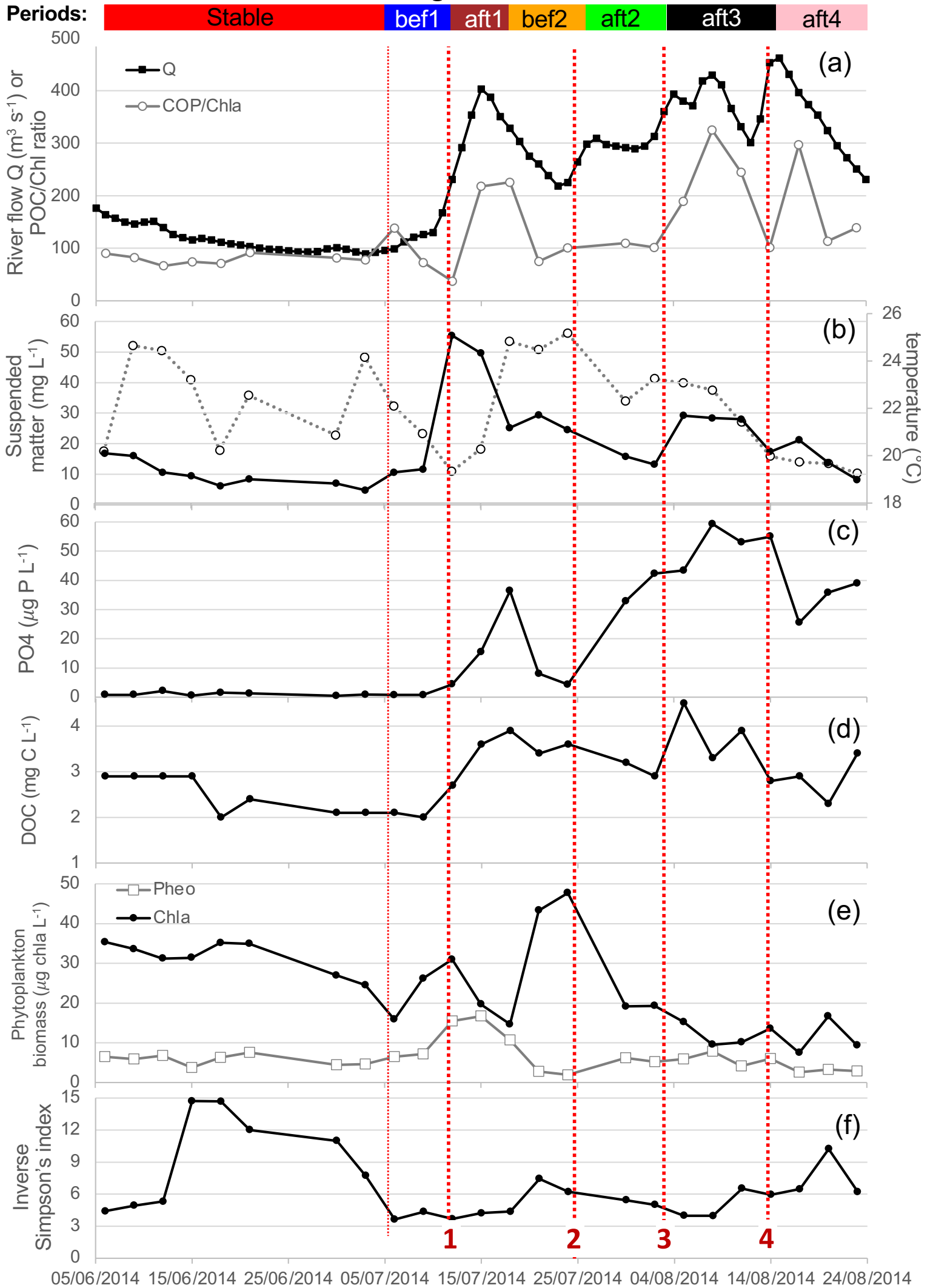


Figure 6.

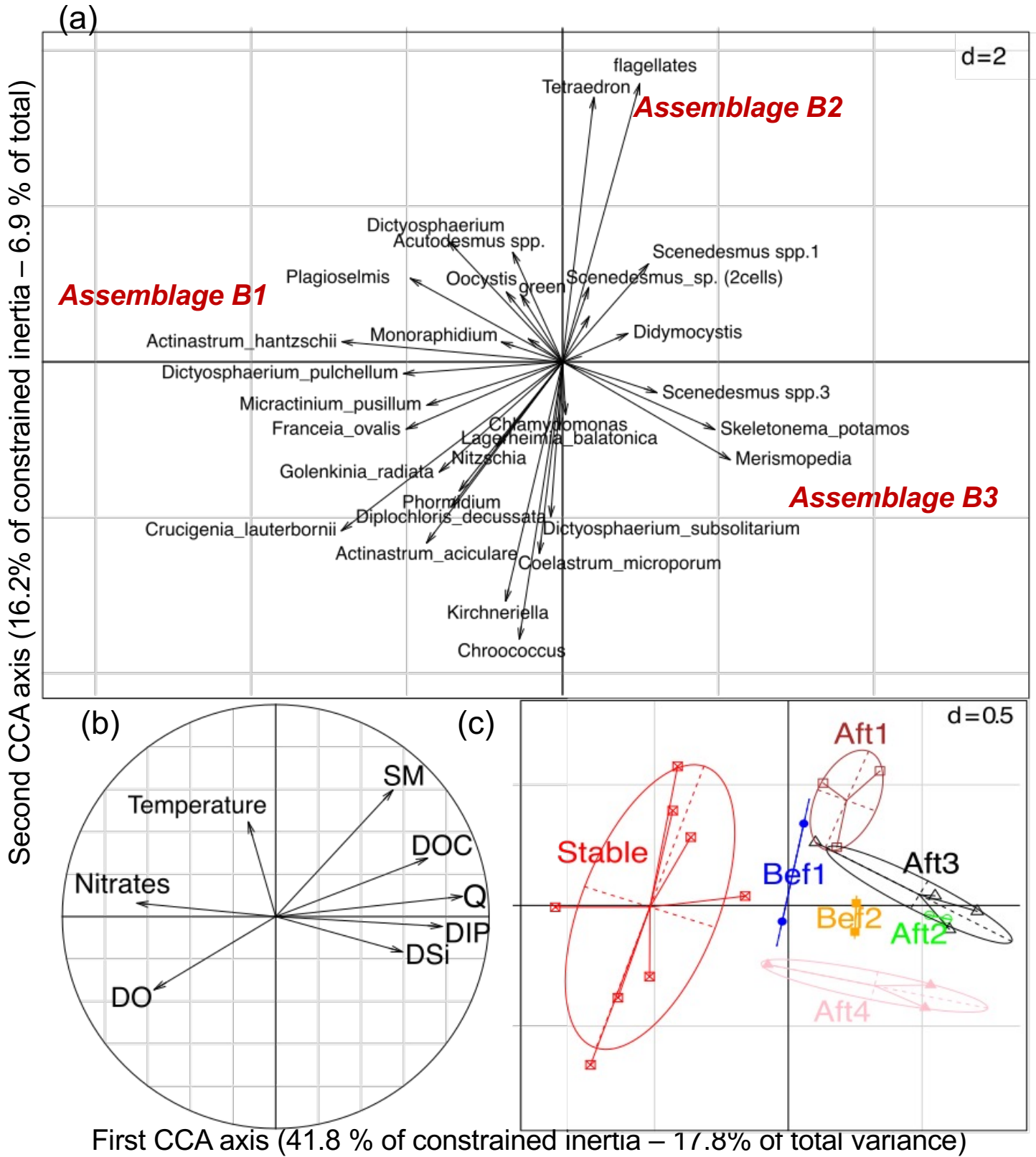


Figure 7.

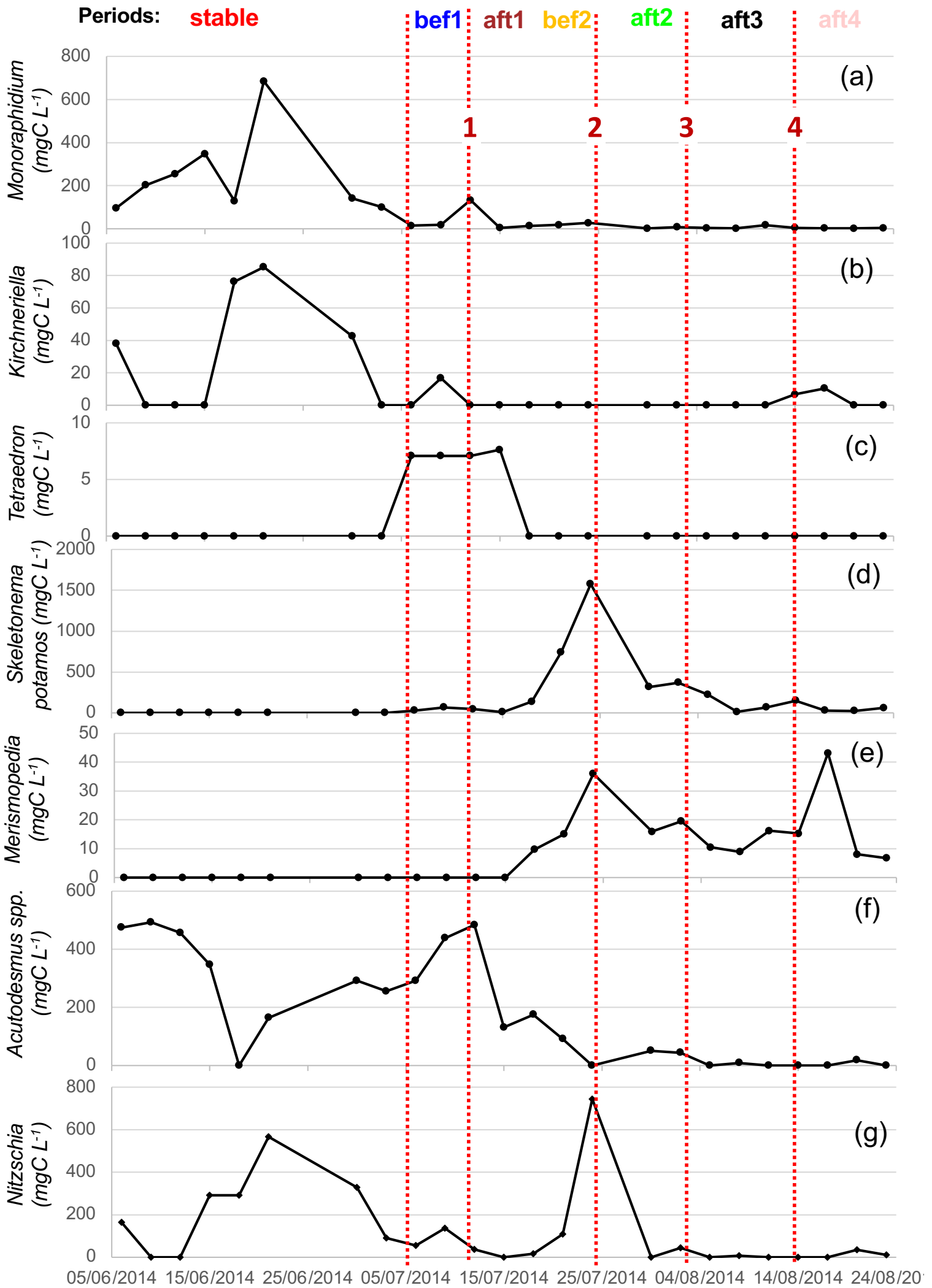
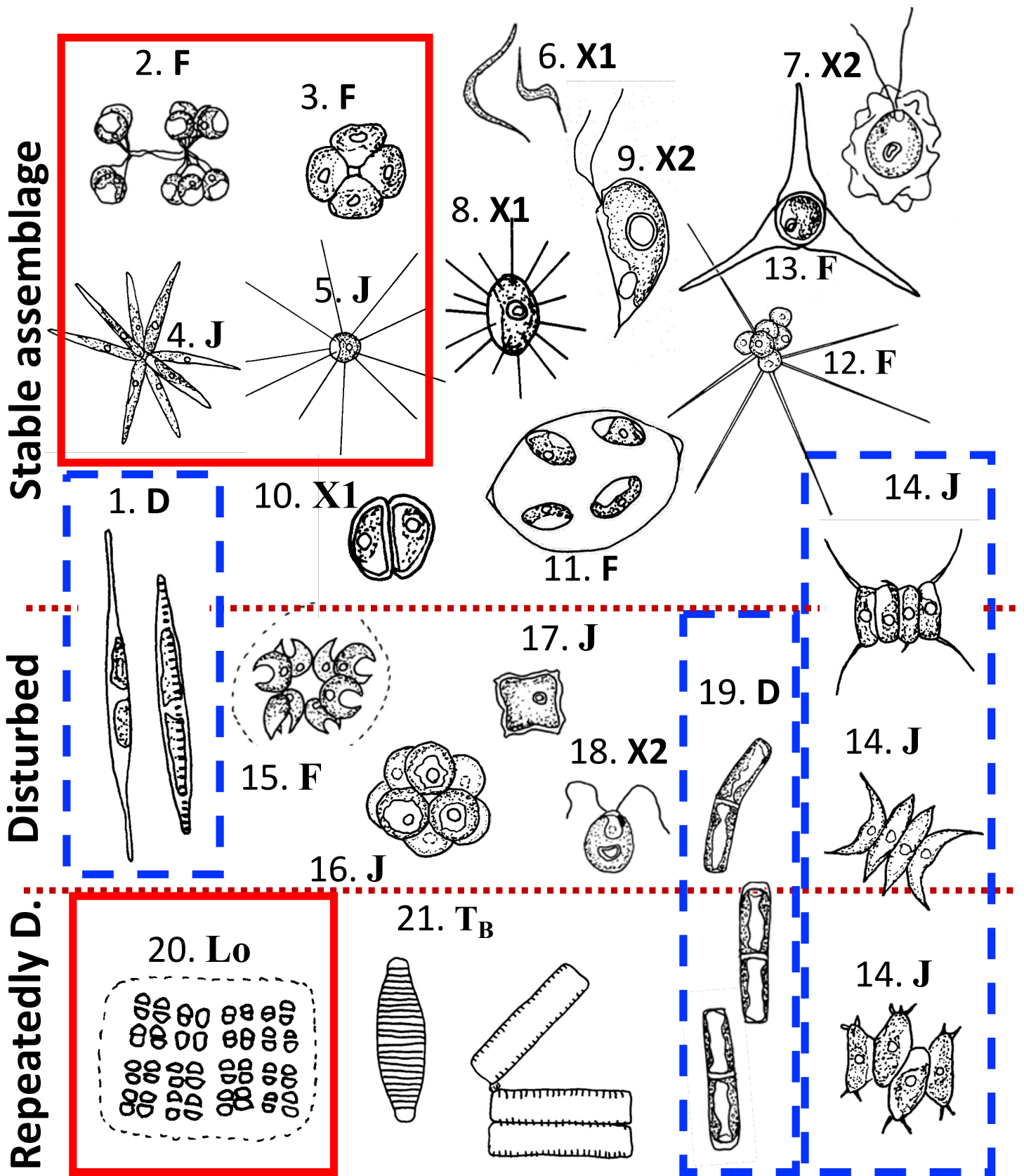


Figure 8.



@drawings from Maria Leitao

Figure 9.

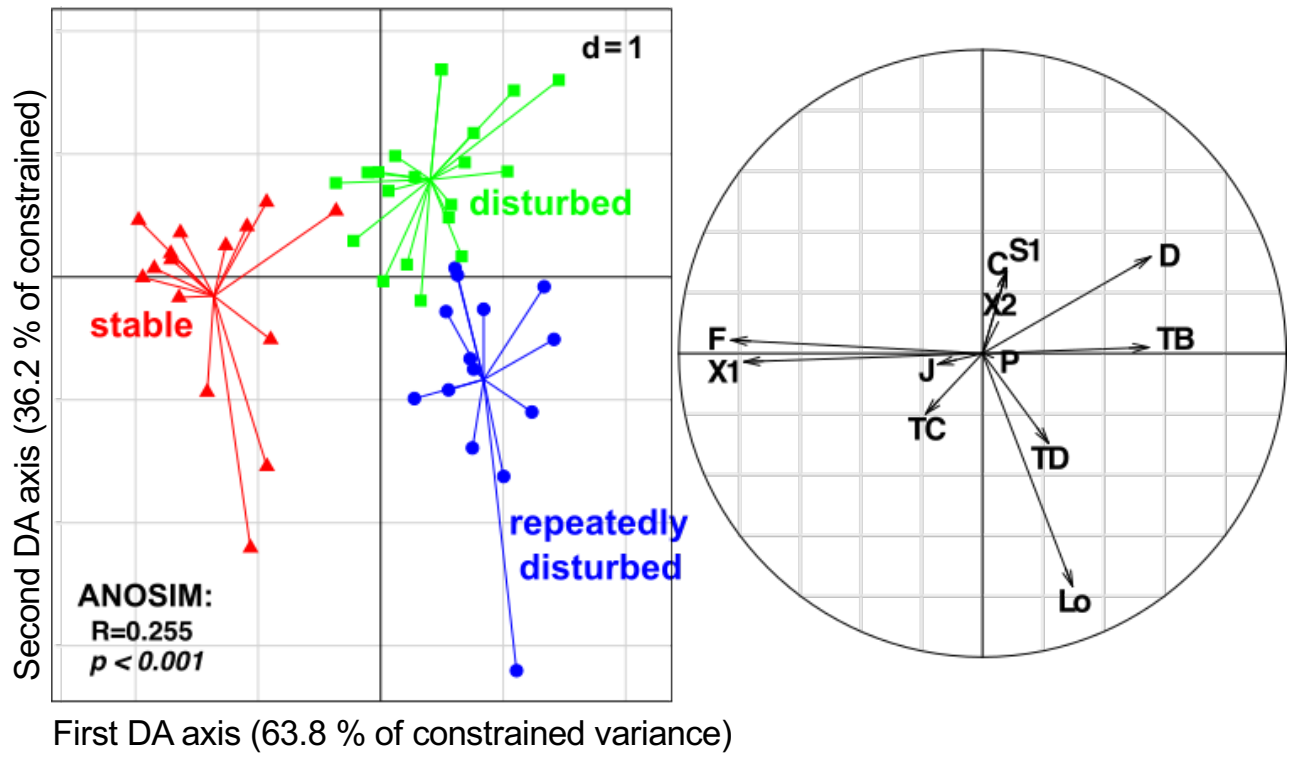


Figure 10.

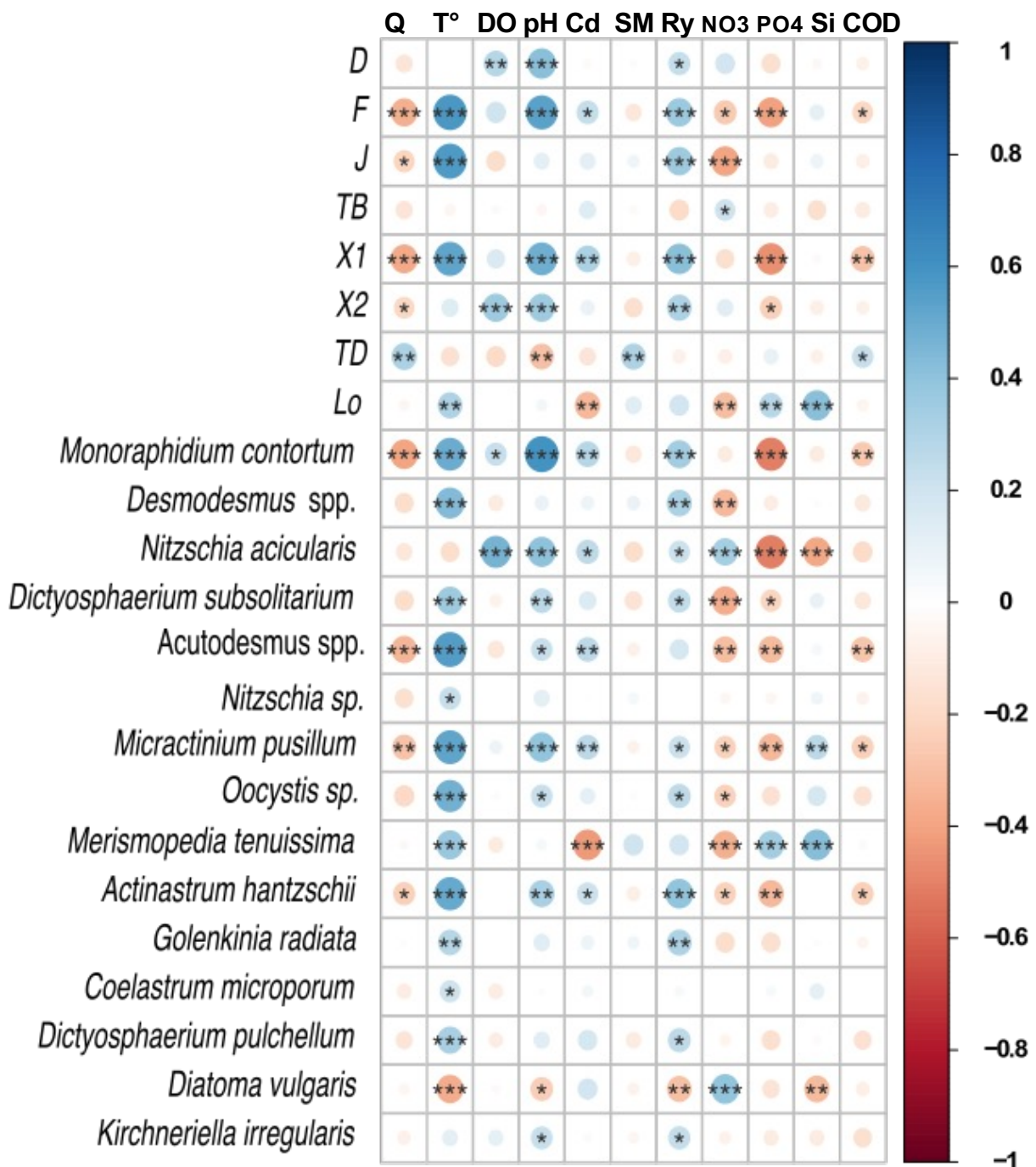


Figure S1.

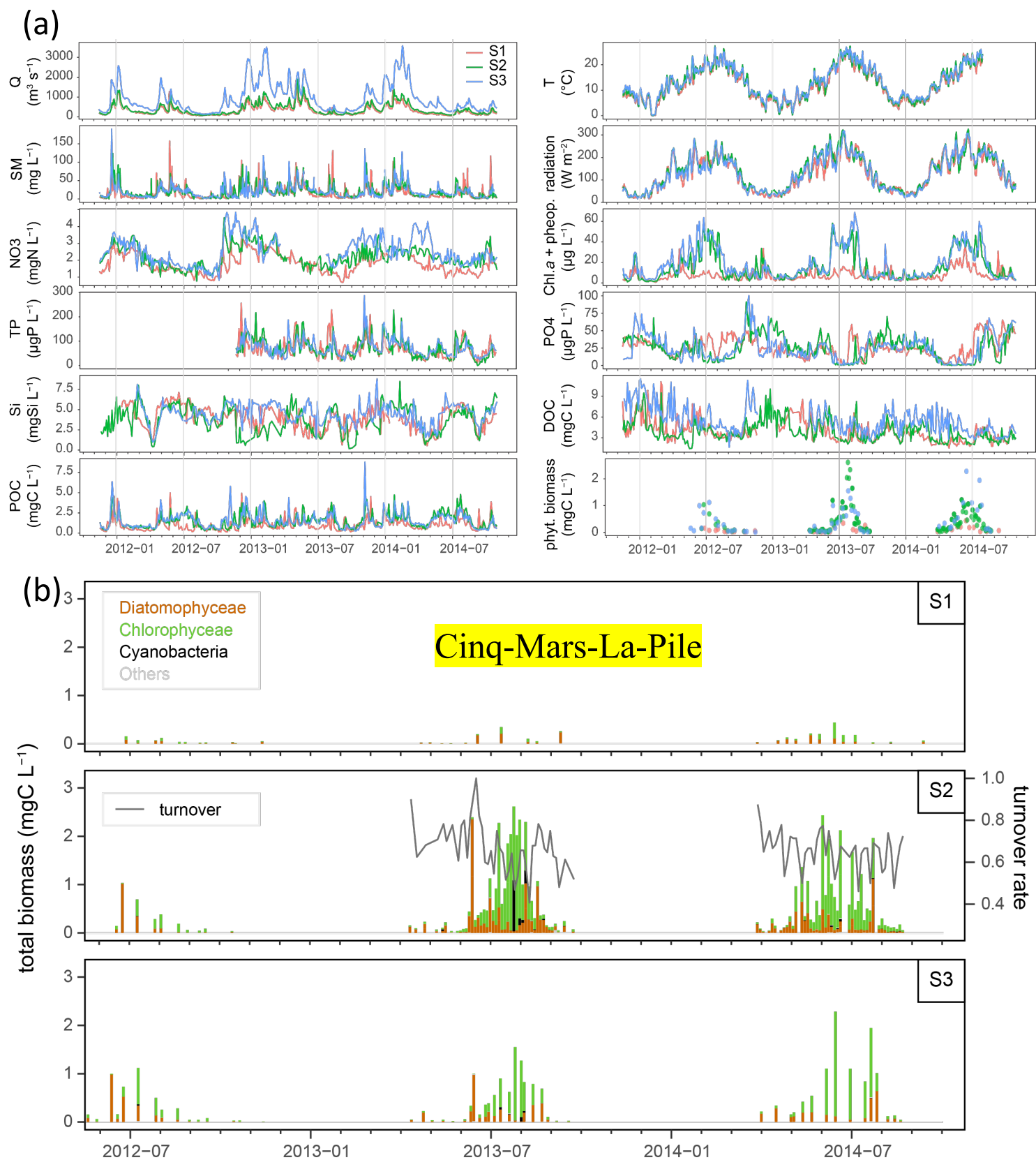


Figure S2.

