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Assessing phytoplankton structure and spatio-temporal dynamics in a freshwater ecosystem using a powerful multiway statistical analysis

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ABSTRACT

Phytoplankton dynamics and diversity are particularly difficult to analyze, especially when (i) the scale of the analysis is situated at the species level, (ii) such a diversity is high, (iii) the study covers several seasons, and (iv) sampling has been performed at many stations of the ecosystem. Fortunately, some powerful statistical methods have been developed with which each species identified can be considered in detailed spatio-temporal analyses. The Partial Triadic Analysis, a method issued from the STATIS family, was applied on a dataset corresponding to 6 stations of the largest French reservoir (Reservoir Marne) sampled 22 times over two years (2006–2007) between March and September. Three key sampling periods that were consistent with those exhibited with the Plankton Ecology Group model (i.e. early spring, late spring–early summer, late summer–early autumn) were unambiguously recognized, with some specific species associated with each of them. Furthermore, a potential reference sampling station was identified among all stations investigated, an information very relevant to both scientists and water managers. It remains that 3 other stations could also be monitored, regularly or from time to time, because of specific phytoplankton characteristics.

1. Introduction

One of the European Water Framework Directive (WFD) aims is to resist against eutrophication, which is of particular concern for water management and treatment, in order to reach and maintain a "good ecological state" by year 2015 (Borja and Elliott, 2007). Recognition of the ecological state (i.e. water quality and functioning) of a lake depends upon evolving bio-indicative criteria related to the presence of species drawn from several categories of organisms. One of them, phytoplankton, is of major importance for the ecological monitoring and understanding of hydrosystems and constitute a potential bio-indicator of both water quality and changes in response to local or more global influences such as nutrient or micro-toxic pollution, temperature or UV increase and species invasion (Wetzel, 2001; Kalff, 2002). Presently, the main technique to estimate the phytoplankton biomass is based on cell chlorophyll *a* concentration. In order to measure this parameter, a set of *in situ* sensors has been developed by scientists and water body managers, including immergeable fluorimeters (e.g. Beutler et al., 2002) or flow cytometers-like machines (e.g. Thyssen et al., 2008). However, like satellite-borne biosensors (another category of potential detectors of phytoplankton biomass), those devices are unable to give precise information on species composition and if the interest of the study lies on characterizing phytoplankton dynamics, it is often necessary

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to combine those methods with classical light microscopy. In fact, this latter technique remains the only one capable of yielding sufficiently precise information about species diversity and composition. In other words, nothing has replaced human-eye observation and expertise so far, and the indices proposed to diagnose the ecological status of water bodies within the European WFD are based indeed on lists of species requiring microscopic identification (Kaiblinger, 2008).

It is noteworthy, however, that phytoplankton identification and counts by microscopy are very time-consuming and labor intensive. This is one of the reasons why classical surveys based on taxonomy are generally reduced both in time and space. It remains that the decision to reduce sampling effort should be the consequence of preliminary intensive data acquisition and treatment that would have allowed the identification of key temporal periods and key spatial places in a single ecosystem. Such information might help to guide future sampling strategies, particularly in selecting precisely when and where the samples should be taken. The introduction of the Plankton Ecology Group model (PEG-model) in 1986 proposed 24 sequential statements which describe step by step the seasonal events which occur in the phytoplankton and zooplankton of an ''idealized standard lake'' (Sommer et al., 1986). The statements concerning phytoplankton can be summarized in four key temporal periods related to the succession of the phytoplankton species. First, towards the end of winter, Cryptophyceae and small centric diatoms develop in response to nutrient availability and increased light. Secondly, the crop of small algae is grazed upon herbivorous zooplanktonic species. As a consequence, phytoplankton biomass decreases rapidly to very low levels to reach a 'clear-water' equilibrium phase in spring. Then, herbivorous zooplanktonic species become food-limited and fish predation accelerates the decline of herbivorous planktonic populations. Under these conditions, phytoplankton summer crops start to build up. Succession during summer is highly pronounced. At first, the edible Cryptophyceae and the inedible green algae become predominant. Competition for phosphate leads to a replacement of green algae by large diatoms. Silica-depletion leads to a replacement of the large diatoms by large Dinophyceae and/or Cyanobacteria. Nitrogen depletion favors a shift to nitrogen-fixing species of filamentous blue-green algae. Thirdly, after a minor reduction of algal biomass in response to changes in physical factors, an algal community develops which is adapted to being mixed. Large unicellular or filamentous algal forms appear. Among them diatoms become increasingly important with the progress of autumn. To finish, a reduction of light energy input results in a low or negative net primary production and an imbalance with algal losses which causes a decline of algal biomass to the winter minimum. Said that, it remains obvious that the taxonomic composition of the phytoplankton community may be highly variable among lakes and/or reservoirs (Reynolds, 1999). Concerning key spatial places, it is often recommended to sample the deepest station of a lake but this might not be adapted to very large lakes/reservoirs that can present a highly spatial heterogeneity in their horizontal phytoplankton distribution (Reynolds, 1984).

Another problem with detailed species-specific data lies on their analysis. Hopefully, the last decades have seen the development of some useful multiway statistical tools that reflect, with considerable precision, the multilinear structures in higher-order datasets (Acar and Yener, 2009). Among these multiway analyses, the three-way data analysis called STATIS (Abdi and Valentin, 2007), introduced by L'Hermier des Plantes (1976) and Robert and Escoufier (1976) then developed by Lavit (Lavit, 1988; Lavit et al., 1994), has been used in many research fields such as sensory evaluation (Qannari et al., 1995; Schlich, 1996), molecular imaging (Coquet et al., 1996), brain imaging (Kherif et al., 2003), chemometrics (Stanimirova et al., 2004), marketing (Perez Aparicio et al., 2007) and food science (Martin et al., 2000; Meyners et al., 2000; Meyners, 2002; Chaya et al., 2004; Perez-Hugalde et al., 2004; Perrin et al., 2008). The related approach is known as ''procrustes matching by congruence coefficients'' in the English speaking community (Korth and Tucker, 1976). In aquatic ecology, the STATIS method has been especially applied to coastal marine ecology (Gaertner et al., 1998; Licandro and Ibanez, 2000; Lekve et al., 2002; Gailhard et al., 2003; Muiño et al., 2003; Simier et al., 2004; Lobry et al., 2006). In limnology, this method was rarely used but two applied studies are fundamental. The first one by Centofanti et al. (1989) revealed a spatial scheme of a reservoir distinguishing five sectors as a function of several physico-chemical variables. The second study, performed by Anneville et al. (2002), helped to identify three homogeneous periods over 25 years (i.e. 1974–1985, 1986–1991 and 1992–1998) in the temporal evolution of the summer phytoplankton community in Lake Geneva. With our dataset, the use of STATIS was not possible as we had a balanced experimental design (i.e. the data matrices had the same number of lines and columns). Consequently, we used the Partial Triadic Analysis (PTA), a method derived from the ''STATIS family''. This approach was originally described by Jaffrenou (1978), and then introduced to ecology by Thioulouse and Chessel (1987) (see also Kroonenberg, 1989 and Thioulouse et al., 2004 for a detailed description). The PTA has been used in several ecological studies (Blanc et al., 1998; Blanc and Beaudou, 1998; Gaertner, 2000; Rossi, 2003; Jiménez et al., 2006; Ernoult et al., 2006; Carassou and Ponton, 2007; Pavoine et al., 2007) but, to the best of our knowledge, it has never been applied to freshwater phytoplankton ecology.

With this study of phytoplankton ecology of Reservoir Marne, the largest in Western Europe, two main objectives have been pointed out. First of all, using the PTA, we were able to identify the key seasonal periods exhibiting the dynamics of phytoplankton diversity in comparison to those highlighted by the PEG-model. Secondly, we could determine the stations that represent the best the phytoplankton dynamics in the Reservoir Marne. Consequently, we are able to provide some advices to water managers concerning the sampling effort and strategy to operate.

2. Materials and methods

2.1. Site description and dataset

The dataset issues from the monitoring of the Reservoir Marne (48°34′55″N 04°45′23″E) located in the Champagne region, 200 km east of Paris, France (see Table 1 for additional

Table 1 – Some physical and chemical characteristics of the stations sampled in the Reservoir Marne for both years. Values are expressed as means and standard deviations over the two years 2006–2007.

	J	K	G	N	I	H
Mean Z[a] (m)	8.6 ± 0.7	8.3 ± 0.3	6.7 ± 1.5	8.5 ± 1.9	11.5 ± 1.7	12.9 ± 1.7
Max Z[a] (m)	10.8	8.9	8.4	11.1	13.8	14.8
Mean pH	8.0 ± 0.2	8.0 ± 0.2	8.0 ± 0.3	8.0 ± 0.3	8.0 ± 0.3	8.0 ± 0.3
Mean Temp.[a] (°C)	18.2 ± 4.3	18.5 ± 4.3	18.4 ± 4.2	17.7 ± 4.7	17.4 ± 4.5	17.3 ± 4.3
Mean Transp.[a] (m)	2.8 ± 1.4	1.9 ± 1.1	2 ± 1.1	2.4 ± 1.4	2.6 ± 1.3	3 ± 1.5
Mean photic zone thickness (m)	7.0 ± 3.5	4.8 ± 2.8	5 ± 2.7	6.1 ± 3.6	6.5 ± 3.1	7.4 ± 3.7
WRT[a] (months)	3–12	3–12	1–12	1–12	1–12	1–12
Mean TP[a] (μg L^{-1})	15.3 ± 4.8	38.0 ± 14.2	40.2 ± 24.4	18.8 ± 6.9	18.7 ± 7.7	22.3 ± 8.6
Mean TN[a] (μg L^{-1})	736.8 ± 585.4	1003.0 ± 746.0	1801.7 ± 1077.2	1981.2 ± 940.0	2086.1 ± 984.0	2009.2 ± 920.2
Mean Chl *a* (μg L^{-1})	4.7 ± 2.0	11.0 ± 8.6	15.8 ± 10.7	6.7 ± 4.0	6.5 ± 3.5	7.1 ± 3.8

[a] Z: depth; Temp: temperature; Transp: transparency; WRT: water residence time; TP: total phosphorus; and TN: total nitrogen.

information). This large reservoir (48 km^2) was constructed in 1974 to control flooding in winter and early spring and to enhance low flows in summer. The water level varies between 2 and 15 m through the hydrological cycle, with a maximum water volume (309 Mm^3) in summer (July) and a minimum (29 Mm^3) in late autumn (November). Depending on summer climate conditions (wind, temperature) and management strategies, the water column may be stratified for a few weeks. Over the 2-year survey of the reservoir, 22 field campaigns were performed, 11 samplings in 2006 and 11 samplings in 2007 between March and September at 6 stations (Fig. 1). Stations K and J correspond to two basins devoted to recreational activities (e.g. sailing, bathing, windsurfing, fishing) and they are separated from the reservoir by a breakwater. Station G receives water from two input channels, stations I and H are close to the output channels and finally station N is approximately in the middle of the reservoir (Fig. 1). This sampling strategy was defined in order to obtain the best picture of the structure of the phytoplanktonic organisms compatible with practicalities of sampling and analysis.

2.2. *Phytoplankton sampling and analysis*

Phytoplankton samples were collected at a depth of 3 m beneath the surface, using a 5-L Van Dorn bottle, and were immediately preserved in Lugol's Iodine solution for phytoplankton counting with an inverted microscope (Zeiss Axiovert 135) following the Utermöhl procedure (Utermöhl, 1958). Algal species were identified and counted at high magnification (×640) along 2 diameters of the sedimentation chamber. Then, the whole slide was scanned at lower magnification (×200) to determine rare species. Abundance was calculated considering the surface area of the 2 diameters counted, the surface of the sedimentation chamber and the volume of water sedimented. Then, the biovolume, that corresponds to the space occupied by a cell or a group of cells in the water column, was estimated considering the different geometric formulae proposed by Hillebrand et al. (1999) depending on the form of the cells.

2.3. *Data preparation*

During this analysis, 142 species out of the 297 identified during the 2-year survey, for a total of 138 samples, were taken into consideration. Each of them represented more than 0.01% of the total abundance and more than 0.01% of the total biovolume. These criteria were chosen because most of the other species occurred rarely, some being observed on as few as one or two occasions during the entire study period. Thus, we considered that these very rare species were not really

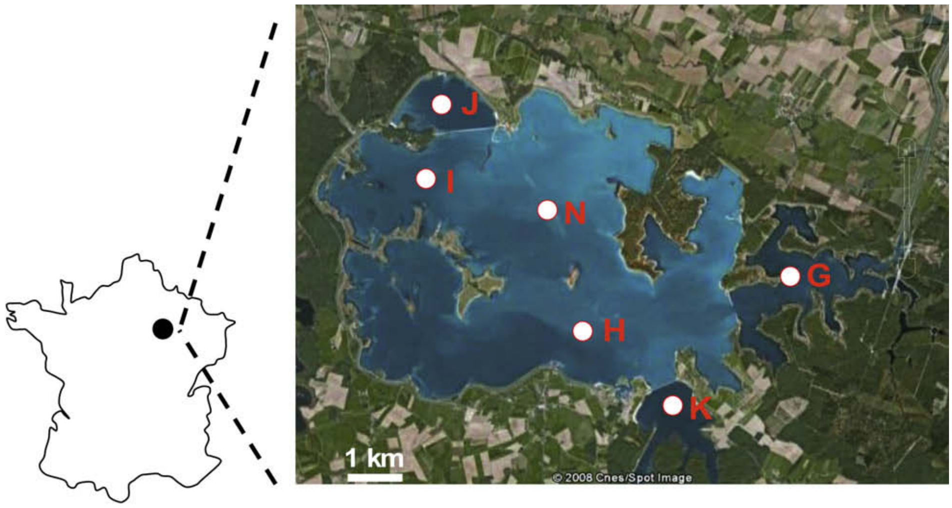

Fig. 1 – The reservoir Marne (source: Google Earth) and location of the sampling stations.

characteristics of the environment and could be omitted from the statistical analysis. Moreover, from a water management perspective, we know that only well-represented species are important and that these can be viewed as potential indicators of phytoplankton dynamics, water quality and ecosystem functioning.

In fine, these data were assembled inside a matrix comprising 142 columns and 132 rows, in which each column corresponded to a variable (species biovolume) and each sample occupied a row. This matrix was then subdivided into 6 sub-matrices, each corresponding to one station. In order to compare the annual variations of the species biovolumes between the sub-matrices, the data of each one were first centered and normalized. All the analyses were run using the package ADE-4 (Chessel et al., 2004; Dray et al., 2007) with R Software (R Development Core Team, 2007).

2.4. The Partial Triadic Analysis

The PTA is based on the logic of the Principal Component Analysis (PCA). It is designed to study simultaneously several sub-matrices of quantitative data and to detect within the structure any pattern common to these different sub-matrices.

The first step of the analysis is called the inter-structure analysis. It consists of the comparison of the structure of the 6 different sub-matrices (stations) and the identification of the stations sharing a similar annual structure. The calculation of the RV coefficient matrix between stations allows the comparison of the stations and the representation of the proximity between stations. The function of this step is to attribute a weight to each station sub-matrix (α_k coefficients). The second step is called the construction of the compromise and its analysis involves the building of a mean matrix of maximum inertia (referred to as the compromise matrix). It is derived from the initial sub-matrices in proportion to their weight. A dimensionless value, the $\cos^2$, constitutes an indicator of how much the compromise expresses the information contained in each sub-matrix (we talk about the $\cos^2$ between a sub-matrix and the compromise). Then, the matrix representing the vectorial correlations between the different stations sub-matrices (RV coefficients) provides an indication of the strength of the links among the different sub-matrices from the various stations (Robert and Escoufier, 1976). In the compromise matrix, a greater importance is thus given to stations which have a similar structure. This leads to the establishment of a common temporal typology shared by those stations; in other words, the compromise will express the spatially stable part of the annual structure. Finally, the last step is called the intra-structure or reproducibility of the compromise. The 6 subsets are projected separately onto the compromise to highlight which station fits best to the compromise.

Thus, the results of the Partial Triadic Analysis is made of three successive steps, which, in our case, successfully revealed the (1) proximity between stations, (2) pattern of phytoplankton dynamics through the two sampling years, and (3) stability and reproducibility of this pattern for each station.

3. Results

3.1. Analysis of the inter-structure (between-stations analysis)

Fig. 2-A illustrates the detection of the similarities between the stations concerning the structure of the phytoplankton community. The representation of the first eigenvalues and eigenvectors shows the similarity between the stations based on their annual phytoplankton successions. The first eigenvalue issued from the inter-structure analysis was isolated from the others and was found to explain 40% of the total inertia. The representation of the eigenvectors on the

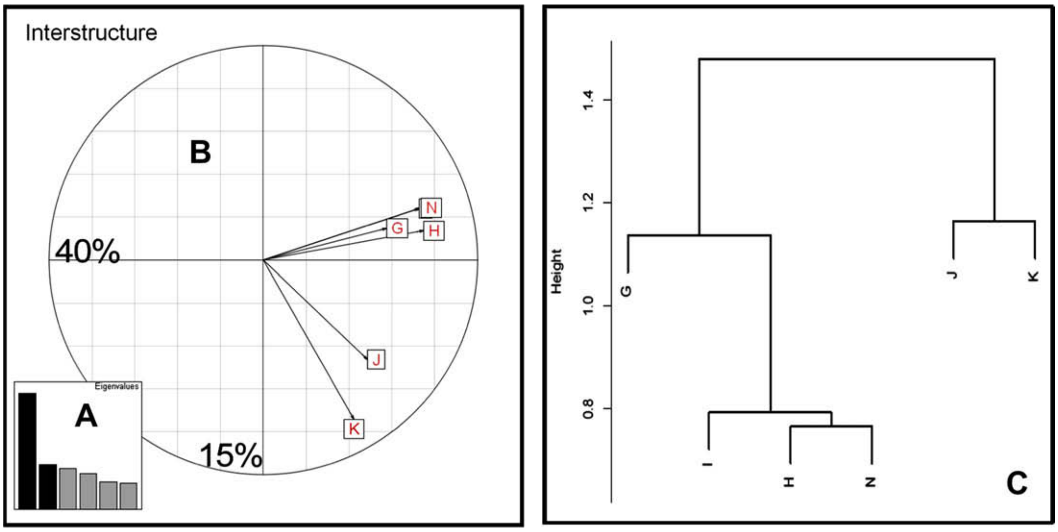

Fig. 2 – The inter-structure analysis. (A) Eigenvalues histogram based on the diagonalization of the vectorial correlation matrix. (B) Coordinates of the 6 data sub-matrices (stations) given by the first two eigenvectors of the vectorial correlation matrix. (C) Tree topology obtained by a Ward clustering method on 1-RV that indicates the following groups of stations ((G, (I, H, N)), (J, K)).

Euclidean space (Fig. 2-B) shows that the 6 components (stations) of the first eigenvector had high values on the first axis. Such a distribution on this axis, which explains most of the total inertia, indicated a strong common spatial structure. On the second axis, the inter-structure analysis emphasized a segregation of groups of stations. It indicated differences in the annual phytoplankton structures between stations. Two groups can be seen on the second axis (Fig. 2-B): a group that includes the stations K and J (the two basins) and another one that gathers the stations G, H, I and N (the four stations within the Reservoir Marne). The second eigenvector explained only a minor part of the total inertia (15%). However, such a distribution in the Euclidean space suggested the existence of two main alternatives in the annual pattern identified.

Then, the matrix presenting the vectorial correlations (RV) between the stations sub-matrices (Table 2) showed that the strongest correlation ($RV = 0.46$) was observed between the stations H and N whereas the stations G and J pointed out the weakest one ($RV = 0.14$). Moreover, considering the results of the Ward clustering method (Fig. 2-C), stations were classified and it confirmed that the stations G, H, I, and N seemed to be linked whereas the other ones (K and J) could be considered as different based on the composition of their phytoplankton community.

Another piece of information derived from the analysis of the inter-structure is the contribution of each sub-matrix in the construction of the compromise defined as α_k coefficients (Table 2). They represent the weight of each sub-matrix in the definition of the compromise. It seems that the sub-matrices H, I and N contributed a larger part in the definition of the compromise suggesting that the other stations had more particular structures leading to a weaker weight. Moreover, looking at some chemical characteristics of the reservoir (mean total phosphorus (TP), total nitrogen (TN) and chlorophyll *a* (chl *a*) concentrations), it can be confirmed that the three former stations are mutually more similar, as compared to the three latter ones (Table 1). The last interesting piece of information derived from the initial tables in proportion to their weight is the $\cos^2$ (Table 2). It constitutes an indicator of how much the compromise expresses the information contained in each table. The station H was the one that fits best with the compromise ($\cos^2 = 0.75$), followed by stations N and I ($\cos^2 = 0.74$ and 0.73, respectively) whereas the compromise represented with less accuracy the annual phytoplankton dynamics at stations G, J and K ($\cos^2 = 0.58$, 0.48 and 0.42, respectively).

Table 2 – Matrix of vectorial correlation coefficients between the tables (RV), weight of each table (α_k) in the construction of the compromise, and quality index of the compromise's structure ($\cos^2$) for each station.

Tables	RV						Weight (α_k)	$\cos^2$
H	1						0.49	0.75
N	0.46	1					0.48	0.74
I	0.45	0.44	1				0.47	0.73
G	0.29	0.31	0.3	1			0.37	0.58
J	0.25	0.23	0.23	0.14	1		0.32	0.48
K	0.21	0.17	0.17	0.18	0.18	1	0.27	0.42

3.2. Analysis of the compromise

The first three axes only accounted for 48% of the total inertia with 26% for axis I, 12% for axis II and 10% for axis III. However, given the great number of variables (i.e. 142) they provided a good summary of the temporal species organization over the 6 stations for the two sampling years. The projection of the samples (dates) on the Euclidean planes I–II (Fig. 3-A) and II–III (Fig. 3-C) provides a graphical representation of the compromise, whose interpretation requires consideration of the correspondences with the species. In fact, the species contributing the most to the annual phytoplankton structure are shown in Fig. 3-B and D. To facilitate Fig. 3 reading, each sampling date has been associated with a number (see Table 3I for correspondence). Moreover, the Kendall τ rank correlations (Kendall, 1976) between the species and the Euclidean coordinates (Fig. 4) allowed the selection of the 89 species that are most responsible for the observed annual distribution. As these 89 species accounted for the major part of the phytoplankton biovolume (73.6% of the average phytoplankton biovolume per sample), their changes were considered to be representative of those of the whole phytoplankton community.

The first axis of the analysis was defined by two distinct assemblages (Figs.3-B and 4) essentially composed of microphytoplankton and to a lesser extent of nanophytoplankton. The first assemblage could be divided into two groups (positive part of the first axis). Half of the major taxa belonged to the Chlorophytes and they were mainly represented by non-motile species. They were found in the colonial form (for example *Scenedesmus* spp., *Crucigenia tetrapedia*, *Pediastrum* spp., *Coelastrum* spp., *Crucigeniella rectangularis*, *Tetrastrum triangulare*) as well as in the individual form (for example *Tetraedron minimum*, *Golenkinia radiata*, *Dydimocystis bicellularis*, *Lagerheimia ciliata*, *Monoraphidium minutum*). Some Cryptophytes (*Cryptomonas* sp., *Rhodomonas minuta*, *Rhodomonas minuta* var. *nanoplanctica*) were also part of this group. Moreover, some individual Euglenoids (*Trachelomonas* spp., *Phacus* spp., *Euglena* sp.), Desmidiates (*Closterium aciculare*, *Closterium acutum* var. *variabile*, *Staurastrum* sp.) considered as ''R'' strategists (Ruderal species i.e. they need high resources but low energy) and Cyanobacteria (*Aphanizomenon* spp., *Chroococcus limneticus*, *Planktothrix agardhii*, *Woronichinia naegeliana* to name the most important ones) often viewed as specialized species (''S'' strategists or Stress-tolerant i.e. they are adapted to low resources water systems) (Grime, 1979; Reynolds, 1988; Padisak, 2004) constitute another cluster within this first assemblage. The second assemblage located in the negative part of the first axis was composed of larger species in the colonial form (*Dinobryon sertularia*, *Fragilaria crotonensis*) or in the individual form (*Gymnodinium helveticum*, *Cryptomonas rostratiformis*, *Cyclotella bodanica*). These were all observed to be relatively more common in spring and early summer. Then, the projection of the sampling dates on the compromise (Fig. 3-A) showed that the two clusters of the first assemblage characterized the end of summer (August) and the beginning of autumn (September) for both years (8, 9, 10, 11 in 2006 and 19, 20, 21, 22 in 2007). In contrast, in the negative part of the first axis, the sampling dates were related to the first half of

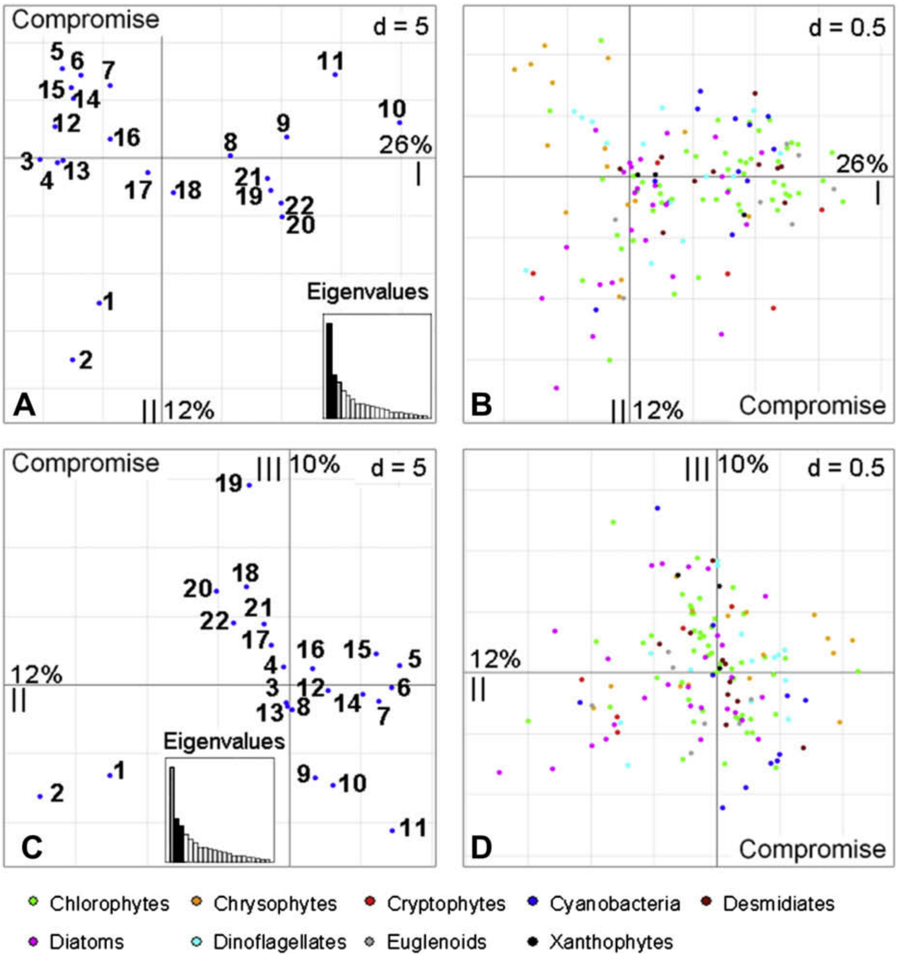

Fig. 3 – The compromise analysis (average station). (A) Coordinates of the sampling dates in the first plane (axes I–II) of the compromise and histogram of eigenvalues identifying the prominence of the two first axes that define the average spatial structure. (Table 3 contains the correspondence between numbers and dates). (B) Projections of the variables (species) in the first plane (axes I–II) of the compromise. (C) Coordinates of the sampling dates in the second plane (II–III) of the compromise and histogram of eigenvalues identifying the contribution of the second and third axes in the construction of the compromise. (D) Projections of the variables (species) in the plane defined by the axes II and III of the compromise.

the year including spring and early summer (1, 2, 3, 4, 5, 6, 7 in 2006 and 12, 13, 14, 15, 16, 17 in 2007). Thus, axis I defined a spring–early summer assemblage and a late summer–early autumn assemblage.

The second axis was defined by two distinct assemblages (Fig. 4). One assemblage was dominated by colonial Chrysophytes (*Dinobryon* spp.), the individual flagellate Chlorophyte *Phacotus lendneri*, some Desmidiates from the genus *Cosmarium* and a Dinoflagellate called *Peridinium aciculiferum* whereas the second one was essentially composed of large individual Diatoms (*Gyrosigma acuminatum*, *Nitzschia acicularis*), little Chlorophytes species (undetermined small Chlorophytes, *Monoraphidium kormakovae*) and some others. Thus, the axis II appeared to reflect a gradual change from a winter–spring assemblage to a summer one with gradual shifts from the dominance of larger forms towards small colonial or unicellular species characteristics of warmer seasons. In addition, the distribution of the sampling dates on the compromise reflected a transition from March–May 2006 (1–3) to June–July 2006 (4–7) and to a lesser extent from April–May 2007 (12–14) to June–July 2007 (15–18). In fact, axis II showed with precision the changes that occurred during the first half of the year 2006 rather than 2007 and it made the differentiation between species characteristics of winter–spring and early summer within the phytoplanktonic community of the Reservoir Marne.

Then, the third axis is also defined by an assemblage composed of some undetermined spherical cyanobacteria that were at the opposite of another group characterized by a mixed assemblage with some well-identified large Diatoms (*Rhizosolenia longiseta*, *Eunotia* sp. and *Acanthoceras zachariasii*), a colonial Cyanobacterium (*Microcystis aeruginosa*), small unicellular (undetermined Chlorophytes and *Schroederia setigera*) and colonial (*Scenedesmus longispinus* and *Micractinium pusillum*) Chlorophytes as well as some small unicellular Chrysophytes (*Salpingoeca frequentissima* and *Chrysolykos planctonicus*) (Fig. 3). The distribution of the sampling dates (Fig. 3-C) showed that axis III mainly reflected the differences of the late summer–early autumn phytoplankton assemblages between the two sampling years. In fact, late August and

Table 3 – Correspondence between the sampling dates and their number on the different figures.

Samples' number	Dates
1	06/03/2006
2	04/04/2006
3	03/05/2006
4	07/06/2006
5	28/06/2006
6	04/07/2006
7	24/07/2006
8	07/08/2006
9	22/08/2006
10	05/09/2006
11	19/09/2006
12	18/04/2007
13	16/05/2007
14	30/05/2007
15	12/06/2007
16	20/06/2007
17	03/07/2007
18	25/07/2007
19	07/08/2007
20	29/08/2007
21	11/09/2007
22	26/09/2007

September 2006 (9–11) were opposed to late July and August 2007 (18–20). The correspondence with the species (Fig. 3-D) showed that the 2006 assemblage was characterized by several Cyanobacteria in the unicellular form (undetermined spherical Cyanobacteria), in the colonial form (*W. naegeliana*) and in the filamentous form (*Aphanizomenon flos-aquae*, *P. agardhii* and *Pseudanabaena limnetica*) as well as a filamentous Chlorophyte, *Mougeotia gracillima* and a unicellular one *Treubaria triappendiculata*. On the contrary, the 2007 assemblage was defined by the presence of large Diatoms, a potentially toxic colonial Cyanobacterium (*M. aeruginosa*) and some other algae cited above (small unicellular chlorophytes and chrysophytes as well as colonial chlorophytes).

To summarize, following the analysis of the three axes, it seems that three temporal periods can be highlighted considering the distribution of the dates and the arrangement of the species on the first two axes. The first one corresponds to early spring, the second one is related to late spring and early summer and the third one refers to late summer and early autumn.

3.3. *Analysis of the intra-structure (reproducibility of the compromise)*

The reproducibility of the compromise for the stations can be represented for species (Fig. 5-B) and for dates (Fig. 5-A). It allows the discussion about the spatial evolution of species-dates links (internal typology for each sub-matrix). To do that, the lines (Fig. 5-A) and the columns (Fig. 5-B), from the separated analyses of each sub-matrix, have been projected on the first plane of the compromise. These projections confirm that the analysis is centered on the station sub-matrices H, N and I because the general pattern for the distribution of the points for the dates and for the species is in accordance with the pattern pointed out by the compromise. This observation implies that there were only a few differences between seasonal changes in the composition of the phytoplankton community between these three stations and the compromise. Moreover, this confirms the information given by the elevated values of the α_k and the $\cos^2$. On the contrary, the general pattern observed for stations K, J and G concerning the distributions of the dates and the species differed from the distribution obtained with the compromise. In fact, they had their own structure compared to the other three stations. The projection of the sampling dates on the axes of the compromise for each of these three stations revealed a distribution that was different from the compromise's one, indicating that the phytoplankton community had its own seasonal dynamics in the stations K, J and G. Finally, the species distribution as a whole differed from the distribution of the species on the compromise indicating that species diversity was not the same in these three stations.

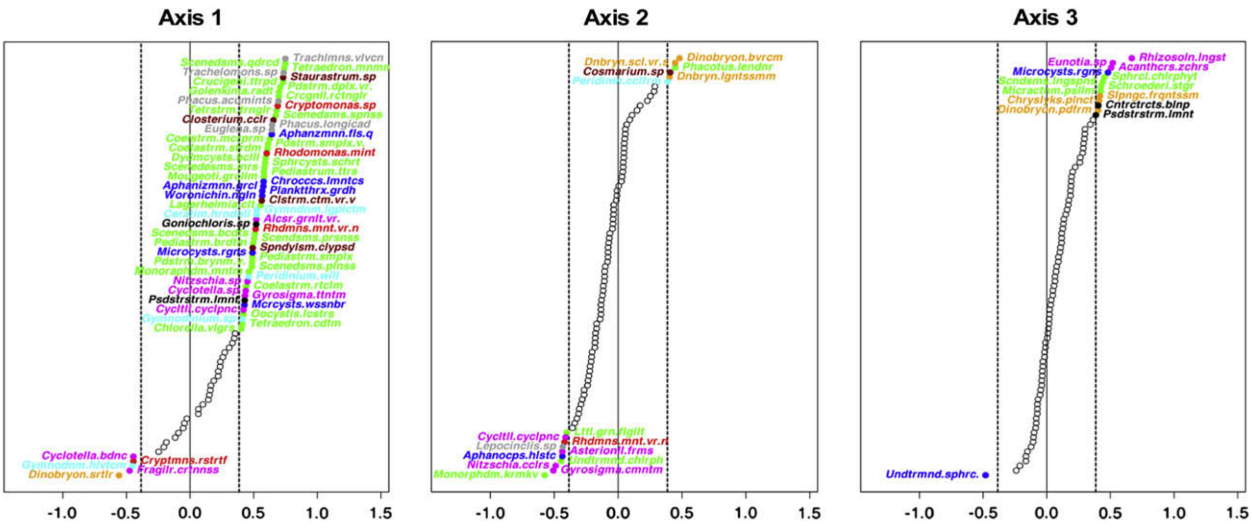

Fig. 4 – Kendall τ rank correlations between species biovolume and factorial coordinates on the first three axes: 89 species were found to be significantly correlated with these axes (for $\alpha = 1\%$).

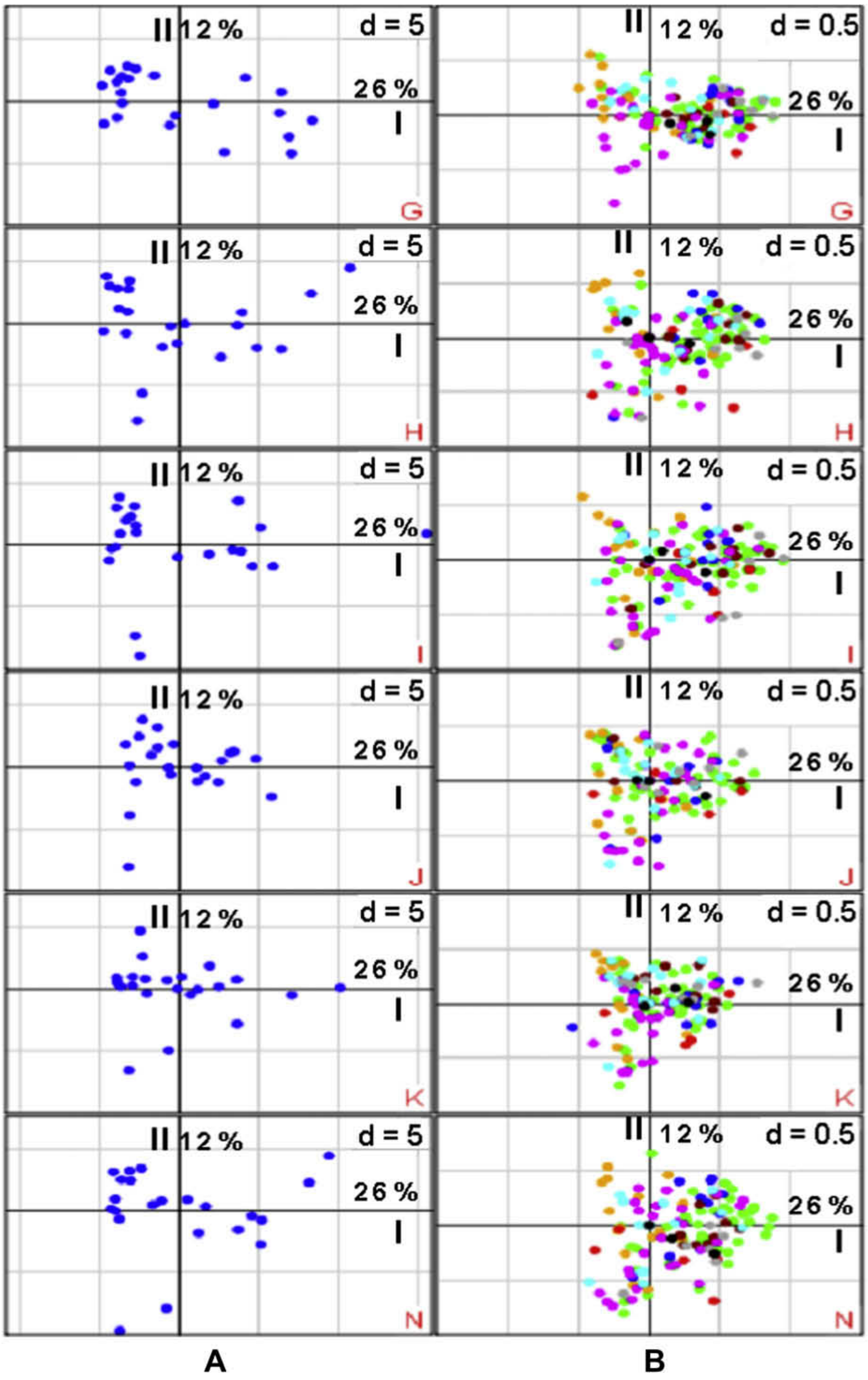

Fig. 5 – Analysis of the reproducibility of the compromise structure. (A) Multiwindowed projection (by station) of rows (dates) on the first plane of the compromise. (B) Multiwindowed projection (by station) of columns (species) on the first plane of the compromise.

4. Discussion

According to the PEG-model (Sommer et al., 1986), some basic trends of planktonic succession in lakes are well known. This can be related to a variety of different factors such as the trophic status, the hydrological regime, the relative importance of the heterotrophic compartment to name only a few. The overriding differences between lakes and reservoirs relate mainly to hydrography and to the hydraulic exchanges (Reynolds, 1999). For example, the Reservoir Marne is prone to important level fluctuations along the year, and the water residence time is short (between 1 and 12 months depending on the sampling station). Consequently, stratification in this reservoir is absent or very weak and this is likely to have an impact on phytoplankton composition in selecting for species that are more or less tolerant to mixing.

4.1. Seasonal dynamics of the phytoplankton community

The early spring assemblage was judged exclusively by the species represented in 2006, because no sampling was carried out in March 2007. The species present in April 2007 were dominated by species of spring and early summer, according to the vectorial coordinates on the second axis. In March and April 2006, *G acuminatum* and *N. acicularis* were the two main Diatoms. The PEG-model generalizes that small centric Diatoms often develop in early spring (Sommer et al., 1986) but some authors have observed that large pennate diatoms can make a significant contribution to the biovolume of the phytoplankton community during this period in rivers (Leland et al., 2001; Ha et al., 2002), ponds (Rojo et al., 2000) or estuaries (Roy et al., 1996). In fact, these species, often considered as ''R'' strategists, have low nutrients requirements (Grime, 1979; Reynolds, 1988; Padisak, 2004). Moreover, they can live in strong-flowing waters that come from the rivers that feed the reservoir and consequently rely on physical perturbations to remain in suspension. The physical mixing in the upper lit layers is essential to the continued suspension of non-motile species with no other means of offsetting a constant tendency to sink. In addition, the coexistence of large diatoms and small chlorococcales has been observed in the eutrophic temperate lake Vechten (Holland) (Gulati and Parma, 1982) and two shallow lakes with a weak stratification, Lake Tjeukemeer (Holland) (Gulati and Parma, 1982) and Lake Heimdalsv (Norway) (Larsson et al., 1978). This could confirm the importance of small undetermined Chlorophytes during this period, i.e. cosmopolitan species growing fast.

An assemblage of several species (*D. sertularia*, *F. crotonensis*, *C. bodanica*, *G. helveticum* and *C. rostratiformis*) characterized the 2006 and 2007 spring and early summer periods (negative part of the first axis and positive part of the second axis). *Cryptomonas* spp. are considered to be fast-growing and opportunistic species and they are known to be part of the key species that establish and infest the water systems in spring (Sommer, 1985a). These small species are generally considered as ''C'' strategists (competitive species, i.e. they need high resources and energy) with high intrinsic growth rates and high metabolic activity (Grime, 1979; Reynolds, 1988; Padisak, 2004). They also benefit from high concentrations of nutrients and low grazing pressure. In addition, Diatoms such as *F. crotonensis* can be associated with the beginning of the summer period in shallow temperate lakes with a mesotrophic status (Yang et al., 1996). According to Vollenweider and Kerekes (1982), the trophic status of the Reservoir Marne can thus be considered as mesotrophic for most of its capacity (stations H, I, N, J) whereas the stations K and G seem more eutrophic (Table 1). Thus, it is not surprising to find this Diatom in the reservoir during this period of the sampling season. In addition, the dependence upon physical mixing is strongly apparent, requiring a continuous or semi-continuous mixed layer of 2–3 m in thickness. Diatoms can also be associated with Desmidiates (Townsend and Luong-Van, 1998; Watanabe et al., 2000; Negro et al., 2003). *G. helveticum* has never been identified with *F. crotonensis* and *C. bodanica* but it has been shown that Desmidiates can be more or less abundant than Diatoms in this kind of associations (Reynolds et al., 2002). Moreover, *G. helveticum* seems to present its maximum development in spring, during the decline of the Diatom bloom whereas in summer, the species is almost completely absent from the epilimnion and occupies the meta- and hypolimnion (Wille and Hofmann, 1991). Then, we can see that *D. sertularia* was a summer species. This species is often found in nutrient-rich water systems and the position of this species in the spring–early summer period can be viewed as a transition through a mature summer assemblage essentially composed of Chrysophytes (Barbiero and McNair, 1996; Clegg et al., 2003). In fact, *Dinobryon* spp. (*Dinobryon bavaricum*, *Dinobryon sociale* var. *stipitatum*, *Dinobryon elegantissimum*), often defined as ''S'' strategists, appeared as typical summer members of the plankton community (positive part of the second axis). These species are obligate CO_2 users, their sensitivity to enrichment and relative absence in high-alkalinity waters are down due to difficulties of carbon acquisition (Reynolds et al., 2002; Padisak, 2004). On the contrary, species like *Cosmarium* sp. tend to be present in more eutrophic waters (Spijkerman and Coesel, 1996; Stamenkovic and Cvijan, 2008). Surprisingly, the dinoflagellate *P. aciculiferum* seemed to be one of the species characterizing the positive part of the second axis that represented the early summer 2006. This species is known to be present in winter plankton for a short time (February–March) and it can be a dominant species in March. A possible explanation for this incoherence can rely on a mistake in the identification. In fact, some *P. aciculiferum* morphotypes could be confused with some *Peridinium umbonatum* morphotypes (Popovsky and Pfiester, 1990). The size range of the former can fit into the size range of the latter. Moreover, as plates are not always visible on samples preserved in Lugol's Iodine solution and spines can be located at the same place in both species, it might be possible that we identified *P. aciculiferum* instead of *P. umbonatum*. Like *Peridinium willei*, this species is actually considered as a cosmopolitan species living in water systems from oligotrophic to mesotrophic status and whose abundances can be high in all seasons (Popovsky and Pfiester, 1990; Lewis and Dodge, 2002). Concerning *P. lendneri*, high abundances have been found in summer in Lake Geneva (Anneville et al., 2002) leading to bloom formation in some cases (Bluszcz et al., 2008). In addition, this species is widely distributed all year long, growing in waters whose temperature fluctuates from 15 to 25 °C and whose trophic status varies from oligo- to hypertrophic water systems (Schlegel et al., 1998). Given the high mean temperatures found in the Reservoir Marne as well as the mean TP concentrations (Table 1), the results obtained in our study are consistent with what has been found in previous studies.

Finally, the phytoplankton dynamics during late summer and early autumn showed that different species with various ecological strategies share the same habitat (positive part of the first axis) and are the main contributors to the phytoplankton biovolume. This is in agreement with the PEG-model that describes the seasonal succession of algae and insists on the development of a rich summer algal growth typical for nutrient-rich water systems (Sommer et al., 1986). In fact, colonial Chlorophytes and Cryptophytes often form the dominants in the summer phytoplankton. These large algal species have a slower growth rate than small ones that have short generation time. Nevertheless, they present an exponential increase within a few days (Sommer et al., 1986). Most of these species are characteristics of shallow, enriched lakes (Reynolds et al., 2002) and are found in summer in Lake Geneva (Anneville et al., 2002). Then, in late summer and early autumn, several classes of algae can be represented in the phytoplankton community. First of all, Cyanobacteria are the typical phytoplankton dominants of all lakes with rich summer algal growth. Species identified in the Reservoir Marne were both filamentous (*P.i*, *Aphanizomenon* spp.) and colonial (*W. naegeliana*). These specialized species are often of large size with low surface to volume ratios. In addition, they are stress-tolerant species with special adaptations such as the ability to utilize organic resources or to store nutrients (Reynolds et al., 2002). Their main selective advantage is their high resistance to grazing because of their size, their high resistance to sedimentation due to their motility or buoyancy and their ability to migrate vertically (Mur et al., 1999). Sometimes, they can be accompanied by Dinoflagellates but this was not observed in the Reservoir Marne. Later on in the early autumn period, Desmidiates appear. The three species identified (*C. aciculare*, *C. acutum* var. *variabile* and *Staurastrum* sp.) are generally found in nutrient-rich water systems and their growth is known to be favored when the water column is mixed instead of being stratified. Then, despite the lack of information on Euglenoids in the PEG-model, it is well known that these cosmopolitan species occur in shallow, nutrient-rich systems when mixing process increases due to changes in wind velocity during summer and early autumn (Samuels and Mason, 1997; Celik and Ongun, 2006). As the Reservoir Marne is a highly exposed water mass, this results in nutrient replenishment available for the Euglenoids' growth. To finish, we can mention, as it was done in Reynolds et al. (2002), that some water systems can support algal flora which have not been well characterized. Several functional groups can be mixed as it is the case for the positive part of the first axis. As an example, we can find, in shallow and enriched systems, species of groups D (Diatoms), J (*Scenedesmus*, *Pediastrum*, *Coelastrum*), X1 (*Chlorella*, *Ankyra*, *Monoraphidium*, *Golenkinia*, *Treubaria*), Y (*Cryptomonas*) and W (Euglenoids, Chrysophytes, Desmidiates) all together (See Reynolds et al., 2002 for more details).

4.2. *Differences between the two sampling years for the late summer–early autumn period: the importance of the third axis of the compromise*

As presented in the results, the third axis clearly separated the 2006 late summer–early autumn period from the 2007 one. In 2006, undetermined spherical Cyanobacteria contributed to a great part of the biovolume. These Cyanobacteria are assumed to be isolated cells of *M. aeruginosa* because of their size, their shape and their pigmentation. Generally, these algae are found in the colonial form but as samples are preserved in Lugol's Iodine solution, it might be possible that they were broken. This alga is one of the most widely reported, and typically forms blooms that may persist throughout the summer in enriched lakes (Mur et al., 1999). The other algae that characterized this period were also Cyanobacteria, in the colonial (*W. naegeliana*) or filamentous form (*A. flos-aquae*, *P. agardhii* and *P. limnetica*). *W. naegeliana* can also contribute to a great part of the cyanobacterial biovolume during the end of summer in mesotrophic lakes but is rarely a major component of blooms (Reynolds et al., 2002). The autumnal assemblage also included filamentous Cyanobacteria and a filamentous Chlorophyte, *M. gracillima*, whose morphological and functional properties make them close to K-selected species (i.e. they grow slowly but can better exploit scarce resources). The heterocysteous Cyanobacteria *A. flos-aquae*, a dinitrogen-fixing species (tolerant to low nitrogen concentrations in the water) is often found in eutrophic systems and can form dense blooms in temperate zones. This is a characteristic species of the autumnal period in Lake Geneva (Anneville et al., 2002). *P. agardhii* and *P. limnetica* are two photoadapting solitary filamentous Cyanobacteria from the so-called functional group "S1" (Reynolds et al., 2002). They are commonly found among enriched, exposed and generally shallow lakes at most latitudes, where they can aspire to monocultural populations persisting throughout the year. Another distinctive Chlorophyte, *T. triappendiculata*, part of the group "J" (mainly non gelatinous, non-motile Chlorococcales) (Reynolds et al., 2002) has the characteristics to be prominent in shallow, highly enriched systems and completed the list of the different species that characterize the 2006 late summer–early autumn assemblage. As we can see, all these species are found in nutrient-replete water systems and this is in agreement with the mesotrophic status of the Reservoir Marne whose annual mean TP concentrations are between 15 and 40 $\mu g\,l^{-1}$ depending on the stations.

Then, the 2007 species that are at the opposite of the 2006 species belong to several classes. The large Diatoms (*R. longiseta*, *Eunotia* sp. and *A. zachariasii* as well as *Asterionella formosa*) generally started to develop in early summer, in parallel with the development of the early summer species. Since they are better adapted for autumnal conditions (deepening of the mixed layer, decreasing vertical temperature gradient and light intensity), they become dominant in late summer and autumn. Diatoms become increasingly important as autumn progresses and the community shifts to the winter species. In addition, elevated silicate concentrations can contribute to Diatoms growth (Sommer, 1985b). In fact, during mixing process at the end of summer and the beginning of autumn, Diatoms can become dominant because dissolved silicate is replenished from deeper water. Some authors also suggest that the Diatoms growing at the end of summer are those who required important nutrient concentrations (Miyajima et al., 1994; Benson-Evans et al., 1999; Heo and Kim, 2004). However, some others pointed out that the mixed water system in autumn decreases competition for nutrients and leads to a shift to algae with progressively lower light requirements (Sommer et al., 1986; Reynolds, 1987, 1999). The autumnal species replacements can thus be understood as a sequence of species with increasingly lower light requirements. Therefore, direct physiological effects of temperature and sedimentation should play less of a role than traditionally assumed. Among Chlorophytes, small unicellular (undetermined Chlorophytes and *S. setigera*) and colonial (*S. longispinus* and *M. pusillum*) species have been identified to be characteristic of the 2007 late summer period. They are non-flagellate and non-motile species, thus favored by water column mixing. Moreover, these colonial species possess spines that can be considered as a way to resist against predation.

The colonial Cyanobacterium *M. aeruginosa* could be characteristic of the 7th August 2007. It is well known that today's populations are not the product of today's conditions and the responses always lag by days (cells) to weeks (populations). In the present study, the weeks preceding the beginning of August presented some specific features related to meteorological conditions. In fact, previous weeks were hot and well insolated but they were also the windiest. Consequently, the water column was not stratified during this period even though this species generally develops in stratified water layers. Thus, it might be possible that the windy conditions associated with the shallow depth suspended the *Microcystis* colonies that were detectable and presented an elevated biovolume during this period.

Part of the explanation for the differences between the two years can rely on meteorological conditions. Summer 2006 was hot and shiny whereas summer 2007 was cool and windy. In September 2006, the phytoplankton community was still a late summer community whereas in 2007, the phytoplankton composition turned to an autumn community much more rapidly. The 7th August 2007 could be the turning date to autumn because *M. aeruginosa* is often considered as an early autumn blooming species. Then, the following dates are more associated with a late autumn community composed of large Diatoms, small opportunistic Chlorophytes and Chrysophytes rather than a late summer one. Moreover, the bad meteorological conditions and the strong wind exposure could also explain that Cyanobacteria were not characteristic of the 2007 sampling year whereas in 2006, conditions were quiet, with low turbulence due to calm winds and high irradiance that favored their growth. All these results highlight also that 2 years is a minimal duration for ecosystem water quality survey.

4.3. *Stations K, J, G versus the others and identification of a reference station*

One of the great interests of the statistical method used here relied on the possibility to identify the stations that represented with the most accuracy the situation described by the compromise and consequently to point up a potential reference station after having extensively sampled the water system. We assume that this is of particular relevance for water managers to define an adequate sampling strategy and plan accurate management policy. As presented in the results, the stations H, N and I were good candidates as reference stations for the whole reservoir whereas the stations K, J and G were more atypical with their own seasonal trends in phytoplankton composition. Somehow, this agrees with the fact that K and J are located in two closed basins that are not directly connected to the main reservoir. The station J could be viewed as a mesotrophic station whereas the station K could be an eutrophic station, with elevated annual mean TP and chl *a* concentrations agreed with. In fact, the latter receives polluted water from a small stream whose trophic status is hypereutrophic and causes the development of invasive algae. The station G is also a nutrient-rich station, with an elevated annual mean TP concentration, that receives water from two feeding channels. Historically, the basin including the station G was the Reservoir Marne in itself, inaugurated in 1938. Then, in 1974, it was enlarged to allow the storage of larger volumes of water. This station, in turn, could be regarded as the feeding station of the reservoir because it communicates with the stations H, N and I that are part of the extended reservoir. Those stations, as they are quite identical to the seasonal trends and the phytoplankton distribution on the compromise could be considered as reference stations. Strictly regarding the values of the $\cos^2$, the station H can be proposed as the reference station to chose for water quality survey of this short-time water residence ecosystem. Nevertheless, this does not mean that the other stations are not important or interesting for an ecological perspective. Typically, as the stations K and J are the places for recreational activities, they should be taken into account in the sampling strategy and be at the center of the water managers' interests, especially regarding the cyanobacterial risk in summer. The station G, as it is the receptacle of water from the channels and consequently the rivers Marne and Blaise, could also be an important station to sample and monitor, for the same reason than above.

5. Conclusion

The PTA revealed three key sampling periods with associated key species, the first one corresponding to early spring, the second one to spring–early summer and the last one to late summer–early autumn which is in agreement with the PEG-model. Moreover, four stations could be chosen for the survey of the reservoir water quality, the station H as the reference and stations K, J and G for their own specificity. This is particularly important to define the best sampling strategy protocol for water managers in the context of the European WFD. With this objective in mind, the PTA appears as a very relevant tool to determine a valid strategy to operate. Most of the water masses possess huge phytoplankton datasets and this kind of statistical technique should constitute an interesting tool for the choice of a representative management strategy. It will be particularly useful for managers who now, more than ever, require decision support to determine adequate policy, i.e. priorities and actions to carry out.

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