

FACTORS CONTROLLING PHYTOPLANKTON COMMUNITY STRUCTURE IN AN ALKALINE VERSUS A SOFTWATER LAKE

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SUMMARY

The objective of this paper is to compare nutrient resources that might control phytoplankton species composition and succession in two Spanish lakes located in very different geological areas but at the same latitude. The lakes, Banyoles and Sanabria, are respectively located on Eocene gypsum carbonate rocks and in a Pre-Cambrian region dominated by granitic rock. Their species compositions are quite different: the first lake is dominated by diatoms, the second by chroococcal cyanobacteria.

Our hypothesis is that the limiting nutrient in soft-water Lake Sanabria will be nitrogen, and in the alkaline Lake Banyoles, phosphorus (because of its strong precipitation with calcium or coprecipitation with CaCO_3).

In order to test this hypothesis we used principal component analyses with physico-chemical and biological variables on the one hand and species composition on the other. The results show nitrogen to be the more important nutrient, controlling species succession in both lakes. This element is relatively low in both ecosystems during the summer.

KEY WORDS: Phytoplankton, Lake Sanabria, Lake Banyoles, nutrient limitation.

INTRODUCTION

The factors responsible for the seasonal variation of phytoplankton as a whole and of its particular component species may be grouped roughly as: 1) partly independent physical factors - that is, temperature, illumination, and turbulence; 2) interdependent chemical factors - nutrients, accessory organic compounds (vitamins) and antibiotics; and 3) biological factors - predation, competition and parasitism (HUTCHINSON, 1967).

The chemical characteristics of waters - soft-water versus alkaline - could be important in characterizing regional

differences in the specific composition of algal communities, as was demonstrated by SPARLING & NALEWAJKO (1970) in natural lakes or by MARGALEF *et al.* (1976) in the phytoplankton characterization of Spanish reservoirs. Species affinity to water type can be a direct effect, such as for example the need for Ca by some haptophyceae with coccolith deposits, or an indirect effect related to the pH-carbon dioxide-bicarbonate system (REYNOLDS, 1984) or to the control of macronutrients as is the case of calcium and phosphorus (MARGALEF, 1983; AVNIMELECH, 1984).

In relation to water chemistry and phytoplankton association, most research carried out during the first part of this century was based on the importance of the monovalent to divalent cation ratio. For example, communities dominated by diatoms were associated with a lower ratio, and desmid and chrysophyceae communities with a higher ratio (PEARSALL, 1922). Although cation concentrations in the water could be important to the regulation of the osmotic pressure in algal cells (MARGALEF, 1983) it is more probable that the difference in species composition in communities living in more or less mineralized waters is related more to nutrient availability than to the abundance of a specific cation or anion. This fact is clearly illustrated by African tropical lakes which show a wide range of chemical characteristics and resource limitations which vary accordingly (KALFF, 1983; KILHAM *et al.*, 1986). If the physical conditions of the lakes are similar, the response of the phytoplankton depends on changes in the N:P supply ratio (SUTTLE & HARRISON, 1988) which will govern the species succession.

The objective of our study is to compare the nutrient resources that might control phytoplankton species composition in two Spanish lakes located in very different geological areas but at the same latitude, ensuring that physical factors controlled by annual irradiation are very similar. The lakes are Banyoles and Sanabria.

In order to arrive at this objective we used principal component analyses with physico-chemical and biological variables on the one hand and species composition on the other. The data for Lake Banyoles were taken from the 1970-1971 cycle (PLANAS, 1973) and for Lake Sanabria from the 1973-1974 cycle studied by Planas in collaboration with the Comisaría de Aguas del Duero (Planas, unpublished data).

Our hypothesis is that the limiting nutrient in soft-water Lake Sanabria will be

nitrogen whereas in the alkaline Lake Banyoles, phosphorus, because of its strong precipitation with calcium or coprecipitation with CaCO_3 , will be the controlling factor. Nitrogen has been found to be the limiting nutrient in some low conductivity temperate lakes where phosphorus concentration is very low (GOLDMAN, 1981).

CHARACTERISTICS OF THE LAKES

Lake Sanabria and Lake Banyoles are the largest natural water bodies in Spain. Both are pre-alpine lakes and are located geographically at $42^{\circ}1' \text{ N} - 3^{\circ}1' \text{ W}$ and $42^{\circ}7' \text{ N} - 2^{\circ}45' \text{ E}$, respectively. They are situated in very different geological regions and have very different origins. Lake Sanabria is located in a Pre-Cambrian region dominated by granitic rock. It occupies the valley excavated by two convergent glaciers closed by the Riss moraines (MARGALEF, 1955). Lake Banyoles is located in Eocene gypsum overlying carbonate rocks of the same geological period. It has a karstic origin and is the remainder of a much larger Tertiary lake (SOLÉ-SABARÍS, 1958).

Water inflow derives mainly from the surface (the Tera river) in Lake Sanabria and from the bottom in Lake Banyoles (PLANAS, 1973; in press).

The first lake is bigger: its surface area is three times, its volume six times and its mean depth twice that of Lake Banyoles. The renewal time of the water in the former is eight times faster than in Lake Banyoles due to its geographical location: Lake Sanabria is located in the wettest part of Spain with a yearly mean precipitation of 1446 mm, whereas Lake Banyoles receives only 837 mm of rain per year.

The main anion is sulphate in Banyoles, and bicarbonate in Sanabria. The dominant cations are respectively calcium and magnesium.

According to their respective nutrient

concentrations, Lake Banyoles is considered to be oligo-mesotrophic (PLANAS, 1973) and Lake Sanabria oligotrophic. The major nutrient differences are in nitrate and silica concentrations. Nitrate concentrations are four times greater in Lake Banyoles than in Lake Sanabria. Silica, which is very abundant and shows strong seasonal variations (0.25 μM to 200 μM) in the epilimnion of the alkaline lake, has a concentration typical of a pre-Cambrian lake (40 to 74 μM) in the soft-water Lake Sanabria. Phosphorus concentration in Lake Banyoles is twice that in Lake Sanabria.

MATERIALS AND METHODS

Data used for the two principal component analyses (PCA) were integrated from samples taken at different depths of the euphotic zone of each lake. The thickness of this zone varied from 2.6-10 m in Lake Banyoles (LB) and from 8-16 m in Lake Sanabria (LS). The samples came from the deepest station of the euphotic zone of each lake: 40 m in Banyoles and 50 m in Sanabria.

Lake Sanabria sampling began at the end of July 1973 and finished in mid-October 1974. In Lake Banyoles sampling took place from the end of October 1969 to January 1971. Symbol identification for the various dates is given in Table I.

For the chemical and biological methods used in Lake Banyoles see PLANAS (1973); the same methods were used for Lake Sanabria. The first lake was sampled fortnightly, the second every three weeks during stratification and monthly during the winter period.

The variables used for the physico-chemical-biological principal component analysis (PC-PCA) were: the nutrients, phosphorus (PO_4) measured as total soluble reactive phosphorus and nitrogen ($\text{NO}_3 = \text{nitrates} + \text{nitrites}$); water transparency (SD); phytoplankton biomass,

TABLE I. Lakes Banyoles and Sanabria sample number identification. * Mixing period.

BANYOLES		SANABRIA	
NUMBER	DATE	NUMBER	DATE
1	14.02.70	1	27.07.73
2	28.03.70	2	10.08.73
3	14.03.70	3	11.09.73
4	28.03.70	4	27.09.73
5	11.04.70	5	19.10.73
6	25.04.70	6	31.10.73*
7	09.05.70	7	16.11.73*
8	25.05.70	8	10.12.73*
9	09.06.70	9	20.12.73*
10	20.06.70	10	07.02.74*
11	06.07.70	11	27.03.74*
12	20.07.70	12	25.04.74*
13	03.08.70	13	16.05.74*
14	18.08.70	14	30.05.74*
15	31.08.70	14b	16.06.74*
16	14.09.70	15	25.06.74*
17	28.09.70	16	11.07.74*
18	10.10.70	17	26.07.74
19	24.10.70	18	09.08.74
20	07.11.70	19	21.08.74
21	21.11.70	20	11.09.74
22	05.12.70	21	26.09.74
23	19.12.70	22	16.10.74
24	02.01.71		
25	16.01.71		
26	30.01.71		

as calculated from chlorophyll-a concentrations (CHL); and cell numbers (CN). In Lake Banyoles, silica (Si) was also included as a nutrient, because the dominant species are diatoms, and silica, which presents a marked cycle, could act as a limiting factor. Since Si was analysed only from June onwards, the PCA for this lake comprises only the sampling data collected during the stratification period (June to October 1970). In Lake Sanabria we did not include this variable since, as mentioned above, it behaves as a rather conservative element. Another difference in the variables used in the PC-PCA of each lake is the primary production (PP). We included it in Lake Banyoles' PC-PCA in which case we had a complete cycle, but not in Lake Sanabria', where it was only measured 9 times out of 22.

For the species principal component analysis (S-PCA) we retained the species

which represented more than 10% of the total for at least one sampling, except if the species was observed only once, in which case it was excluded.

In discussing the distribution of the objects in the reduced space of the PCA, we considered only the axes with an eigenvalue near or above 1. We considered that descriptors with a component greater than or equal to 0.60 defined the axes.

For each PCA we determined object (in this case sampling date) clustering by applying a hierarchic classification (LEGENDRE & LEGENDRE, 1979).

RESULTS

The first three axes of the PC-PCA in Lake Banyoles (LB) contribute 82.63% of the variance, with Axis I explaining 37.45%. The loading variable which defines the positive part of the Axis is Si (0.70) and those for the negative part are CN (-0.73) and SD (-0.72). Axis II explains 26.34% of the variance. The descriptors that

characterize this axis are NO₃ (-0.84) and PP (-0.83).

These two axes clearly separate the stratification period (Cluster 1) from the mixing period (Clusters 2 and 3). The separation of the clusters is highly significant (Fig. 1a). In general the stratification period is characterized by low nitrogen and silica concentrations, low primary production and relatively high transparency (PLANAS, 1990) and phytoplankton cell density (Fig. 2).

Axis III contributes 18.83% of the variance. The most important loading variables on this axis are nutrients. This axis separates a few dates of the stratification period from those of the mixing period (Fig. 1b).

The objects in the principal component analysis of Lake Banyoles using species as descriptors (S-PCA) are spatially distributed on five axes, which explain 71.72% of the variance. Axis I explains 24.78% of the variance. It is defined by the following species: *Rhodomonas minuta* (-0.91), *R. minuta nannoplanctonica*

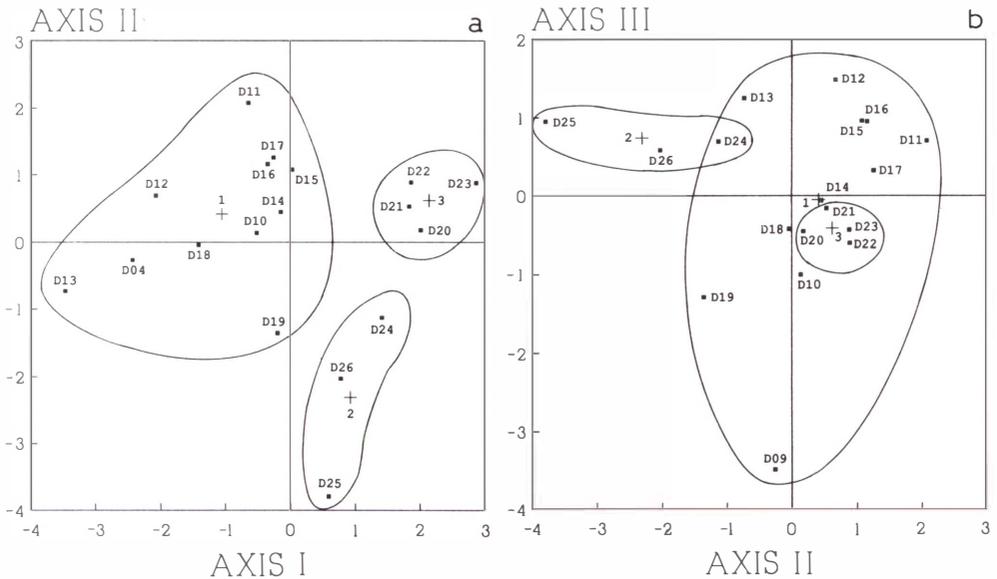


FIGURE 1. Lake Banyoles sample distribution using the physico-chemical and biological variables. (a) Axes I and II. (b) Axes II and III. For identification of object numbers, see Table I.

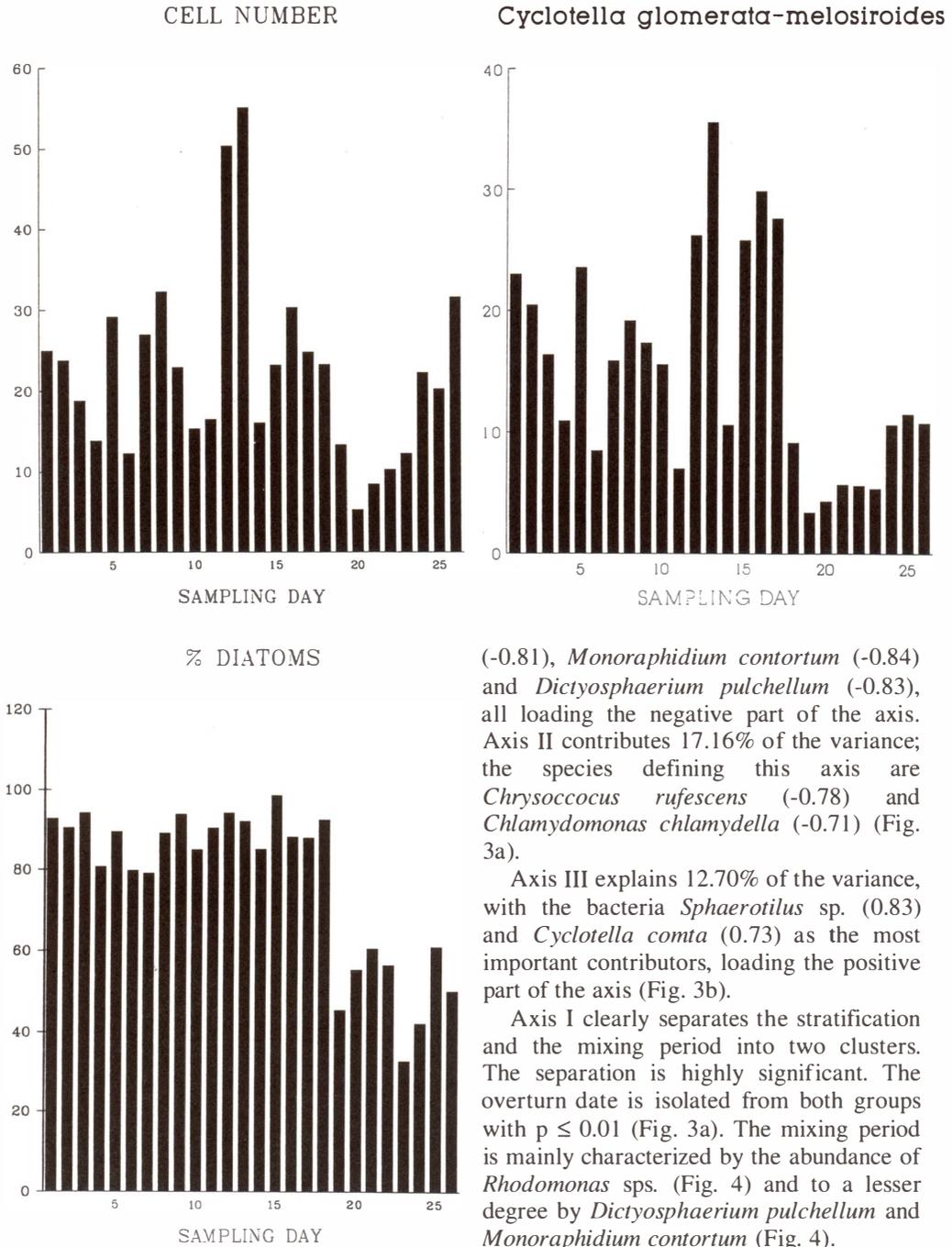


FIGURE 2. Temporal evolution of Lake Banyoles variables: Cell number ($\text{cell m}^{-2} \times 10^9$), *Cyclotella glomerata-melosiroides* ($\text{cells m}^{-2} \times 10^9$), and percentage of diatoms.

(-0.81), *Monoraphidium contortum* (-0.84) and *Dictyosphaerium pulchellum* (-0.83), all loading the negative part of the axis. Axis II contributes 17.16% of the variance; the species defining this axis are *Chrysococcus rufescens* (-0.78) and *Chlamydomonas chlamydelta* (-0.71) (Fig. 3a).

Axis III explains 12.70% of the variance, with the bacteria *Sphaerotilus* sp. (0.83) and *Cyclotella comta* (0.73) as the most important contributors, loading the positive part of the axis (Fig. 3b).

Axis I clearly separates the stratification and the mixing period into two clusters. The separation is highly significant. The overturn date is isolated from both groups with $p \leq 0.01$ (Fig. 3a). The mixing period is mainly characterized by the abundance of *Rhodomonas* sp. (Fig. 4) and to a lesser degree by *Dictyosphaerium pulchellum* and *Monoraphidium contortum* (Fig. 4).

Axis II separates the sampling period around overturn into two groups; the sampling dates before overturn, and those after it. This period is characterized by a

relatively greater abundance of *Chrysococcus rufescens* (Fig. 5a). The greater abundance of *Chlamydomonas chlamydeila* (Fig. 5b) in the overturn period isolates this date from the other clusters.

Axis III separates the sampling dates where *Cyclotella comta* was more abundant (Fig. 5c). These correspond to the samples taken at the beginning of the stratification period. At that time there was a proliferation of the bacteria *Sphaerotilus* sp.

In Lake Sanabria (LS) the first three axes of the PC-PCA explain 81.86% of the variance. The variables loading the positive and negative part of the first axis (40.35% of the variance) are CN (0.76) and SD (-0.75) respectively.

Axis II contributes 25.16% of the variance. The variables which define the positive side of the axis are nutrients: NO_3 (0.72) and PO_4 (0.62). Axis III explains 16.35% of the variance. The descriptor highly associated with the negative part of this axis is CHL (-0.71).

The first axis in the PC-PCA of this lake (LS) mainly separates 1974 stratification dates from the mixing period. Axis II discriminates objects corresponding to the 1973 late summer period (Fig. 6a) when PO_4 was high (Fig. 7a) from winter samples with high NO_3 concentrations (Fig. 7b). Axis III discriminates objects with high CHL concentrations (Fig. 7d).

The spatial distribution of the objects in the three axes could be clustered into four groups. Statistically, Groups 1 and 2 are very highly significantly different; 3 and 4, highly significantly. The first cluster includes samples with high PO_4 and CHL. The sampling dates clustered in 2 are characterized by high transparency (Fig. 7c) or high NO_3 . In Cluster 3 the sampling dates are characterized by high CN (Fig. 9a) and in Cluster 4 by elevated PO_4 concentration. If we eliminate Cluster 4, its objects are absorbed into Cluster 3, in the positive part of the axis (Fig. 6a). The difference between the three remaining groups thus becomes very highly

significant.

In the principal component analysis of LS, using phytoplankton species composition to separate objects, the first 5 axes explain 75% of the variance. Axis I contributes 21% of the variance. The species loading the negative and positive

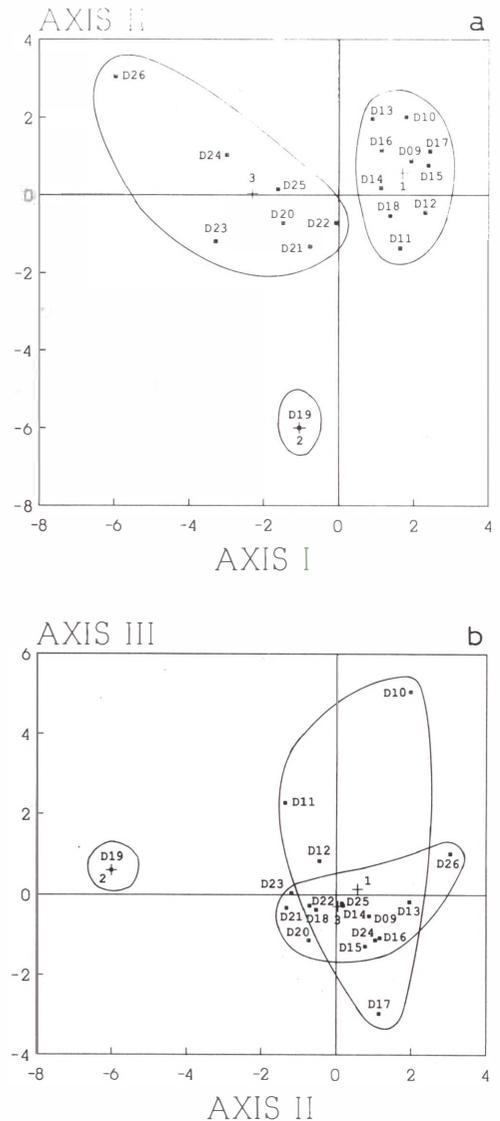
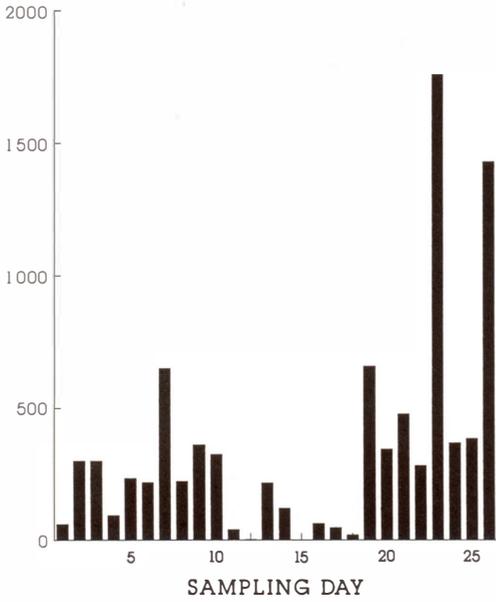
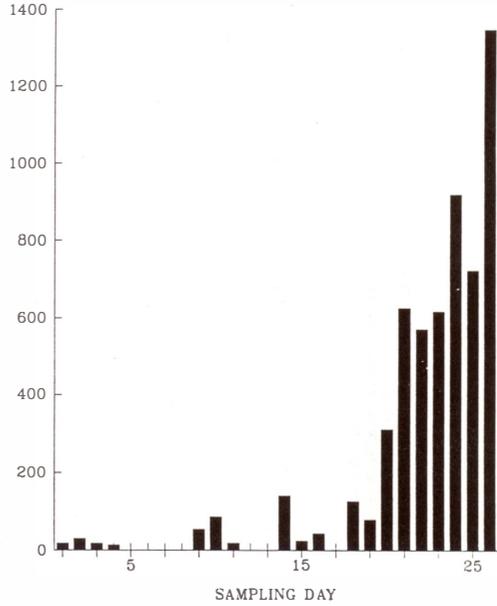


FIGURE 3. Lake Banyoles sample distribution using species composition as descriptors. (a) Axes I and II, (b) Axes II and III. For identification of object numbers, see Table I.

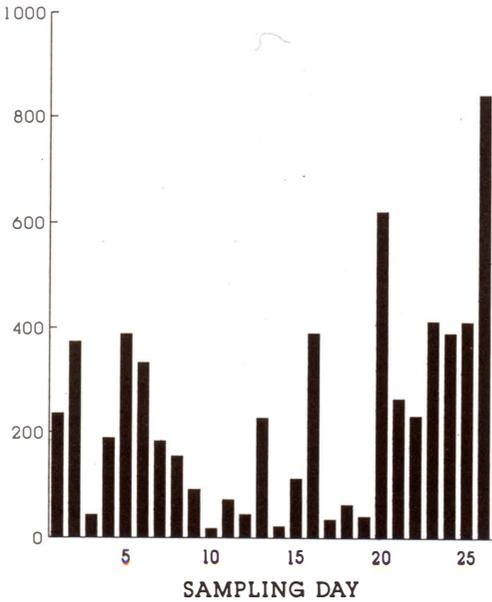
Rhodomonas minuta



Rhodomonas minuta var. *nannoplanctonica*



Monoraphidium contortum



Dictyosphaerium pulchellum

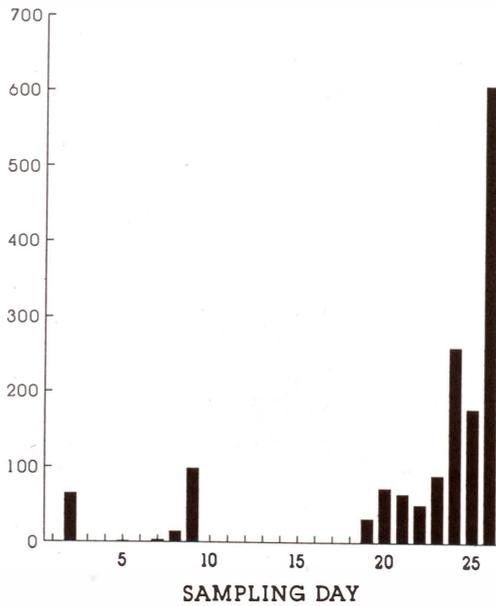


FIGURE 4. Temporal evolution of Lake Banyoles species loading the first axis (cells m⁻² x 10⁶): *Rhodomonas minuta*, *R. minuta nannoplanctonica*, *Monoraphidium contortum* and *Dictyosphaerium pulchellum*.

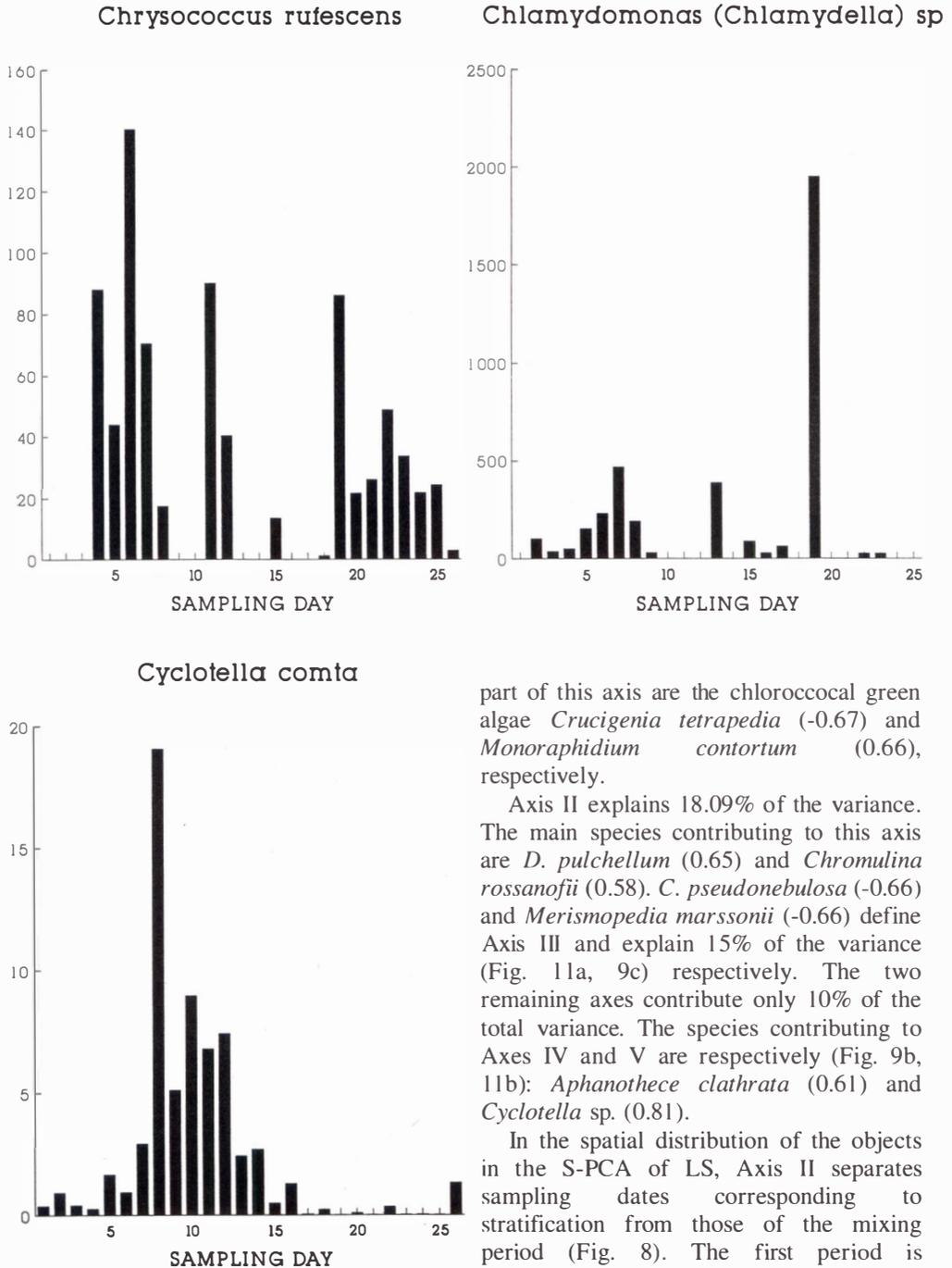


FIGURE 5. Temporal evolution of the species (cells m⁻² × 10⁶) loading Axes II and III: *Chrysococcus rufescens*, *Chlamydomonas chlamydella*, and *Cyclotella comta*.

part of this axis are the chlorococcal green algae *Crucigenia tetrapedia* (-0.67) and *Monoraphidium contortum* (0.66), respectively.

Axis II explains 18.09% of the variance. The main species contributing to this axis are *D. pulchellum* (0.65) and *Chromulina rossanofii* (0.58). *C. pseudonebulosa* (-0.66) and *Merismopedia marssonii* (-0.66) define Axis III and explain 15% of the variance (Fig. 11a, 9c) respectively. The two remaining axes contribute only 10% of the total variance. The species contributing to Axes IV and V are respectively (Fig. 9b, 11b): *Aphanothece clathrata* (0.61) and *Cyclotella* sp. (0.81).

In the spatial distribution of the objects in the S-PCA of LS, Axis II separates sampling dates corresponding to stratification from those of the mixing period (Fig. 8). The first period is characterized by the abundance of *D. pulchellum* (Fig. 10c). Axis I contributes to separating the summer dates where *C. tetrapedia* presents its maximum density

(Fig. 10a), from samples where for the same period in the former year *Cyclotella* sp. was very abundant (Fig. 11b).

The spatial distribution of samples in Axes II and III (Fig. 8b) is determined by the absence of *C. pseudonebulosa* (Fig. 11a). Its cell density was greatest in the summer of 1974, especially from August to September.

DISCUSSION

The phytoplankton species richness in Lake Sanabria was higher than in Lake Banyoles: 232 and 77 species respectively. The first lake could be characterized as a myxophycean plankton lake, the second as a diatom plankton lake (HUTCHINSON, 1967). Cyanobacteria of the chroococcal order dominated Lake Sanabria throughout the year (Planas, unpublished data); the more abundant species were *Aphanothece clathrata* and *Merismopedia marssonii*. In Lake Banyoles the diatoms *Cyclotella glomerata* and *C. melosiroides* were dominant during the whole study period (PLANAS, 1973; Fig. 2b).

The dominance of diatoms in the

silica-rich, alkaline Lake Banyoles (Fig. 2c) was to be expected, although diatoms could have been limited by other nutrients or by light (KILHAM *et al.*, 1986). HUTCHINSON (1967) characterizes oligotrophic diatom plankton as being present in nutrient-poor lakes with neutral or slightly alkaline water.

The dominance of cyanobacteria in Lake Sanabria is more striking. Some species of these algae are normally associated with waters low in nitrogen, as is the case of the nitrogen fixing species which dominate in eutrophic ecosystems where phosphorus concentrations are high (SCHINDLER, 1978). They are also very abundant at high phosphorus and nitrogen concentrations (VOLLENWEIDER, 1968). However, these trophic characteristics do not correspond to Lake Sanabria, which, as we mentioned before, might be classified as oligotrophic. The two chlorococcal species that dominate this lake are very abundant in the low conductivity waters of the Canadian Shield (Planas, personal observation), especially after the spring outburst when nitrogen and phosphorus are not detectable in the water. These Canadian shield lakes are naturally quite rich in dissolved organic matter, as is

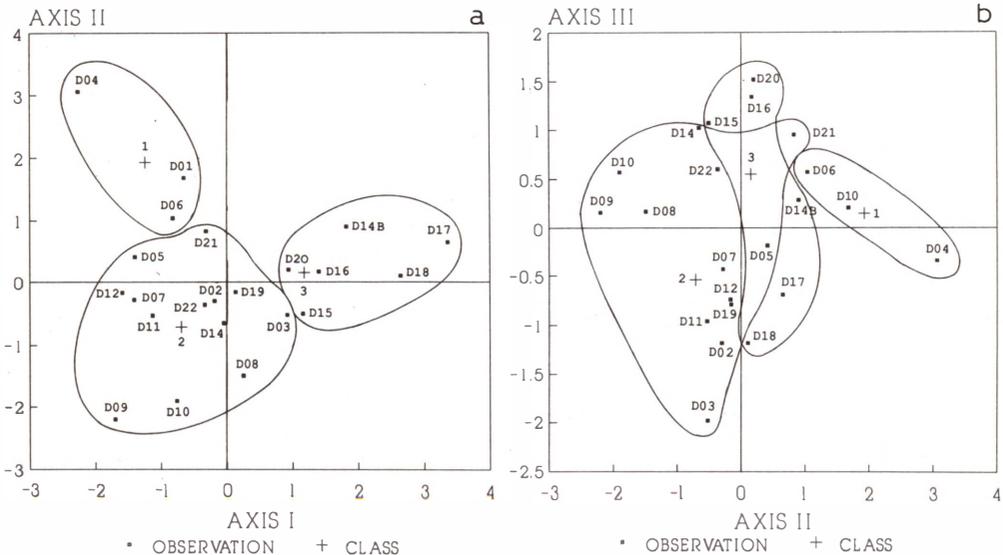


FIGURE 6. Lake Sanabria sample distribution using the physico-chemical and biological variables. (a) Axes I and II. (b) axes II and III. Points, observations; crosses, classes. For identification of object numbers, see Table I.

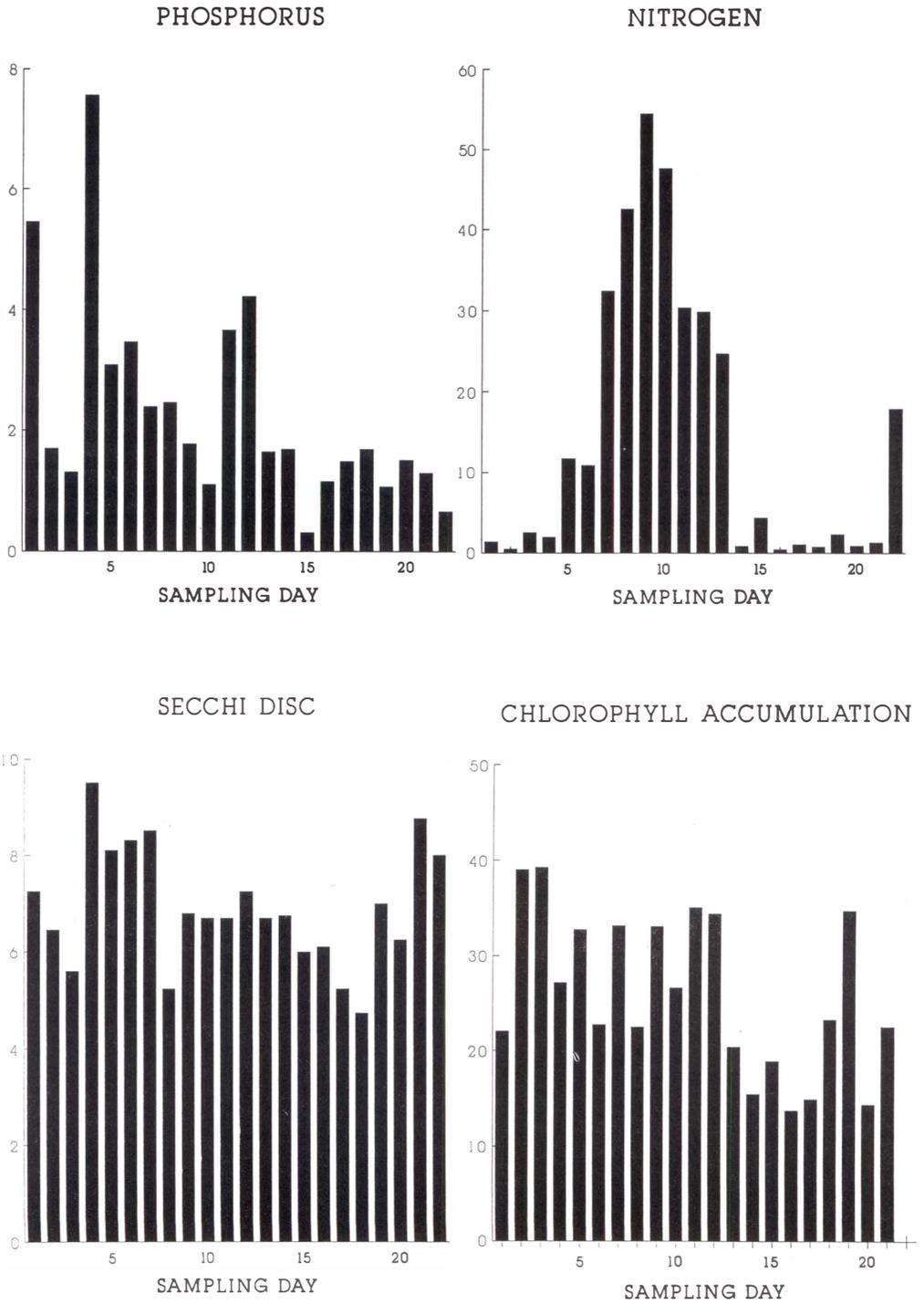


FIGURE 7. Temporal evolution of Lake Sanabria variables: phosphate (mM m^{-2}), nitrates + nitrites (mM m^{-2}), Secchi disc depth (m) and chlorophyll-a (mg m^{-2}).

the case of Lake Sanabria (Planas, unpublished data). It has been mentioned in the literature, on several occasions and for different parts of the world, that planktonic blue-greens are favoured by dissolved organic matter (FOGG *et al.*, 1973). This, however, does not imply that such compounds are needed by cyanobacteria, as the same authors show that no freshwater cyanobacteria species require exogenous organic growth factors.

For both lakes and particularly for Lake Banyoles, we cannot speak of true succession, at least not in reference to the dominant species, since they were present throughout the study period. Phytoplankton succession is a general phenomenon observed not only in temperate lakes (HUTCHINSON, 1967; REYNOLDS, 1984) but also in tropical and subtropical lakes, if one can rely on the little information that exists (GANF & VINER, 1973; MELACK, 1979; LEWIS, 1978 a, b; HECKY & KLING, 1981).

The two dominant cyanobacteria species of LS constitute more than 50% of the total cell counts during lake stratification and early mixing. *M. marssonii* was more

abundant at the beginning of stratification than *A. clathrata* but the latter species attained its maximum in October 1974. HUTCHINSON (1967) mentions that *Aphanothece* sp. develops in productive lakes of temperate regions during the warmest month, usually when the combined nitrogen in the water is low and PO₄ undetectable. This does not correspond to the conditions found in LS during the summer, where the species was most abundant when PO₄ was either detectable or at its maximum. *Merismopedia* are generally considered to be oligotrophic indicators (DROUET & DAILY, 1956).

In LB the dominant species (Fig. 2b) constitute 90% of the population from early spring to overturn. Thereafter they decrease to 20-50% of the total cell number (Fig. 2b; PLANAS, 1973) but continue to be dominant. According to Grim's study of Lake Constance (GRIM, 1939) the same diatom species were dominant throughout the year. The author mentions that the only non-diatom species with a significant contribution was the cryptomonad *R. lacustris*, which was abundant towards the end of the winter when the temperature of

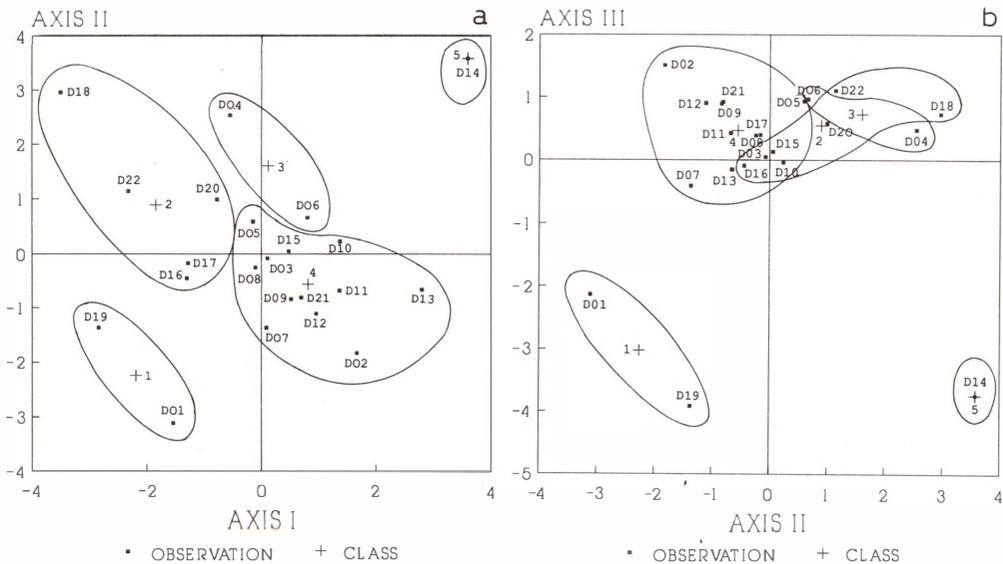


FIGURE 8. Lake Sanabria sample distribution using species composition as descriptors. (a) Axes I and II, (b) Axes II and III. Points, observations; crosses, classes. For identification of object numbers, see Table I.

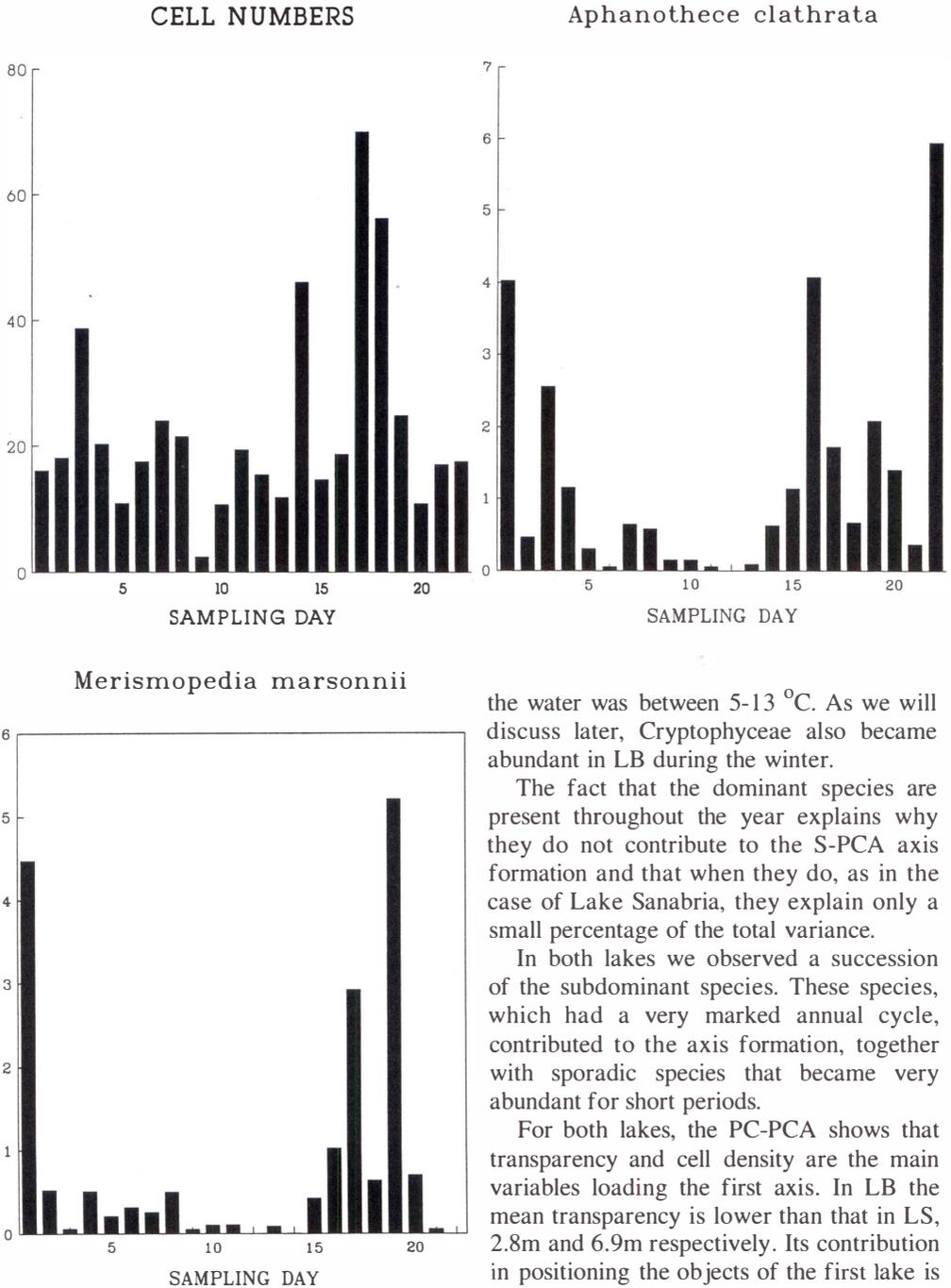


FIGURE 9. Temporal evolution of Lake Sanabria phytoplankton density ($\text{cell m}^{-2} \times 10^9$) and dominant species: *A. chlathrata* ($\text{colonies m}^{-2} \times 10^9$), and *Merismopedia marsonnii* ($\text{colonies m}^{-2} \times 10^9$).

the water was between 5-13 °C. As we will discuss later, Cryptophyceae also became abundant in LB during the winter.

The fact that the dominant species are present throughout the year explains why they do not contribute to the S-PCA axis formation and that when they do, as in the case of Lake Sanabria, they explain only a small percentage of the total variance.

In both lakes we observed a succession of the subdominant species. These species, which had a very marked annual cycle, contributed to the axis formation, together with sporadic species that became very abundant for short periods.

For both lakes, the PC-PCA shows that transparency and cell density are the main variables loading the first axis. In LB the mean transparency is lower than that in LS, 2.8m and 6.9m respectively. Its contribution in positioning the objects of the first lake is low. SD is more important in Lake Sanabria where it distributed the sampling dates around overturn. Overturn corresponds to the period of maximum

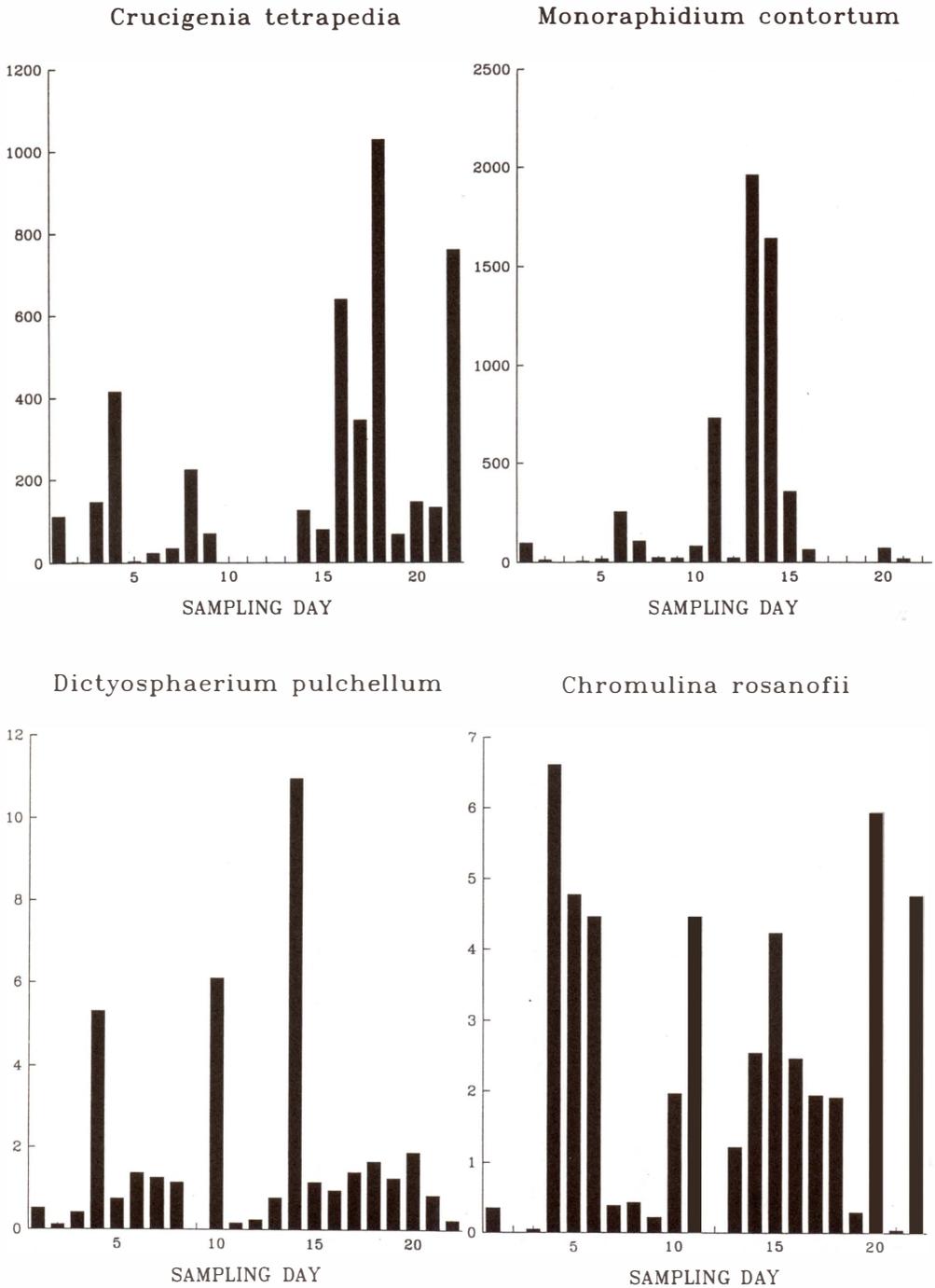


FIGURE 10. Temporal distribution of Lake Sanabria species loading the first two axes: *Crucigenia tetrapedia* (cells m⁻² x 10⁶), *Monoraphidium contortum* (cells m⁻² x 10⁶), *Dictyosphaerium pulchellum* (cells m⁻² x 10⁹), and *Chromulina rosanofii* (cells m⁻² x 10⁹).

transparency in this lake.

As stated above, cell numbers also contribute to the formation of Axis I. It is interesting to note that the two variables which contribute to Axis I have different signs in each lake. In LB both variables loaded the same sign of the axis, whereas in Sanabria SD loaded the negative part of the axis and CN the positive. The factors which contribute to light transmission in each lake could explain this difference. During our study cycle of LB, suspended matter increased after overturn due to a high underwater inflow during the autumn rains (PLANAS, 1973). The transparency then remained very low until the next summer stratification. In Lake Sanabria transparency seems related more to phytoplankton abundance, although not to biomass as measured by CHL. In both lakes, the maximum in CN occurred in the summer. The smaller size of the dominant species in LS probably induced more light

scattering than the diatoms which dominated LB.

Nitrogen contributes to Axis II formation in both lakes. This nutrient was more abundant in winter than in summer, both in LB and LS. In the latter lake, NO₃ increased after overturn and remained relatively high until spring. In LB, although a slight increase occurred during the fall overturn, NO₃ became really abundant only in January when the lake mixed completely (PLANAS, 1973, 1990). In LB, primary production as well as NO₃ load the negative part of Axis II. Although the maximum of PP in this lake occurs in the spring, another maximum is present in winter concurrent with the nitrogen increase (PLANAS, 1990). Both variables thus seem to influence the positioning of the same sampling stations.

In LS, besides NO₃, phosphorus also contributes to Axis II, but in the opposite direction. It increases slightly during

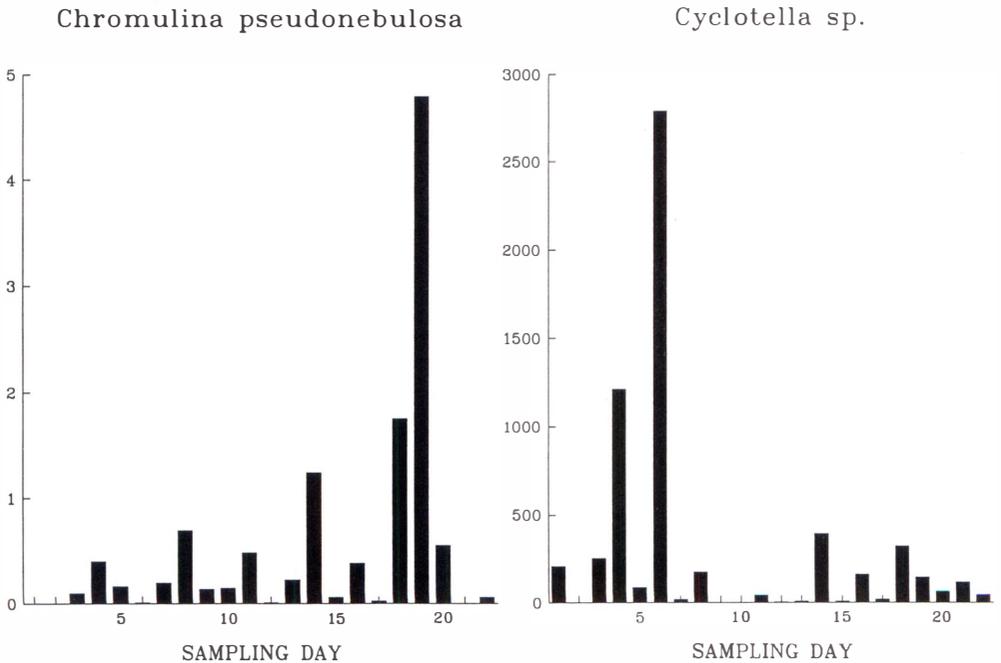


FIGURE 11. Temporal distribution of Lake Sanabria species loading Axis III: *Chromulina pseudonebulosa* (cells m⁻² x 10⁶), and Axis V: *Cyclotella* sp. (cells m⁻² x 10⁶).

overturn but attains its maximum towards the end of the summer of 1973, which does not correspond at all to the nitrogen pattern.

In Lake Sanabria, Chlorophytes, which as a taxon contributed the greatest percentage of identified species (Planas, unpublished data), were the most important in defining Axes I and II. *Crucigenia tetrapedia* is a summer species more abundant in 1974 than in 1973. It explains the formation of Cluster III. The sampling data of this period were characterized by very low NO_3 and moderate PO_4 concentrations; the biomass as measured by chlorophyll-a was high.

Dictyosphaerium pulchellum was most abundant towards the end of the mixing period as well as at the end of the stratification. *Monoraphidium contortum* was abundant during the whole winter. These species position a few objects characterized by either higher PO_4 or NO_3 concentrations.

The Chrysophyceae and the Cyanobacteria contributed to the formation of Axis III in the S-PCA of SL. *Chromulina pseudonebulosa* had a pulse in the second part of the summer of 1974 when PO_4 and NO_3 concentrations were very low and biomass (measured as chlorophyll-a) was relatively high. *M. marssonii* became abundant at the same period. Its abundance during a period when both nutrients were low confirm its capacity for growth in poor waters (DROUET & DAILY, 1956).

Aphanothece clathrata defines the spring data with relatively low biomass, when NO_3 is becoming scarce and phosphorus less abundant. This species has been found in small productive lakes (REYNOLDS, 1984) but as mentioned before its presence is associated with low nutrient concentrations. This fact, as well as its abundance in ultra-oligotrophic lakes of the Canadian Shield, suggest that this species can develop in waters very low in phosphorus and nitrogen, independently of water temperature, contrary to the statement

made by HUTCHINSON (1967).

In Lake Banyoles the subdominant species that characterize the mixing period are species very abundant in winter such as *Rhodomonas minuta*, *R. minuta nannoplanctonica* and the two green species also abundant in LS during this period, *D. pulchellum* and *M. contortum*. The two green species characterize samples clustered in Group III. They correspond to environmental conditions where Si and NO_3 are abundant, and PO_4 relatively low. Maximum density for the Cryptophyceae occurs when NO_3 concentration is at its peak and PO_4 is still low. As mentioned for Lake Constance, the *Rhodomonas* sps. are usually very abundant in winter, in oligotrophic lakes of temperate regions. We do not think that temperature is the variable that controls its growth but that nitrogen could be a more important factor. In the acidifying lakes of North America (YAN, 1978), where 1/3 of the acidity of rain is due to NO_x (LIKENS *et al.*, 1979), the Cryptophyceae generally increase during the summer. This would seem to confirm the importance of nitrogen in the proliferation of this taxon.

The sampling dates characterized by *Chrysococcus rufescens* and *Chlamydomonas chlamydes* correspond to a period of low productivity in LB. This low productivity was associated with low nitrogen concentrations (Planas, in press). The first species was more abundant at the beginning of stratification and the second at overturn.

The species that contributed to Axis III appeared sporadically at the beginning of stratification. *Sphaerotilus* sp. had a very short pulse; *Cyclotella comta* persisted longer, until the middle of stratification. These species characterize the sampling dates corresponding to a period of high transparency. They also become abundant in Lake Constance towards the end of the summer (GRIM, 1939). In this lake their outburst correspond to a decrease in the dominance of *C. melosiroides* and *C.*

glomerata, but this is not the case in LB where the maximum of *C. comta* occurred when the dominant species were very abundant, just prior to their peak.

In summary, the nutrient which seems to control the succession in species composition in the two lakes studied is nitrogen. This element is relatively low in both ecosystems during the summer and becomes more abundant at overturn. Phosphorus (measured as total dissolved reactive phosphorus) seems to have relatively less importance in the species composition evolution. In both lakes the concentration of this nutrient seems related more to recycling in the water column or its inflow by surface runoff, than to fluxes from the sediments or deep hypolimnetic waters. This would explain the relatively constant phosphorus concentrations, independent of the lakes' temperature regime.

Nitrogen, on the contrary, has a very marked cycle and its abundance in the euphotic zone seems more closely associated with water turnover. It is striking that in both lakes its low concentrations during the summer do not favor the nitrogen fixing cyanobacteria. It is probable that the affinity of these cyanobacteria to phosphorus is very low and consequently the concentration present in both lakes did not satisfy their needs. The abundance of phosphorus during the mixing period might possibly explain the appearance or increase of the same green algae species (*M. contortum*, *D. pulchellum*) in both lakes during the winter.

The chemical differences in the two lakes considered, an alkaline and a moderately acidic lake, seem to determine the type of phytoplankton at the dominant species level. In the alkaline lake, the availability of silica and possibly other minor ions determine its diatom dominance throughout the year.

The dominance of Cyanobacteria in Lake Sanabria is more difficult to interpret. In this lake, silica and phosphorus

concentrations are lower than in Lake Banyoles. Silica, due to its relatively constant concentration, does not seem to be a determining factor in phytoplankton succession, but the low concentration of phosphorus could be. In Lake Sanabria phosphorus concentration was half that measured in Lake Banyoles. In studies carried out by SUTTLE & HARRISON (1988) on the natural phytoplankton populations of two ultraoligotrophic lakes of the Rocky Mountains with nutrient characteristics close to those of Lake Sanabria, a chroococcal cyanobacteria (*Synechococcus*) showed the highest affinity to phosphorus; this species could develop at very low phosphorus concentrations contrary to the diatoms, which are better competitors at low nitrogen levels.

These findings could explain the dominance of the blue-greens and the scarcity of diatoms in Lake Sanabria as well as the abundance of diatoms in Lake Banyoles but, as was mentioned before, the water alkalinity and the high abundance of silica could also be determining factors.

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