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Annual cycles of plankton species composition and physical chemical conditions in Slapy Reservoir detected by multivariate statistics

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With 8 figures and 2 tables in the text

Abstract

Data on phytoplankton and zooplankton species composition and abundances as well as on physical and chemical conditions from Slapy Reservoir were treated by different methods of multivariate statistics. Three to four consecutive years with rather diversified, extreme hydrological conditions were elaborated. The following multivariate methods were used: classification of samples (dissimilarity: Euclidean distance; hierarchical clustering: WARD'S method and average linkage), classification of species and physical – chemical factors (similarity: correlation coefficient, hierarchical clustering: average linkage) and ordination (by principal component analysis, correspondence analysis and constrained ordinations: redundancy analysis and canonical correspondence analysis). In addition, the method of classification of sequences was used, for the first time for limnological data.

Agglomerative classification of samples based on standardized data yielded five distinct groups: winter samples, late winter to spring samples, mainly summer samples, full summer samples and the winter *Closterium* aspect. Other classifications, although differing, follow the basic seasonal pattern.

In the ordination space defined by two principal component axes, three community compositional patterns were distinguished for phytoplankton: the September to April with low biomass of many species, the May peak characterized by the *Cryptomonas* aspect and the June – August peak with Chlorophyta and blue-greens. The summer peak composition was different for the three years observed. In the dry years with strong stratification blue greens were highly developed, whereas during the most wet years with reduced stratification a strikingly low phytoplankton biomass was observed.

Introduction

Dynamic models are used primarily on the level of large groups, like total phytoplankton, zooplankton etc., where the causal and dynamical relationships may be (at least roughly) estimated and/or studied experimentally. When we are seeking for spatial or temporal patterns in species composition, the causal relationships are less obvious and statistical rather than causal description is more appropriate. Both the community composition and environmental characteristics are typically multivariate variables and hence, the methods of multivariate statistics come in question. They are used particularly in plant community ecology to detect compositional patterns and/or linkage between species composition and environmental conditions. In hydrobiology, these methods were used by ALLEN & KOONCE (1973) and MARGALEF (1975) for phytoplankton and then by many other authors. The studies by BREZONIK & SHANNON (1971) or RECKHOW (1978) are

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examples for a typical use of these techniques in water quality investigations. Two basic approaches may be used – classification and (both direct and indirect) gradient analysis. According to TER BRAAK (1987) the multivariate methods of indirect gradient analysis are called (unconstrained) ordinations and methods relating species composition to multivariate environmental data constrained ordinations. In direct gradient analysis, the species composition is related directly to environmental variables, whereas in the indirect one, the ordination axes are extracted on the basis of species composition only. The use of methods of multivariate gradient analysis (particularly those of the direct one) was promoted by the appearance of new powerful techniques, which are included in the CANOCO computer program package (TER BRAAK 1987).

Four years which differed most profoundly with respect to hydrology were selected for the study. Limnological conditions in the Slapy Reservoir depend heavily on discharges and retention times (STRAŠKRABA et al. 1973). Therefore, two hydrologically extreme types of years were selected: the dry year 1964, which was immediately followed by the extremely wet years 1965 and 1966. An incomplete data set from 1967, a fairly dry year, was also analyzed for some examples. The aim was to follow differences in the patterns in years with similar discharges and in years characterized by a highly aberrant throughflow.

Phytoplankton samples represent euphotic zone values; they were obtained by means of a 4 m tube (JAVORNICKÝ & KOMÁRKOVÁ 1973). The 36 species or species groups distinguished are listed in Table 1. Our evaluation of importance is based on biomass of particular species [g. m^{-3} or mg. l^{-1} fresh weight]. The biomasses differ considerably both between samples and between species.For computations, the values were subject to logarithmic transformation (transf. (x) = log (x + 1)).

A set of 14 environmental limnological variables was used (temperature, transparency, DO, BOD_5, conductance, alkalinity, pH, nitrate N, NH_3–N, total N, phosphate P, total P, total biomass of Cladocera and of zooplankton, for details see PROCHÁZKOVÁ et al. (1973). For application of methods of gradient analysis, all limnological environmental data were standardized and centred to zero mean and the unit standard deviation or the standardization was implicit in the method.

Gradient analysis

Most of methods of multivariate gradient analysis are based either on the linear response model or on the unimodal response model (cf. TER BRAAK (1987). The first one expects the linear response of species importance to environmental gradient. The second model expects, that species have an optimum on the (composite) environmental gradient. Of methods based on the linear model, principal components analysis (PCA) was used for indirect, and redundancy analysis (RDA) for direct gradient analysis. Two variants were calculated: – with data standardized by sample norm and without standardization. Both centred (by species) and noncentred PCA were used. The standardization by a sample norm removes the effect of total biomass changes on the resulting ordination and only the species composition plays role in the standardized analysis. Of methods based on unimodal response model, the correspondence analysis (CA) was used for indirect and canonical correspondence analysis (CCA) for direct gradient analysis. Both methods were applied in two versions: standard and "detrended" (i. e. DCA and DCCA). Note, that in these methods, the standardization is implicit and the results are not affected by differences in the total biomass. All the analyses were performed using the CANOCO program (TER BRAAK 1987).

Classification

Both the **agglomerative** and **divisive** strategies were applied for classification of samples. In the agglomerative approach, the Euclidean distance, both standardized (chord distance, ORLÓCI 1978) and unstandardized distances were used as between sample dissimilarity measures. We have used WARD'S procedure (minimal dispersion) for **hierarchical clustering**. The correlation coefficient was used as the similarity measure and average linkage clustering was applied for classification of limnological environmental variables. Divisive classification was performed by the two way indicator species analysis (using the program TWINSPAN, HILL 1979).

The **classification of sequences** was used to evaluate the similarity of particular years. Two step procedure was applied. At the first step the hierarchical classification of all samples from all the years was carried out. Based on this classification, each sample is assigned to a particular group. The cut off level for defining the groups was selected on the basis of ecological interpretability of classification. Each year is then represented by a sequence of states, i. e. the sequence of groups to which the particular samples were assigned. Two approaches were used for measuring dissimilarity of sequences. The first one is based on similarity of transition matrices (DALE et al. 1970). In the second one, the similarity was expressed using the longest common substring of two strings (equivalent to Levenshtein metric, as used by LITTLE & ROSS 1985) adjusted to the length of strings under comparison. The average linkage clustering was then constructed on the similarity matrix.

Table 1. Phytoplankton species and species groups distinguished. For each species an abbreviation used in consequent figures is given.

Anabaena circinalis	Ac
Anabaena flos-aquae	Aa
Aphanizomenon flos-aquae	Aq
Asterionella formosa	Af
Ceratium hirundinella	Ch
Chlamydomonas	Ca
Chlorophyta large (particularly *Oocystis*)	Ol
Chlorophyta medium	Ch
Chlorophyta small	Cu
Closterium limneticum	Cl
Closterium polymorphum	Co
Cryptomonas curvata	Cc
Cryptomonas marssonii	Cm
Cryptomonas reflexa	Cr
Chrysococus sp.	Cs
Cyclotella comta	Cc
Diatomae medium size	Dm
Diatomae small	Ds
Fragilaria crotonensis	Fc
Gymnodinium large	Gl
Gymnodinium small	Gs
Melosira granulata var. angustissima	Ma
Melosira italica	Mi
Microcystis aeruginosa	Me
Microcystis incerta	Mi
Microcystis large	Ml
Nitzschia acicularis	Na
Peridinium aciculare	Pa
Peridinium inconspicuum	Pi
Rhodomonas pusilla	Cp
Scenedesmus sp.	Ss
Staurastrum sp.	St
Stephanodiscus hantzschii	Sh
Synedra acus	Sa
Trachelomonas volvocina	Tv

Results

Classification of basic limnological variables (Fig. 1) has shown a few groups of variables having similar seasonal occurrence in different years. One group consists of dissolved and abiotic particulate nitrogen and its forms. The group consisting of the two phosphorus forms is also obvious, and there is an inverse relation to the nitrogen group at a correlation level of – 0.5. Another major group represents the variables related to phytoplankton and its activity: phytoplankton biomass, pH and O_2. Related is also BOD_5, apparently due to the organic matter release by phytoplankton (STRAŠKRABOVÁ 1975). The zooplankton related variables seem to be nearly independent of the rest, however with a strong relation to temperature. This is perhaps due to the fact, that there is usually a summer zooplankton peak, but phytoplankton shows a depression due to zooplankton grazing at this time. Evidently the phase shift in the occurrence of phyto- and zooplankton, which we know from their dynamics, cannot be uncovered by the classification methods.

Agglomerative classification of particular samples of **phytoplankton species-biomass** data was performed in two ways: with standardized and nonstandardized data. In both cases, the five-group cut-off level was accepted. The results of the two methods differ considerably and will be treated separately.

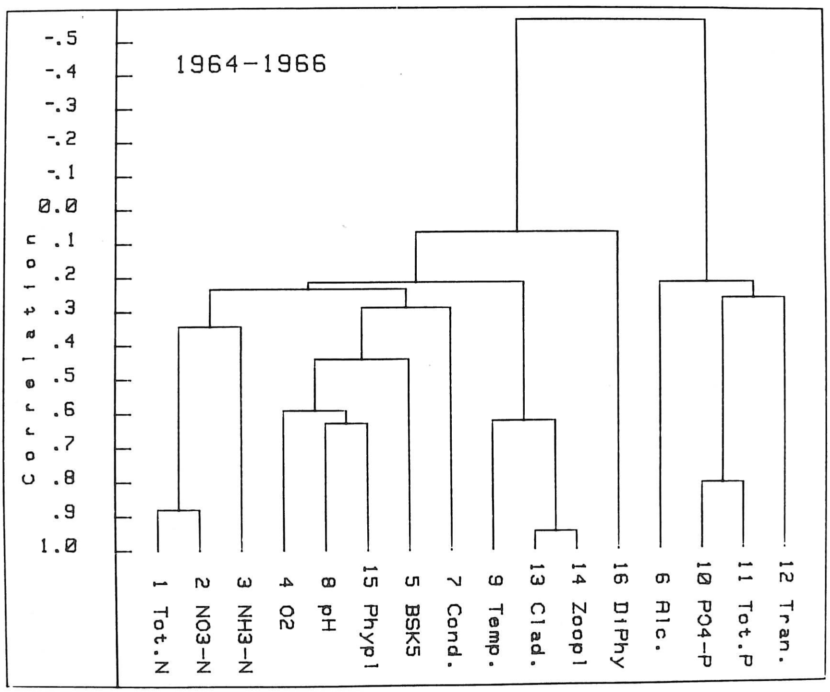

Fig. 1. Result of cluster analysis of the limnological variables (similarity measure: correlation coefficient, clustering algorithm: average linkage). BSK5 stands for BOD_5. Phypl stands for phytoplankton biomass, Diphy stands for phytoplankton diversity.

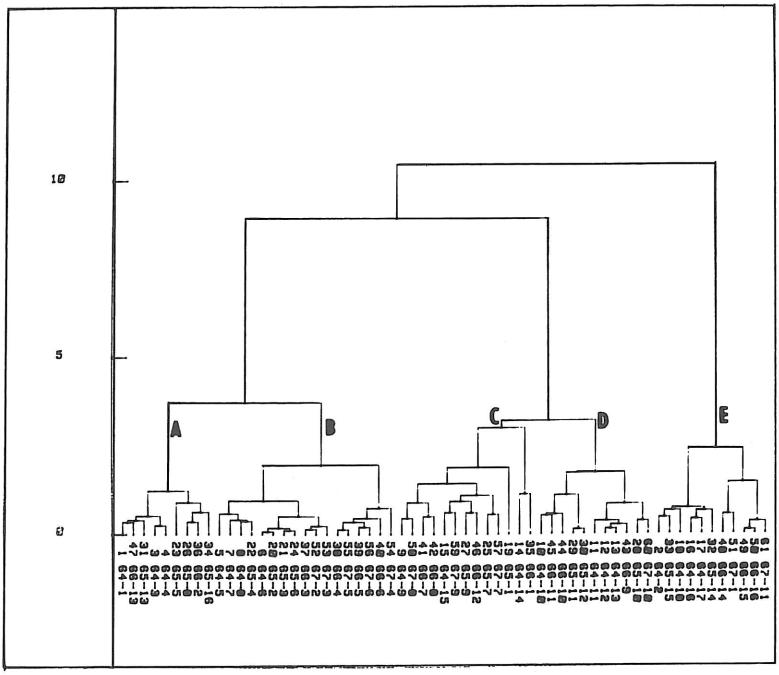

Fig. 2. Classification of particular samples for all four years. Similarity measure: standardized Euclidean distance, clustering algorithm: Ward's method. Every sample is marked by its serial number within the whole data set, year, and the serial number in each year.

Results based on standardized data (Fig. 2) show the following groups of samples:

a) Winter samples (mainly October to January) dominated by species of *Closterium* and *Scenedesmus* species (Group A in Fig. 2). The extraordinary position of the June 1965 sample in this group is caused by heavy throughflow of the reservoir, producing a very low total density of phytoplankton, comparable with winter values.
b) Late winter to spring (February to May) samples with an *Asterionella formosa* and *Cyclotella comta* aspect (Group B).
c) Mainly summer samples, often with blue-greens, but also some winter samples with a rather even species representation (Group C).
d) A homogeneous group of full summer (July to early September) samples with a high bloom of *Aphanizomenon flos-aquae*. (Group D).
e) Winter *Closterium* aspect (Group E).

The five groups obtained by treating the nonstandardized data are as follows:

a) Winter samples (October to February) with low biomass dominated by *Closterium* both *polymorphum* and *limneticum* and large and medium size Chlorophyta, mainly *Oocystis* sp. (Group A). Similarly to standardized data, this group includes also the June 1965 sample.
b) Spring to early summer samples (March to May) with a medium biomass represented by *Cryptomonas* (particularly *C. reflexa* and *curvata*) and also *Peridinium inconspicuum* (Group B).

c) Short spring phytoplankton peak following the previous period (late April to early May) but only in 1966 and 1967, characterized by the same species as in the previous group but with much higher biomass up to 12.00 mg. l^{-1} fresh weight (Group D).
d) Summer samples with biomass increasing up to more than 12.0 mg. l^{-1}, dominated by *Cryptomonas reflexa* and *marssonii*, *Asterionella formosa* and *Chlamydomonas* species (Group C). The occurrence of this group is divided into two periods, interrupted by group E.
e) Short summer period (July to August) of maximum biomass with large species like *Ceratium hirundinella* and the colonies of *Fragilaria crotonensis* (Group E).

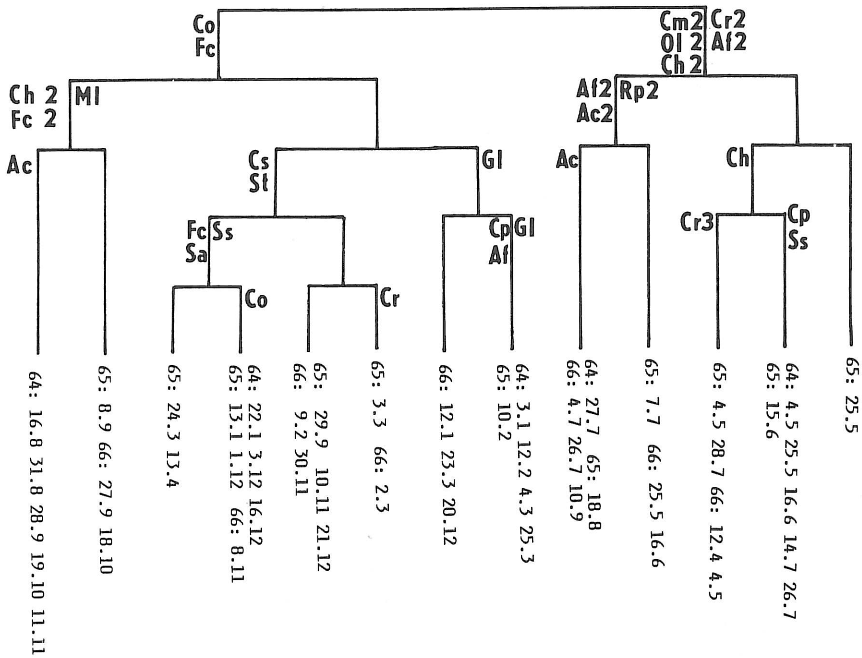

Fig. 3. The result of TWINSPAN classification. Each division is accompanied by indicator species characteristic for the given part of dichotomy. The two-letter symbols for particular species correspond to Table 1. Number 2 or 3 indicates that the species are characteristic only during biomass exceeding 10 or 100 mg. 1^{-1} fresh weight, respectively. Samples are labeled by year: day. month.

Divisive classification of phytoplankton (Fig. 3) was made only for the three complete years, 1964 to 1966. On the highest hierarchical level the summer group on the right side of the dendrogramm was clearly defined. It is characterized by high biomass of several species. However, a certain part of summer samples (those characterized by the high biomass of *Fragilaria crotonensis* and *Ceratium hirundinella*) was classified as a part of the other basic group. The other part of this group consists of all winter samples. On the lower hierarchival level the winter samples are subdivided mostly according to differences of individual years and their specific composition in this period. For example in the group marked by Gl the winter aspect of 1964 was separated mainly by *Rhodomonas pusilla*, *Gymnodinium* and *Asterionella*. The subdivision of the summer group also reflects differences between the years.

The **confrontation of** the two quantitative agglomerative **classifications** with a qualitative estimate of phytoplankton sequence shows a more concise agreement with the one based on nonstandardized data. This is mainly due to the fact that the visual classification is affected by the absolute biomass values much more than by the differences in species representation. For instance, the distinction of group D in classification based on the nonstandardized data is based only on the absolute biomass values of the two dominant species. If so, the standardized classification may be more relevant for detecting the species abundance or biomass grouping. Therefore, the winter samples are here diversified into more groups, while the nonstandardized version reflect only the generally low biomass during the whole winter period.

Comparing the agglomerative and divisive classification we can see, that the latter reflects mainly the differences among years, whereas the former (particularly the standardized one) is mainly due to more or less regular appearence of species sequences with less emphasis on among years differences.

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NON-STANDARDIZED E.D.
1964: AAABBBBBCCEEEAAAAA
1965: AABAABCACECCAAAA
1966: AABBDDCCEECACAAA
1967: ABBBBDCCCEA

STANDARDIZED E.D.
1964: AEAABBBBCDDDDCCEEE
1965: CBBBABCACDDDAEEA.
1966: CABBBBCCDDDCAEEE
1967: EBBBBBCCCDE
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Fig. 4. Sequences of community types (labeled A to E) obtained by nonstandardized and standardized Euclidean distance classification. For standardized classification the types correspond to those given in Fig. 2.

The **classification of sequences of phytoplankton groups** (Figs. 4 and 5) was based on agglomerative classifications described above. Fig. 4 gives the observed sequences of groups A to E during the four observation years. Fig. 5 which represents the similarity among the sequences within different years shows a different result for standardized and nonstandardized data, for two different measures of sequence similarity (the longest common subsequence adjusted to length – LCS and information gain – IG). Except IG applied to standardized data, all classifications show two pairs of similar years: 1964 & 1967 and 1965 & 1966. This reflects the basic hydrological and stratification differences among the given years, as indicated in the introduction.

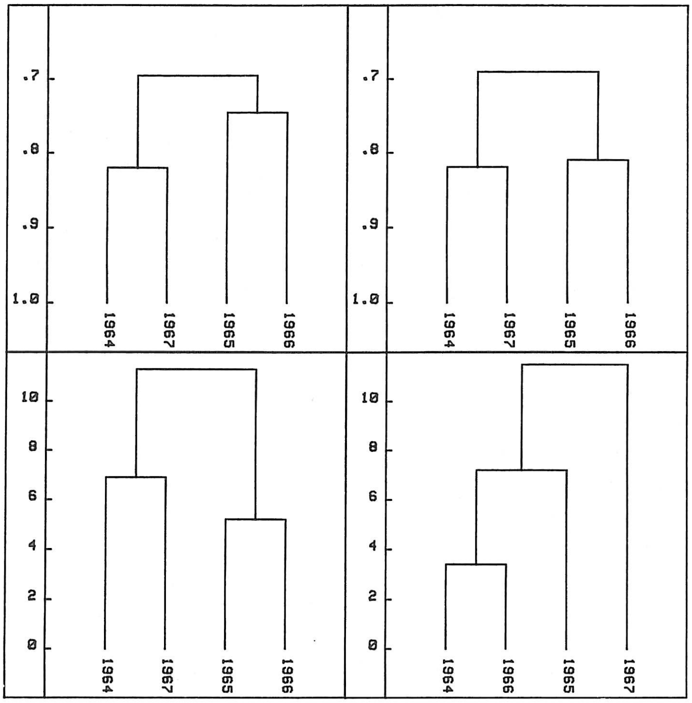

Fig. 5. Comparison of four classifications of sequences. The left column gives classifications based on nonstandardized Euclidean distance, the right one based on standardization. The upper row uses the longest common subsequence, the lower one the information gain (transition matrices).

The centred PCA **ordination** was performed separately for the limnological environmental variables and for the phytoplankton and zooplankton species-biomass composition. Only the three complete years of observation are covered. In all ordinations a characteristic pattern of annual trajectories in the ordination space defined by the two first ordination axes is repeated with some modifications for all three years. The extreme position of the summer samples is typical for the limnological characteristics (Fig. 6). It corresponds to high values of zooplankton biomass, Cladocera biomass, temperature and pH (variables with high factor loadings on the first axis and negative loadings on the second one). The rest of the trajectory is different for the dry year 1964 and both wet years. In 1964 the winter and spring samples are shifted to the lower left quadrant of the ordination diagram, whereas a cyclic pattern from fall through winter to spring is evident for the other years. The winter position corresponds to high phosphorus concentrations (both total and phosphate phosphorus, both variables with high negative loadings on the first axis). A particularly high extreme is seen for spring 1965 corresponding to high values of DO, BOD and nitrogen forms. Correlations with the differences in discharge conditions are therefore evident.

On the phytoplankton ordination diagram (Fig. 7) most conspicuous are the two peaks formed by the May and June to August samples. These peaks correspond to biomass maxima. The accumulation of all September to April samples around the first axis is due to

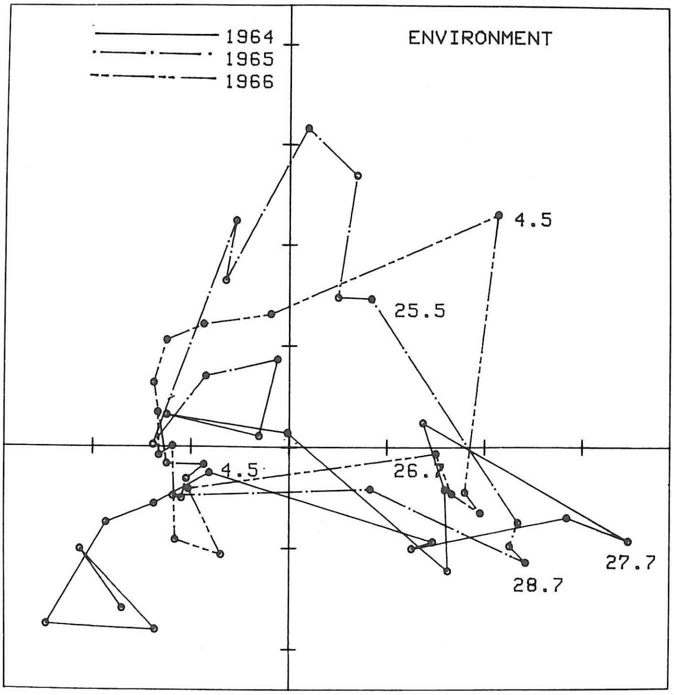

Fig. 6. Ordination diagram of centered PCA based on limnological environmental variables.

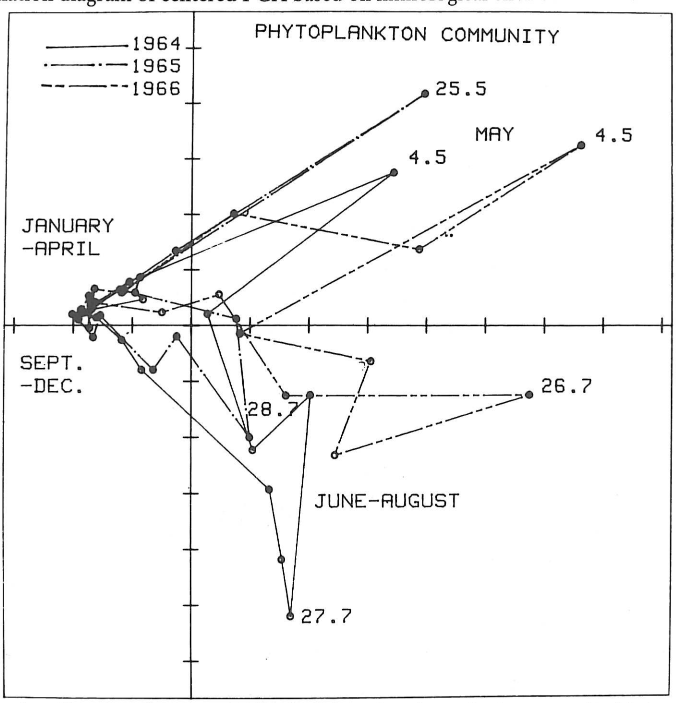

Fig. 7. Ordination diagram of centered PCA based on the phytoplankton species-biomass data.

data centering. The data remain highly skewed also after the log-transformation applied: there are many samples with fairly low biomass and only few high peaks.

The efficiency of four ordination methods and their constrained counterparts (Table 2) was compared for the same data sets on the basis of percentage of the total variance accounted for by the first S axes of the species-environment biplot. The limnological variables were included as well as phytoplankton species-biomass data. Note, that the species axes are related to environmental variables after the axes extraction for PCA, CA and DCA, whereas the axes are extracted in the way maximizing the correlation between the species and environmental axes for the constrained ordinations. Therefore, the percentage of the explained variance must be higher by definition than that for the unconstrained ordinations. The performance of methods based on the linear response model (PCA and RDA) is better than that of methods relying on the Gaussian response (CA, CCA, DCA and DCCA). For the Gaussian response methods, the detrending leads to a decrease of explained variance in both DCA and DCCA. Of the linear methods, the results based on nonstandardized data give higher values. This is mainly due to the inclusion of the obvious dependence of total biomass on the environmental limnological variables. Therefore, the results based on standardized data which follow only the species composition seem to be most important.

Table 2. Comparison of efficience of particular ordinations. Percentage of total variance accounted for by first S axes of the species-environment biplot. Note that for **PCA, CA** and **DCA** the species axes are related to environmental variables after axes extraction. **ns** means that analysis is based on nonstandardized data, **st** means standardization.

S	PCAns	RDAns	PCAst	RDAst	CA	CCA	DCA	DCAA
1	40.6	44.0	6.6	34.3	20.1	23.7	20.1	23.7
2	61.5	67.0	33.2	58.2	36.2	40.6	33.7	38.5
3	74.0	78.7	54.1	67.8	49.6	55.1	39.0	51.7
4	78.7	84.1	63.4	74.6	53.8	64.1	43.6	57.7

The species-environment biplot based on RDA using standardized data, which was shown to be the most relevant, is given in Fig. 8. In this Figure the most important limnological characteristics as well as the characteristic species can be recognized. The cyclic pattern is repeated for all three years, without any conspicuous peaks. Changes of biomass are more abrupt than changes of the relative species representation.

Discussion

The numerical classification and ordination of communities is perhaps most popular in phytosociology. However, after an initial enthusiasm the idea of numerical classification as the only objective method was omitted. A great amount of options exists, including various data transformations, relativizations, standardizations and various algorithms for ordination and classification (GAUCH 1982). Each of them leads to results different from those obtained by other methods while various data operations have some unique meaning. For example, with standardization to sample norm, the changes in total biomass are disregarded and only the species composition is taken into account. Various transformations

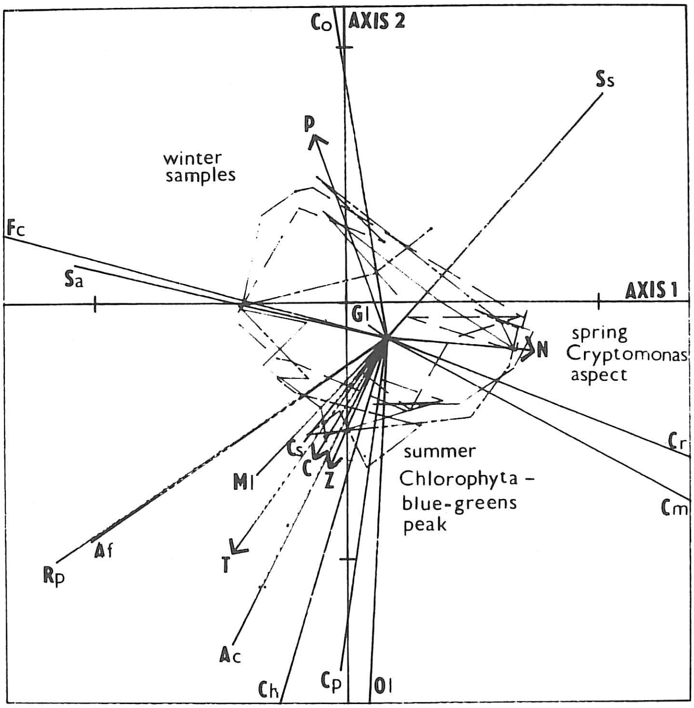

Fig. 8. Map of Pacific Northwest, U.S.A. showing location of Willow Creek Reservoir, Oregon.

weigh the relative importance of dominant and other species differently, affecting the final results considerably (ALLEN et al. 1984).

It was argued as soon as in early '70 (GRIGAL & GOLDSTEIN 1971) that only a combination of various methods is able to give unbiased results. Similarly, each of the methods used here has highlighted some other aspects of the seasonal cycles of environmental limnological variables and plankton species assemblages. Consequently, particular options have to be used intentionally for answering specific questions.

Each ordination method (either constrained or unconstrained) is based on some theoretical model of species response to a gradient. Obviously, for the more heterogeneous data sets the Gaussian response is expected to perform better, whereas for a homogeneous data set the linear response is more appropriate. In accordance with it FÄNGSTRÖM & WILLÉN (1987) found the DCCA to be very useful for their large data set from Swedish lakes, whereas in our study for one reservoir the RDA appears superior.

There are many reasons to apply multivariate statistics in limnology: to distinguish seasonal cycles of species assemblages (GOODMAN et al. 1984), to recognize the basic stratagems of algal ecology (e.g. ALLEN & KOONCE 1973), to distinguish between regional water body types (MARGALEF et al. 1982), to detect human impacted trends in a single water body (BAYBUTT & MAKAREWICZ 1981), to study spatial distribution of species assemblages (ARMENGOL 1984). The aim to recognize detailed temporal and/or spatial correlations between species assemblages and limnological environmental variables, which are difficult to recognize by inspection or by any other approach is common to all. Moreover we have added another more aim: in addition to distinction of seasonal cycles we are interested in between year differences in one water body, which are related to hydrometeorological changes producing deep differences in reservoir stratification and horizontal distribution.

The methods of multivariate statistics have appeared favourable for this goal: the differences in species assemblages among the years of different stratification have been recognized particularly by means of the principal component analysis and divisive classification.

Summary

1) The following methods of multivariate statistics were used: Classification of samples and of species and limnological environmental variables using different measures of similarity and/or dissimilarity (correlation coefficient and Euclidean distance) and of hierarchical clustering (WARD'S method and average linkage), ordination by principal component analysis, correspondence analysis, constrained ordination by redundancy analysis and canonical correspondence analysis. All data were log-transformed and both standardized and nonstandardized data were elaborated. A method of classification of sequences (two approaches) seems to be applied for the first time in limnology.

2) The analysis is based on selected years from Slapy Reservoir, characterized by the most extreme hydrological conditions. The years followed each other and no trend is assumed to bias the comparison of years with fairly different stratification: dry (and sunny) year with very pronounced stratification of temperature, dissolved oxygen and other variables and two wet (and calm) years with stratification nearly absent.

3) Annual cycles of phytoplankton and zooplankton assemblages and their relations to limnological environmental variables were based on species-biomass data. Major characteristic differences between the hydrologically and limnologically different years were encountered. In some instances the results were in agreement with the qualitative limnological ordination and classification while in others different results were obtained.

4) The inverse relationship between the occurrence of nitrogen and phosphorus forms is difficult to explain. The relationship of phytoplankton, oxygen, pH and BOD_5 is limnologically evident. The annual cycle of zooplankton and Cladoceran biomass appeared to be uncorrelated with phytoplankton but related to temperature. Evidently the dynamics cannot be discovered by the classification methods.

5) Agglomerative classification appeared to reflect mainly the regularities of the annual phytoplankton pattern, whereas divisive classification was more useful for detecting between year differences.

6) For our relatively homogeneous data set from one reservoir the ordination methods based on the model of linear dependence between limnological environmental variables and species-biomasses appeared to perform better than methods based on the Gaussian model.

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