Hydrobiologia **344:** 141–153, 1997.

Limnological survey of the warm monomictic lake Trichonis (central western Greece)

II. Seasonal phytoplankton periodicity – a community approach

T. Tafas & A. Economou-Amilli
University of Athens, Department of Biology, Section of Ecology & Systematics, Panepistimiopolis, Athens GR-15784, Greece

Received 17 April 1996; in revised form 14 November 1996; accepted 10 December 1996

Key words: phytoplankton, distribution patterns, species seasonality, diversity, multivariate analysis

Abstract

Phytoplankton assemblages of the warm monomictic lake Trichonis were studied during the period April 1985 to February 1986. Species composition and biomass data are presented along with information on the seasonal periodicity of dominant taxa of microalgae. Multivariate methods were used to analyze community structure and annual succession. Population succession patterns correspond to changes in environmental variables. According to the generalized phytoplankton sequences Trichonis is classified as an oligotrophic lake.

Introduction

Temporal variations in the abundance and composition of phytoplankton have been described in many aquatic ecosystems (see reviews in Hutchinson, 1967; Lund, 1969; Round, 1971, 1981; Kalff & Knochel, 1978; Reynolds, 1984a). A synthesis of similar seasonal events portraying the function of various regulating factors – physical, chemical and biological – has recently induced the development of conceptual models, such as the PEG model for lentic waters (Sommer et al., 1986) and the 'Riverstrahler' model for lotic environments (Billen et al., 1994). Multivariate analysis is a useful tool for providing adequate representation of underlying structures in biological data matrices (Field et al., 1982; Clarke & Green, 1988). This approach has been applied extensively in the study of algal assemblages (e.g. Thorrington-Smith, 1971; Bartell et al., 1978; Stewart et al., 1987; Leskinen & Sarvala, 1988; Goldman et al., 1990; Vyverman, 1992; Sorhannus, 1993).

In the case of the warm monomictic lake Trichonis (for limnological characteristics see Overbeck et al., 1982; Tafas, 1991; Tafas et al., 1997) information is restricted to the taxonomic description of interesting phytoplankton and periphyton species (Economou-Amilli, 1979, 1982; Kristiansen, 1980; Anagnostidis et al., 1985, 1988a, 1988b; Falniowski et al., 1988; Tafas, 1991). While spatial phytoplankton distribution has been related to the abiotic variables (Tafas & Economou-Amilli, 1991), there is a dearth of data on algal community structure and annual succession. The present study analyzes the spatial and temporal distribution patterns of the phytoplankton of lake Trichonis during different stages of annual succession.

Material and methods

Samples were obtained from the euphotic zone (0–20 m) in the central part of the lake (water depth 58 m) at 2 m intervals starting at the water surface for a total of 11 sampling times and 118 samples. Plankton sampling started in April 1985 and was carried out monthly until February 1986. Samples were immediately fixed in Lugol's solution and acetic acid. Identification of algal species was carried out using classical and modern keys and monographs as well as specific taxonomic

Table 1. List of algae found in the phytoplankton of lake Trichonis.

Cyanophyta
Chroococcus turgidus (Kützing) Nägeli
C. minutus (Kützing) Nägeli

Merismopedia punctata Meyen

Coelosphaerium kuetzingianum Nägeli
Gloeothece sp.

Anabaena sphaerica Bornet et Flahault
A. inaequalis (Kützing) Bornet et Flahault

Aphanizomenon sp.

Geitlerinema amphibium (Agardh ex Gomont) Anagnostidis

Planktothrix mougeotii (Bory ex Gomont) Anagnostidis et Komárek

Chlorophyta

Monoraphidium arcustum (Korsikov) Hindák
M. mirabile (W .et G.S. West) Pankow
M. minutum (Nägeli) Komárkova-Legnerová

Ankistrodesmus bernardii Komárek

Chlorella cf. *oocystoides* Hindák
Chlorella homosphaera Skuja
Chlorella vulgaris Beijerinck

Kirchneriella contorta (Schmidle) Bohlin
Quadrigula closterioides (Bohlin) Printz

Tetraedron caudatum (Corda) Hansgirg
T. minimum (A. Braun) Hansgirg

Coelastrum reticulatum (Dangeard) Senn
C. microporum Nägeli in A. Braum

Schroederia planktonica (Skuja) Philipose

Pediastrum boryanum (Turpin) Meneghini
P. simplex var. *sturmii* (Reinsch) Wolle

Oocystis cf. *nephrocytioides* Fott et Cado
O. lacustris Chodat
O. parva W. et G.S. West
O. pusilla Hansgirg
Oocystis sp.

Trochiscia cf. *granulata* (Reinsch) Hansgirg

Eutetramorus fottii (Hindák) Komárek
E. tetrasporus Komárek

Scenedesmus cf. *intermedius* Chodat
S. quadricauda (Turpin) Brébisson
Tetrachlorella alternans (G.M. Smith) Korsikov

Table 1. Continued

Tetrastrum glabrum (Roll) Ahlstrom et Tiffany
T. triangulare (Chodat) Komárek

Closterium aciculare T. West
C. acutum Brébisson

Cosmatium bioculatum Brébisson
C. contractum Kirchner

Staurastrum cf. *cornutum* Archer

Oedogonium sp.

Elakatothrix biplex (Nygaard) Hindák
E. gelatinosa Wille
E. genevensis (Reverdin) Hindák
Elakatothrix sp.

Mougeotia sp.

Spirogyra sp.

Bacillariophyta
Cyclotella radiosa (Grunow) Lemmermann
C. trichonidea Economou-Amilli
C. trichonidea var. *parva* Economou-Amilli

Stephanodiscus neoastraea Håkansson & Hickel
Diatoma vulgaris Bory

Fragilaria pinnata Ehrenberg

Asterionella formosa Hassal

Synedra tabulata (Agardh) Kützing
S. ulna var. *biceps* (Kützing) Kirchner

Cocconeis pediculus Ehrenberg
C. placentula var. *lineata* (Ehrenberg) Cleve

Achnanthes clevei Grunow
A. lanceolata (Brébisson) Grunow
A. minutissima var. *affinis* (Grunow) Lange-Bertalot

Gyrosigma acuminatum (Kützing) Rabenhorst
G. attenuatum (Kützing) Rabenhorst

Navicula cincta (Ehrenberg) Ralfs
N. cryptocephala Kützing
N. rhynchocephala Kützing
N. tripunctata (O.F. Müller) Bory

Amphora perpusilla Grunow

Nitzschia cf. *Lorenziana* var. *subtilis* Grunow
N. fonticola Grunow
N. intermedia Hantzsch ex Cleve et Grunow
N. pusilla Grunow emend. Lange-Bertalot
N. sigmoidea (Nitzsch) W. Smith

Continued on p. 143

Table 1. Continued

Cymbella aspera (Ehrenberg) Cleve
C. cymbiformis Agardh
C. helvetica Kützing
C. parva W. Smith
C. prostrata (Berkeley) Cleve

Gompbonema olivaceum var. *calcareum* (Cleve) Cleve

Chrysophyta
Dinobryon bavaricum Imhof
D. divergens Imhof
D. sertularia Ehrenberg
D. sociale Ehrenberg
Uroglena americana Calcins
Uroglena volvox Ehrenberg

Xanthophyta
Ophiocytium capitatum Wolle var. *longispinum* (Moebius) Lemmermann
O. lagerbeimii Lemmermann

Cryptophyta
Chroomonas acuta Utermöhl

Cryptomonas ovata Ehrenberg

Pyrrhophyta
Ceratium hirundinella (O.F. Müller) Bergh. f. *gracile* Bachman

C. birundinella f. *robustum* (Amberg) Bachman
C. furcoides (Lavander) Langhans

Peridinium cf. *africanum* Lemmermann
P. inconspicuum Lemmermann

papers (cit. in Tafas, 1991). Phytoplankton were counted with a Zeiss inverted microscope using Utermöhl's (1958) sedimentation method. The results of the counts were subject to statistical analysis as described by Lund et al. (1958). Phytoplankton biomass determination was based on the geometric calculation of cell volume and assuming a specific gravity of one (Van Heusden, 1972; Willen, 1976).

Multivariate techniques were used for R-analysis of the phytoplankton data matrix. These techniques are primarily applied to distinguish clusters of species with similar abundance patterns. The software implemented was kindly provided by the Plymouth Marine Laboratory, UK (Carr, 1989). Only species accounting for more than 2% of total abundance in any one sample (i.e. 45 species out of a total of 98) were included in the analysis. Square-root transformation of the raw data was used in the construction of the Bray & Curtis (1957) similarity matrix to scale down the scores of the abundant species. Group Average Cluster Analysis and Non-metric Multidimensional Scaling were applied to the derived species abundance similarity matrix (Field et al., 1982; Pielou, 1984; Clarke & Green, 1988; Clarke & Warwick, 1989; Ludwig & Reynolds, 1988). Abundance data were averaged for all depths on each sampling date for use in species clustering. Abundance data for each separate taxon within each grouping were subsequently transformed into percentage values. The standardized values were plotted using Microsoft Excel. Phytoplankton diversity was calculated using the $\log_2$ version of the Shannon-Wiener Species Diversity Index (Shannon & Weaver, 1949).

Results

Species composition

A total of 98 taxa (Table 1) were identified in the phytoplankton assemblages of lake Trichonis during the examined annual cycle, belonging to 7 algal divisions. Bacillariophyta and Chlorophyta were the most prominent groups in terms of species number with 32 and 41 taxa respectively. The Shannon-Wiener Species Diversity Index based on numbers of individuals ranged between 0.906 and 2522 in May and August 1985 respectively (Figure 1).

Biomass variation

Phytoplankton biomass in lake Trichonis exhibited a typically mono-acmic pattern with peak development in July (Figure 2). The biomass remained low until the end of the overturn at the end of March, to increase rapidly immediately after the onset of stratification. Thus, the mean biomass in the water column (0 to 20 m) increased from 44 mg m^{-3} at the end of March to 241 mg m^{-3} by the end of April, to more than 100-fold by the end of July (4295 mg m^{-3}). The maximum value of 7290 mg m^{-3} was recorded at 6 m of depth. Thereafter, phytoplankton biomass constantly decreased until the end of stratification from 2311 mg m^{-3} in August to 1082 mg m^{-3} in November with the lowest value recorded by the end of December (132 mg m^{-3}).

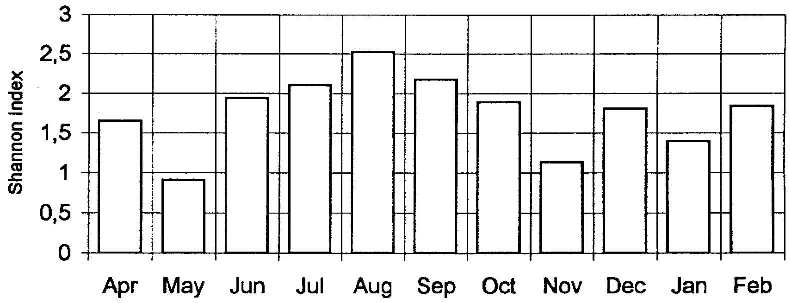

Figure 1. The Shannon-Wiener Species Diversity Index during the studied annual cycle.

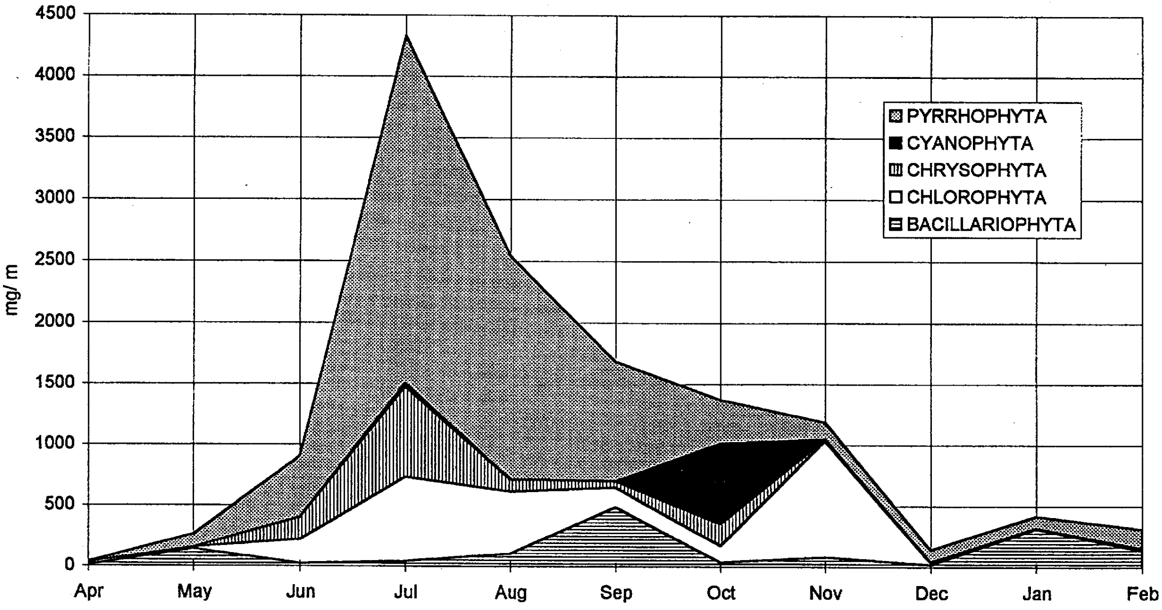

Figure 2. Seasonal biomass variation of the main taxonomic algal groups.

Seasonal phytoplankton periodicity

Seasonal periodicity of major algal groups

Three algal groups were dominant in the phytoplankton biomass of lake Trichonis: dinoflagellates (Pyrrhophyta), diatoms (Bacillariophyta) and green algae (Chlorophyta). Chrysophytes were present at lower numbers, but formed a distinct component of the biomass. Blue-green algae (Cyanophyta), on the other hand, were less significant in terms of numbers and biomass.

Diatoms were the dominant group (Figure 2) at the onset of stratification (end of April) accounting for 58% of the total phytoplankton biomass, but decreased rapidly to 3–4% after the vernal peak in June and July. Phytoplankton communities were dominated by dinoflagellates (over 50% of the total biomass) until September. From September till the end of stratification green algae, chrysophytes and blue-green were abundant. At the onset of turnover, however, diatoms became the dominant group once again, with an abundance value of 50%.

Seasonal periodicity of dominant algal species

By the end of turnover, when biomass values reached a minimum, the dominant species of the phytoplankton assemblage were mainly (a) the chlorophyte *Pediastum simplex* var. *sturmii* as well as *Spirogyra* and *Oedogonium* species, (b) the diatom *Cyclotella trichonidea* (Figure 3), and (c) the cryptophytes *Cryptomonas ovata* and *Chroomonas acuta*. By the end of May – when stratification was well developed (the upper boundary of metalimnion in 10 m of depth) and phytoplankton in its growth phase, the diatom *C. trichonidea* was the dominant species (70%) with dinoflagellates (*Peridinium* cf. *africanum*, *Ceratium hirundinella* f. *gracile*), other diatoms (*C. trichonidea* var. *parva*, *Cyclotella radiosa*) and green algal species as subdominants. The *C. trichonidea* population quickly declined and subsequently, *P.* cf. *africanum* (Figure 4) accounted for 43% of the total phytoplankton biomass. Other dominant species during this phase were *Dinobryon sociale*, *C. hirundinella* f. *gracile*, and *Eutetramorus tetrasporus*. By the end of July, *P.* cf. *africanum* contributed almost 62% of the phytoplankton biomass. This species along with *Dinobryon* spp., *Peridinium inconspicuum*, *C. hirundinella* f. *gracile* and a few species of green algae accounted for 95% of the total biomass.

In August, when total phytoplankton biomass values started to decline, the relative abundance of *P.* cf. *africanum* remained relatively stable. The abundance of *Dinobryon* spp. dramatically decreased from 17% in July to 3%; the dinoflagellates *Ceratium hirundinella* var. *gracile*, *C. furcoides* and *P. inconspicuum* formed 13.5% of the total biomass. The biomass of *P.* cf. *africanum* dropped to 25% of the July value in September. However, this species remained major component of the phytoplankton composition; at the same time, *Asterionella formosa* (Figure 5) developed to form 25.3% of the total biomass. In October, the biomass of *P.* cf. *africanum* was reduced to 6.4% of the total, while the blue-green alga *Chroococcus turgidus* was the major biomass component (48%). In November, *Mougeotia* trichomes were dominated (72%). In December, the abundance of *Mougeotia* dropped to 13.3% with a simultaneous decrease of mean total phytoplankton biomass. Dinoflagellates constituted the bulk of the phytoplankton biomass (67.5%). *Asterionella formosa* became again the dominant species in January, reaching 75% of the total phytoplankton biomass with dinoflagellates accounting for 23%. The concentration of *A. formosa* dropped dramatically from 283 mg m^{-3} in January to 9 mg m^{-3} in February when species of *Cyclotella*, *Ceratium*, *Nitzschia* and *Chlorella* dominated.

Species succession patterns

Cluster analysis and Non-Metric Multidimensional Scaling (Figures 6 and 7) indicate that certain phytoplankton species within the seasonal cycle are included in major groupings (G_1 to G_7). Each of these groupings contains species with high Bray-Curtis similarity; they are not characterized as typical 'clusters' since they have not been selected at a specific similarity level. Very few (5) species have been left out of the classification, their abundance values being only slightly above the 2% limit used for constructing the initial similarity matrix. The species' growth patterns for the groupings are displayed in Figure 8.

– Grouping (G_1) contains several diatom species (*Cymbella helvetica, Diatoma vulgare, Nitzschia intermedia, Tabularia fasciculata, Synedra ulna* var. *biceps*) appearing during overturn.

– Grouping (G_2) consists of green algal species (*Oocystis pusilla, Pediastrum simplex* var. *sturmii, Scenedesmus quadricauda, Chlorella vulgaris, Elakatothrix biplex*) appearing mainly in the beginning of stratification (with the exception of *O. pusilla*).

– Two blue-green algae (*Coelospbaerium kuetzingianum, Chroococcus minutus*) and one cryptophyte (*Cryptomonas ovata*) form a group of species (Grouping G_3) related to the above Grouping G_2, with growth patterns extending throughout the annual cycle.

– Three green algae (*Elakatothrix gelatinosa, Tetrachlorella alternans, Oocystis lacustris*) form Grouping G_4. These species reach their maximum abundance during stratification and gradually disappear afterwards.

– The abundance of species belonging to $G_{5.1}$ and $G_{5.2}$ peaks only once during the annual cycle. Grouping $G_{5.1}$ comprises *Asterionella formosa, Planktothrix mougeotii* and *Mougeotia* sp., while grouping $G_{5.2}$ *Chroococcus turgidus* and *Elakatothrix genevensis*. *A. formosa* is a typical representative of $G_{5.1}$ and $G_{5.2}$ species' growth pattern. Its high abundance coincides with high availability of silicates and other nutrients in hypolimnetic waters both at the end of stratification and during the mixing period.

– Several species dominating the plankton communities during the whole annual cycle are included in Grouping (G_6): *Ceratium hirundinella* fa. *robustum, G. hirundinella* fa. *gracile, Aphanizomenon* sp., *Chlorella* cf. *oocystoides, Cyclotella trichonidea, G. trichonidea* var. *parva*.

– Grouping ($G_{7.1}$) comprises the species *Eutetramorus tetrasporus, Peridinium* cf. *africanum, P. inconspicuum, Dinobryon divergens, D. sociale* with maximum development in the beginning of stratification and a gradual decline afterwards.

– Grouping ($G_{7.2}$) contains species (*Oocystis* cf. *nephrocytioides, Trochischia* cf. *granulata, Dinobryon*

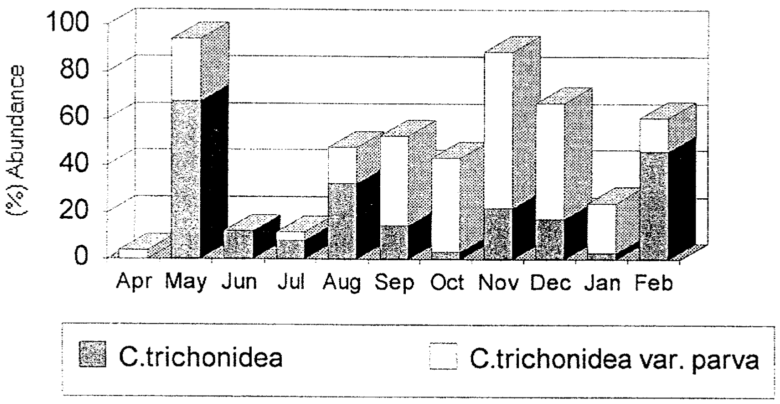

Figure 3. Contribution of the diatoms *Cyclotella trichonidea* and *C. trichonidea* var. *parva* to the total species abundance.

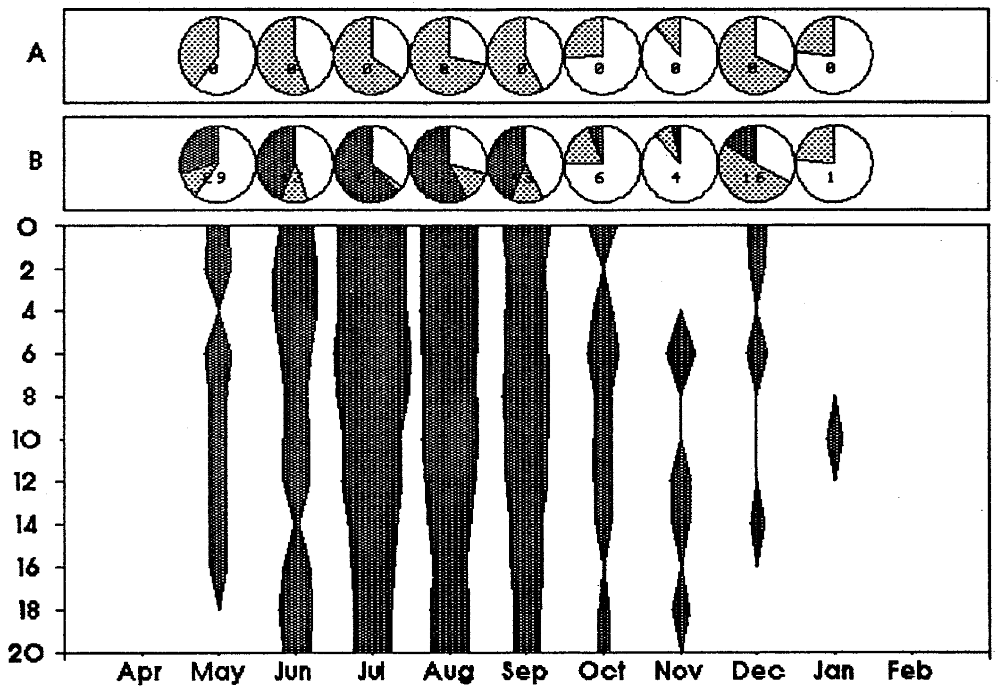

Figure 4. Annual pattern of vertical biomass distribution of *Peridihium* cf. *africanum* expressed in the form of cubic curves (max. biomass 4.8 mg m^{-3}). Pie charts portray the phytoplankton abundance (A) or the total phytoplankton biomass (B); the darker sectors correspond to the participation of *P.* cf. *africanum*, while the dotted sectors to the group (diatoms) participation.

bavaricum, Coelastrum reticulatum, Tetrastrum triangulare) reaching peak abundance at the same time as the species of Grouping $G_{7.1}$, but also exhibits a second peak during stratification.

Discussion

The phytoplankton assemblage comprises mainly cosmopolitan species; several other floristic components are mostly known from the tropics and have restricted distribution (details in Tafas, 1991); the diatoms *Cyclotella trichonidea* and *C. trichonidea* var. *parva* are probably endemic. Generally, periphytic diatoms

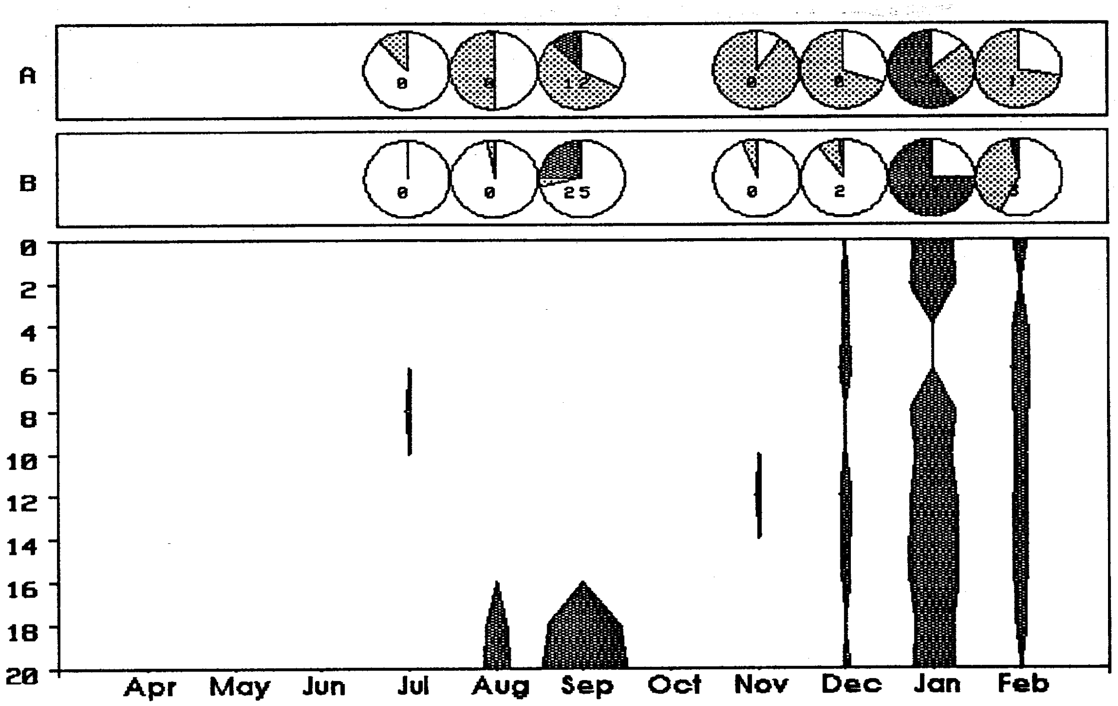

Figure 5. Annual vertical biomass distribution of *Asterionella formosa* expressed in the form of cubic curves (max. biomass 2.7 mg m^{-3}). Pie charts portray the phytoplankton abundance (A) and the total phytoplankton biomass (B); the darker sectors correspond to the participation of *A. formosa*, while the dotted sectors to the group (diatoms) participation.

prevailed during turnover possibly due to enhanced suspension by the mixing of the water column and drift from metaphyton to plankton (see Round, 1981; Reynolds, 1984a).

Minimum values of the Shannon-Wiener Diversity Index in May and November coincided with the dominance of the diatoms *Cyclotella trichonidea* and *C. trichonidea* var. *parva*, which contributed over 80% to the total species abundance (Figure 3). The high diversity values of June to September might be attributed to the onset of the nutrient depletion (Tafas, 1991; Tafas et al., 1997) restricting the dominance of the dominant competitor. High grazing pressure on the two small-celled *Cyclotella* species may have been an important factor for their abundance decrease; zooplankton grazing may also have given a competitive advantage to large inedible dinoflagellate forms.

Based on the annual biomass maximum (Vollenweider, 1982) Trichonis is classified among the oligotrophic lakes with mesotrophic tendencies. However, summer phytoplankton development characterizes eutrophic systems according to the PEG model (Sommer et al., 1986). The second smaller biomass peak during the subsequent turnover of the annual cycle (first peak 381 mg m^{-3} in January; second peak 286 mg m^{-3} in February) might be a consequence of nutrient remobilization, despite the unfavourable water temperature recorded (the lowest temp. <10 °C) of this period (Tafas, 1991; Tafas et al., 1997). On the other hand, a ‘clear water phase’ described from other stratified lakes (Sommer et al., 1986) did not develop in lake Trichonis, despite the dramatic diatom decrease following their vernal peak and the subsequent depletion of SiO_2-Si (Tafas, 1991).

Mono-acmic phytoplankton biomass distribution is typical for oligotrophic lakes in central Europe (Rott, 1984). In Greek lakes of different trophic status other patterns have been recorded: tri-acmic patterns in the eutrophic lakes Volvi and Vegoritis (Moustaka-Gouni, 1988; Moustaka-Gouni & Tsekos 1989; Moustaka-Gouni & Nikolaidis, 1990); and di-acmic patterns in the shallow lake Mikri Prespa (Tryfon 1994; Tryfon et al., 1994) and in the mesotrophic lake Amvrakia adjacent to Trichonis (Spartinou, 1992). Absolute biomass values are significantly lower in lake Trichonis in comparison to the aforementioned Greek lakes as well as to lake Kinneret: maximum biomass values in lake Trichonis are comparable to mean biomass values

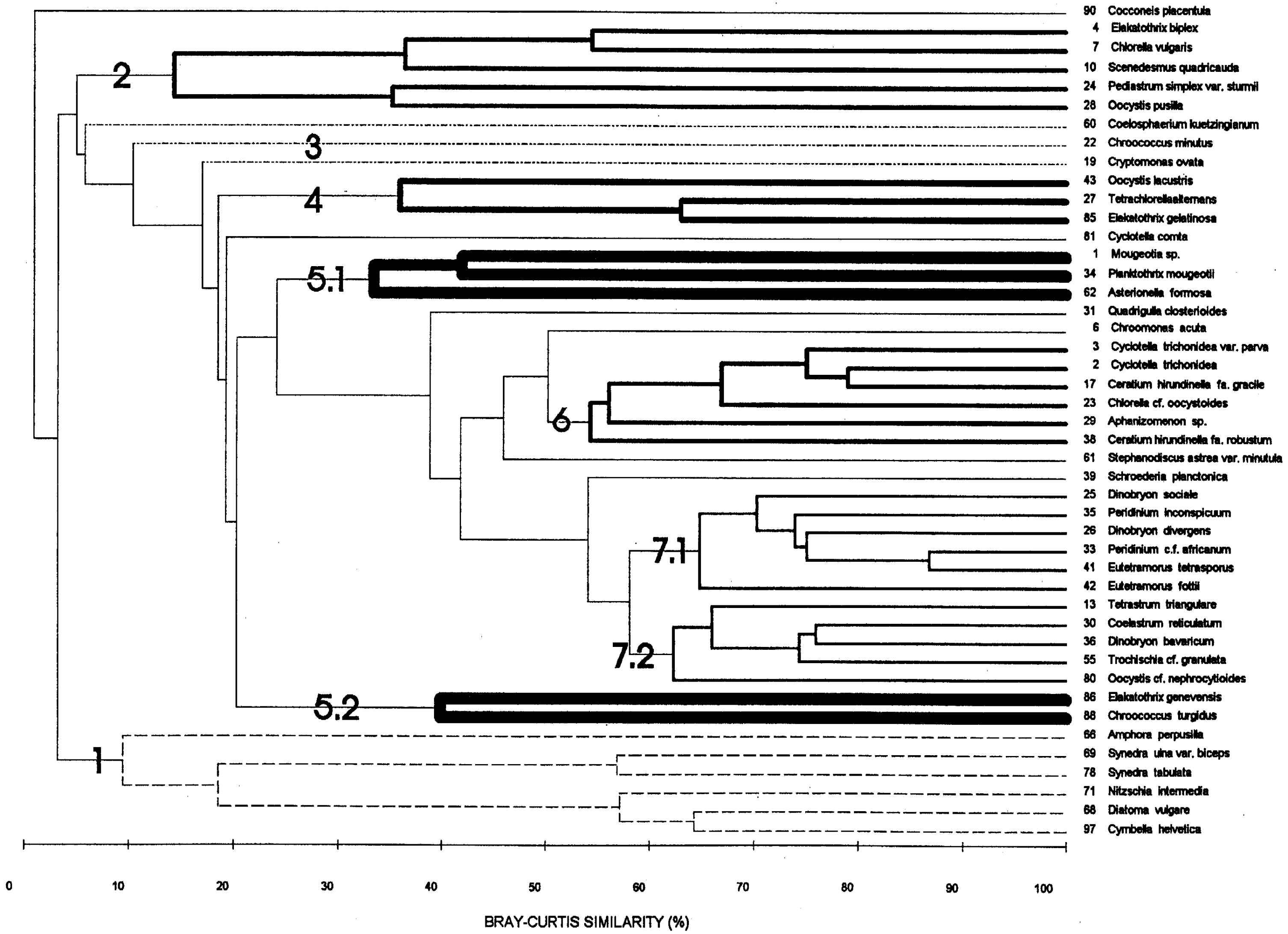

Figure 6. Dendrogram obtained from cluster analysis of those species accounting for more than 2% of the total abundance (code numbers precede the taxon name).

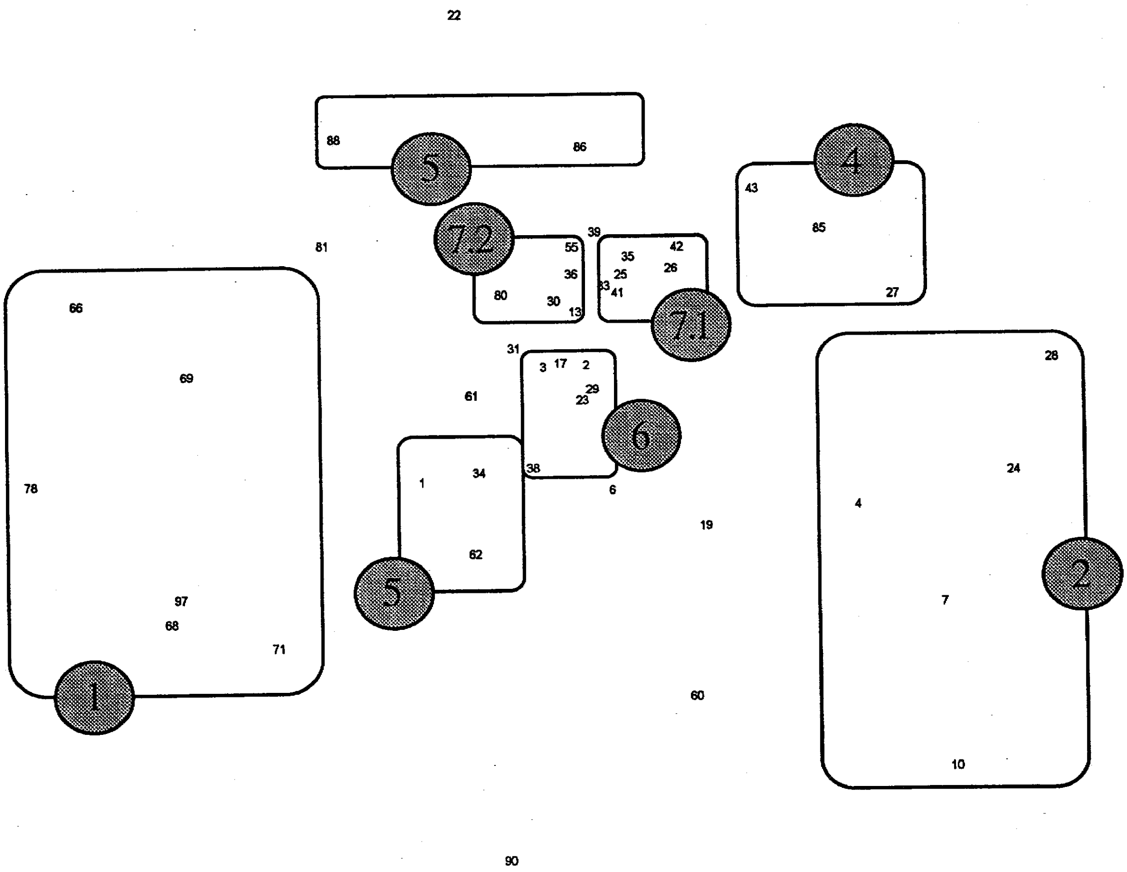

Figure 7. Plot derived from the two-dimensional solution of the Non-Metric Multidimensional Scaling; numbers refer to particular taxa of the previous (Figure 6) diagram.

in lakes Volvi (Moustaka-Gouni, 1988) and Kinneret (Pollingher & Berman, 1978), but lower than those of lake Amvrakia (Spartinou, 1992).

With regard to the annual succession pattern of phytoplankton (Reynolds, 1984b) Trichonis is classified among the oligotrophic lakes. This characterization is corroborated by the zooplankton findings from a later annual cycle (Dumont, unpubl. data) where Rotifera, a group favoured by oligotrophic conditions, dominated in terms of species numbers (>50%). Rare species such as *Leptodora kindti, Kellicottia longispina* and *Ploesoma hudsoni*, which are typical inhabitants of large oligotrophic lakes, were also present in lake Trichonis tending to disappear during eutrophication. In addition, the high proportion of chrysophyte species in relation to coccoid green algae and blue-green algae observed in lake Trichonis is also indicative of oligotrophic conditions. In the case of lake Trummen chrysophytes tripled after restoration (Cronberg, 1982).

The increase of diatoms seems to follow the reduction of the available SiO_2-Si (comp. Tafas, 1991; Tafas et al., 1997). This is exemplified in the period after the vernal diatom peak, where a reduction of the dominant *Cyclotella trichonidea* population from 500 to 100 individuals per liter followed a similar decline in silicates (from 700 to less than 200 μg l^{-1}). The summer increase of diatoms is mainly attributed to the high development of *Asterionella formosa* (Figure 5) in the hypolimnion, where mean SiO_2-Si concentration was higher than 1050 μg l^{-1}. Such a vertical distribution pattern might have been stimulated by the preceding silicate depletion in the epilimnion (mean SiO_2-Si concentration 30 μg l^{-1}), as nutrient-depleted cells are known to sink more rapidly than populations at the exponential growth phase (Tilman & Kilham, 1976a). In contrast, the simultaneous development of other diatoms (*C. trichonidea, C. trichonidea* var. *parva*) in the epilimnion is attributed to the tolerance of

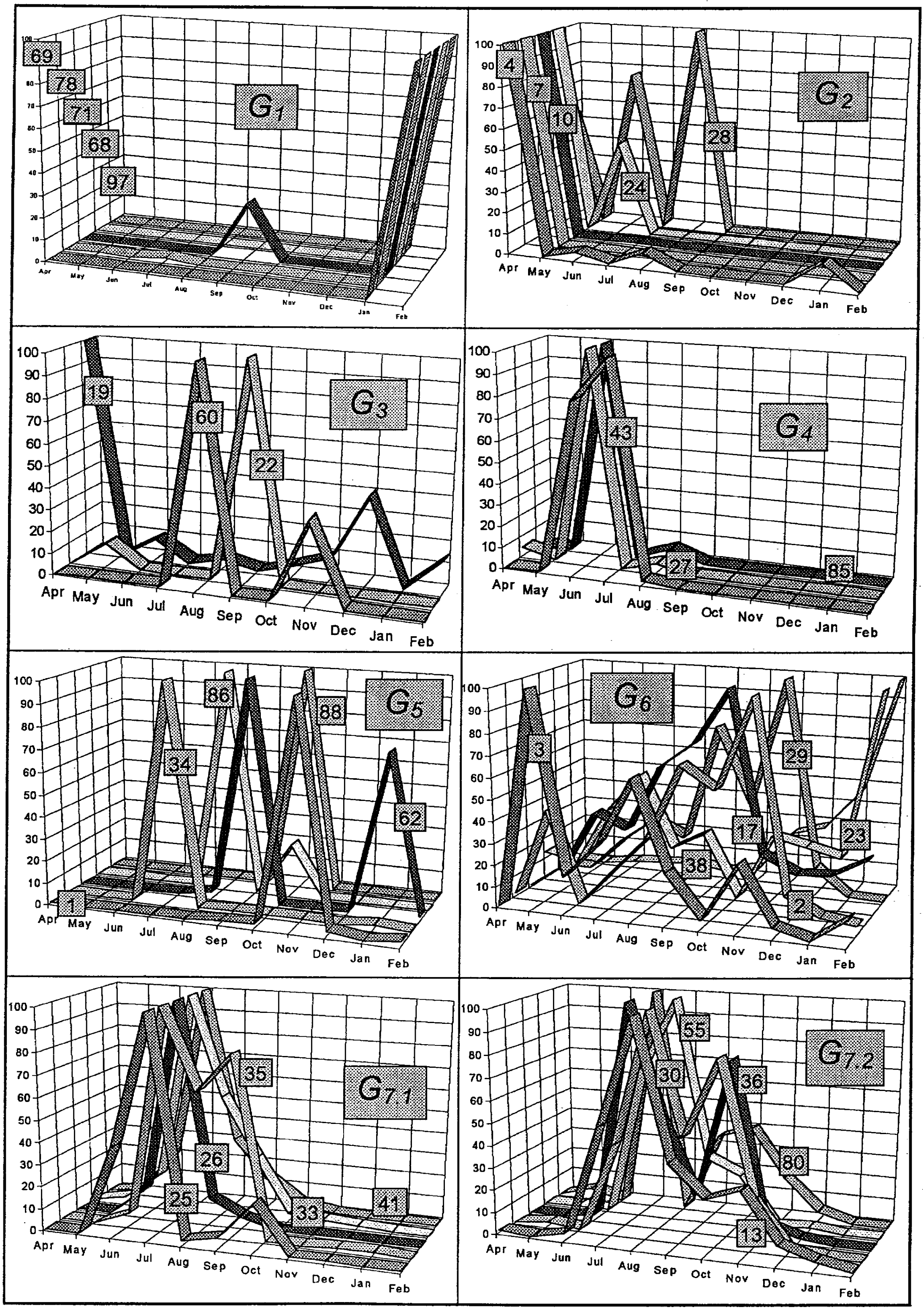

Figure 8. Groupings (G_1–$G_{7.2}$) of algal species portraying the seasonal phytoplankton periodicity over the studied annual cycle; the number on each curve refers to the particular taxon of the previous diagram (Figure 6); Y-axis represents the average percent abundance of each taxon.

certain diatom species for very low silica concentrations (see also Tilman et al., 1976; Tilman & Kilham, 1976b).

The group of diatoms showed a competitive advantage over other algal groups during both the warm and the cold period of the annual cycle. Blue-green algae and especially the nitrogen-fixing species, are poorly represented in lake Trichonis, unlike other warm lakes (Serruya & Pollingher, 1983). The observed distribution pattern of diatoms and blue-green algae is related to the availability of inorganic nitrogen and generally low phosphorus content during this particular annual cycle (Tafas, 1991; Tafas et al., 1997). The observed seasonal periodicity of both groups seems to justify the characterization of many diatoms as superior competitors for phosphorus and inferior competitors for nitrogen, and of many blue-green algae as superior nitrogen and inferior phosphorus competitors. The observations of this study, however, contradict the hypothesis of optimal diatom competitive ability at temperatures lower than 15 °C (Tilman et al., 1986; Tryfon et al., 1994). The maximum development of green algae in late summer and autumn indicates that species of this group may also be good nitrogen competitors. This hypothesis is corroborated by the comparable findings of Tilman, et al. (1986) and Tryfon et al. (1994). On the other hand, the dominance of dinoflagellates during stratification (see also Sommer et al., 1986) might be attributed to their capability to remain in the euphotic zone (Rodhe, 1948) and resistance to grazing due to their large size (Pollingher, 1978).

Examination of the seasonal periodicity patterns of dominant algal species, shows that *Peridinium* cf. *africanum* was the main biomass component during the stratified period (Figure 4). A similar phenomenon has been observed in lake Kinneret, where during the spring bloom, *Peridinium gatunense* – accompanied by green algae, blue-green algae and chrysophytes – constituted more than 95% of the total phytoplankton biomass (Pollinger, 1978; Wyatt & Horwood 1973; see also Berman et al., 1992). The growth of *Peridinium* during the summer and early autumn, i.e. at the time of phosphorus depletion in stratified lakes, has been attributed in lake Kinneret to ‘luxury consumption’ (Serruya & Berman, 1975), while in the Greek lake Mikri Prespa it has been associated with low dissolved inorganic nitrogen rather than low phosphate concentrations (Tryfon et al., 1994). In lake Trichonis the former explanation is more likely (comp. Tafas et al., 1997).

In general, cluster analysis reveals certain succession patterns, and population responses to specific environmental parameters. The similarity between Groupings 1–4 is below 50% of the maximal similarity value (Figure 6). In Grouping G_1, the appearance of diatoms during overturn is accounted by the replenishment of silicates in the hypolimnion at the end of stratification; moreover, diatoms tend to be favoured by the thorough mixing of water columns with transient micro-stratified density gradients (Round, 1981; Reynolds, 1984a). The green algae of Grouping G_2 seem to better exploit the nutrients after overturn replenishment (cf. Padisák & Tóth, 1991). This group is replaced by other dominating species at later stages of annual succession. The high abundance of Grouping G_4 species coincided with the total phytoplankton biomass peak. The abundance of these species declined in the poor nutrient conditions of mid-stratification (August).

The other groupings suggest a closer relationship among the species (Figure 9), which featured either narrow mono-acmic (Grouping $G_{7.1}$) and diacmic (Grouping $G_{7.2}$) growth patterns or wider growth periods. These species appeared mainly during stratification and some of them dominated the phytoplankton assemblage (Grouping G_6). In Grouping G_6, the endemic diatoms *Cyclotella trichonidea* and *C. trichonidea* var. *parva* have complementary abundance patterns, the latter replacing the former at the end of stratification; similar patterns are exhibited by the two forms of *Ceratium hirundinella* (fa. *gracile* and fa. *robustum*). All species of Groupings $G_{5.1}$ and $G_{5.2}$ showed mono-acmic growth patterns, with the exception of *Asterionella formosa* (see also Figure 5). This species is usually present in eutrophic or mesotrophic lakes (Reynolds, 1984b). Its di-acmic growth development in lake Trichonis coincides with the high availability of silicate and other nutrients during overturn, and also during stratification in the hypolimnion (Tafas, 1991; Tafas et al., 1997). A similar annual pattern of *A. formosa* was observed in the adjacent lake Amvrakia (Spartinou, 1992).

In the present case study of lake Trichonis, the annual succession patterns of some species in the same group may appear unrelated to one another and to nutrient availability (e.g. in Grouping G_3, species distribution extended throughout the annual cycle) because the calculation of similarities was based on collective abundance data. Nevertheless, cluster analysis as well as other multivariate methods (e.g. Tafas & Economou-Amilli, 1991) permits a better understanding of species niche preferences, e.g. tolerance to particular environmental conditions, interspecific competition or susceptibility to grazing. Finally, the analysis of annual succession patterns provides useful information for understanding the role of environmental parameters in community dynamics (Reynolds, 1984a, 1988; Sommer et al., 1986, 1993; Duarte et al., 1992; Reynolds et al., 1993; Padisák, 1993; Jacobsen & Simonsen, 1993).

Acknowledgments

The authors are indebted to Dr K. R. Clarke (Plymouth Marine Laboratory, Plymouth, UK) for the assistance provided on the application of multivariate techniques. Thanks are also extended to Dr M. Carr of the same laboratory for providing instructions and making the necessary modifications to the software used. Prof. Dr H. Dumont (Ghent University, Belgium) kindly placed at our disposal data on the zooplankton composition. Research was supported by DG-XII (Contract No. EV4V-0133-GR) of the European Commission.

References

Anagnostidis, K., J. Overbeck & D. Danielidis, 1985. *Oscillatoria* cf. *agardii* var. *isothrix* Skuja from the lakes Amvrakia and Trichonis, Greece. A taxonomic consideration. Arch. Hydrobiol. 104: 205–217.

Anagnostidis, K., A. Economou-Amilli & J. Overbeck, 1988a. *Anabaena azollae* Strassb. and the periphyton of *Azolla filiculoides* Lam. in lake Trichonis and the lagoon of Aetolikon, Hellas (Greece). Arch. Hydrobiol. 113: 321–343.

Anagnostidis, K., A. Economou-Amilli & T. Tafas, 1988b. *Aphanizomenon* sp. from lake Trichonis, Hellas (Greece). A taxonomic consideration in relation to morphological and ecological parameters. Arch. Hydrobiol. Suppl. 80: 1–4, Algological Studies 50–53: 529–543.

Bartell, S. M., T. F. H. Allen & J. F. Koonce, 1978. An assessment of principal component analysis for the description of phytoplankton periodicity in lake Wingra. Phycologia 17: 1–11.

Berman, T., Y. Z. Yacobi & U. Pollingher, 1992. Lake Kinneret phytoplankton: stability and variability during twenty years (1970–1989). Aquat. Sci 54: 104–127.

Billen, G., J. Garnier & P. Hanset, 1994. Modelling phytoplankton development in whole drainage networks: the ‘Riverstrahler’ Model applied to the Seine river system. Hydrobiologia 289: 119–137.

Bray, J. R. & J. T. Curtis, 1957. An ordination of the Oakland forest communities of southern Winskonsin. Ecol. Monogr. 27: 225–349.

Carr, M. R., 1989. ‘Practical notes for using the computer programmes prepared for the training workshop on the statistical treatment and interpretation of marine community data’, organised in the framework of the Long-term Programme for Pollution Monitoring and Research in the Mediterranean Sea (MED POL – Phase II). Athens, 18–29 September 1989, 105 pp.

Clarke, K. R. & R. H. Green, 1988. Statistical design and analysis for a ‘biological effects’ study. Mar. Ecol. Progr. Ser. 46: 213–226.

Clarke, K. R. & R. M. Warwick, 1989. ‘Report on the training workshop on the statistical treatment and interpretation of marine community data’, organised in the framework of the Long-term Programme for Pollution Monitoring and Research in the Mediterranean (MED POL – Phase II), Athens, Greece, 18–29 September 1989, 216 pp.

Cronberg, G., 1982. Changes in the phytoplankton of lake Trummen induced by restoration. Hydrobiologia 86: 185–193.

Duarte, C. M, S. Agusti & D. E. Canfield, 1992. Patterns in phytoplankton community structure in Florida lakes. Limnol. Oceanogr. 37: 155–161.

Economou-Amilli, A., 1979. Two new taxa of *Cyclotella* Kützing from Lake Trichonis, Greece. Nova Hedwigia 31: 467–477.

Economou-Amilli, A., 1982. SEM-Studies on *Cyclotella trichonidea* (Bacillariophyceae). Arch. Hydrobiol. Suppl. 63,1 Algological Studies 30: 25–34.

Falniowski A., A. Economou-Amilli & K. Anagnostidis, 1988. *Valvata piscinalis* O. F. Müller (Mollusca-Prosobranchia) and its epizoic diatoms in lake Trichonis, Greece. Int. Revue ges. Hydrobiol. 73: 327–335.

Field, J. G., K. R. Clarke & R. M. Warwick, 1982. A practical strategy for analysing multispecies distribution patterns. Mar. Ecol., Progr. Ser. 8: 37–52.

Goldman, N., T. B. Paddock & K. M. Shaw, 1990. Quantitative analysis of shape variation in populations of *Surirella fastuosa*. Diatom Res. 5: 25–42.

Hutchinson, G. E., 1967. A treatise on Limnology. II. Introduction to Lake Biology and the Limnoplankton. John Wiley and Sons, New York, 1115 pp.

Jacobsen, B. A. & P. Simonsen, 1993. Disturbance events affecting phytoplankton biomass, composition and species diversity in a shallow eutrophic temperate lake. Hydrobiologia 249: 9–14.

Kalff, J. & R. Knochel, 1978. Phytoplankton and their dynamics in oligotrophic and eutrophic lakes. Annu. Rev. Ecol. Syst. 9: 475–95.

Kristiansen, J., 1980. Chrysophyceae from some Greek lakes. Nova Hedwigia 33: 167–194.

Leskinen, E. & J. Sarvala, 1988. Community analysis of diatom colonization on artificial substrata in a northern Baltic Sea Archipelago: a comparison of methods. Ann. bot. Finnici 25: 21–32.

Ludwig, J. A. & J. F. Reynolds, 1988. Statistical Ecology. A Primer on Methods and Computing. John Wiley and Sons, New York, 339 pp.

Lund, J. W. G., 1969. Phytoplankton. In: NAS Symposium, ‘Eutrophication: Causes, Consequences, Correctives’, Washington D.C., 306–330.

Lund, J. W. G., C. Kipling & E. D. Cren, 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia 11: 143–170.

Moustaka-Gouni, M., 1988. Seasonal variations, annual periodicity and spatial distribution of phytoplankton in lake Volvi. Diss., Univ. Thessaloniki, 230 pp. (in Greek)

Moustaka-Gouni, M. & I. Tsekos, 1989. The structure and dynamics of the phytoplankton assemblages in lake Volvi Greece. II. Phytoplankton biomass and environmental factors. Arch. Hydrobiol. 115: 575–588.

Moustaka-Gouni, M. & G. Nikolaidis, 1990. Phytoplankton of a warm monomictic lake, Lake Vegoritis, Greece. Arch. Hydrobiol. 119: 229–313.

Overbeck, J., K. Anagnostidis & A. Economou-Amilli, 1982. A limnological survey of three Greek lakes: Trichonis, Lyssimachia and Amvrakia Arch. Hydrobiol. 95: 365–394.

Padisák, J., 1993. The influence of different disturbance frequencies on the species richness, diversity and equitability of phytoplankton in shallow lakes. Hydrobiologia 249: 135–156.

Padisák, J. & L. G. Tóth, 1991. Some aspects of the ecology of subdominant green algae in a large, nutrient limited shallow lake (Balaton, Hungary). Arch. Protistenkd. 139: 225–242.

Pielou, E. C., 1984. The interpretation of ecological data. J. Wiley and Sons, New York, 263 pp.

Pollingher, U., 1978. Annual pattern of algal succession. In Serruya, C. (ed.), Lake Kinneret. Dr W. Junk Publishers, The Hague: 243–246.

Pollingher, U & T. Berman, 1978. Biomass and chlorophyll, 247–252. In: Serruya, C.(ed.) Lake Kinneret. Dr W. Junk, The Hague, Boston, London, 501 pp.

Reynolds, C. S., 1984a. The Ecology of Freshwater Phytoplankton. Cambridge Univ. Press., Cambridge, 384 pp.

Reynolds, C. S., 1984b. Phytoplankton periodicity: the interactions of form, function and environmental variability. Freshwat. Biol. 14: 111–142.

Reynolds, C. S., 1988. The concept of ecological succession applied to seasonal periodicity of freshwater phytoplankton. Verh. int. Ver. Limnol. 23: 683–691.

Reynolds, C. S., J. Padisák & U. Sommer, 1993. Intermediate disturbance in the ecology of phytoplankton and the maintenance of species diversity: a synthesis. Hydrobiologia 249: 183–188.

Rohde, W., 1948. The ionic composition of lake waters. Verh. int. Ver. Limnol. 10: 377–386.

Round, F. E., 1971. The growth and succession of algal populations in freshwaters. Mitt. int. Ver. Theor. angew. Limnol. 19: 70–99.

Round, F. E., 1981. The Ecology of Algae. Cambridge Univ. Press, Cambridge, 653 pp.

Serruya, C. & T. Berman, 1975. Phosphorus, nitrogen and the growth of algae in Lake Kinneret. J. Phycol. 11: 155–162.

Serruya, C. & U. Pollingher, 1983. Lakes of the Warm Belt. Cambridge Univ. Press, Cambridge, 569 pp.

Shannon, C. E. & W. Weaver, 1949. The mathematical theory of communications. Illinois Univ. Press. Urbana, Chicago, London, 125 pp.

Sommer, U., Z. Gliwicz, W. Lampert & A. Duncan, 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. Arch. Hydrobiol. 106: 433–471.

Sommer, U., J. Padisák, C. S. Reynolds & P. Juhasz-Nagy, 1993. Hutchinsons's heritage: the diversity-disturbance relationship in phytoplankton. Hydrobiologia 249: 1–7.

Sorhannus, U., 1993. The sister-group of diatoms. An analysis using a combined data set. Diatom Res. 8: 131–143.

Spartinou, M., 1992. The microflora of Lake Amvrakia, Western Greece. A systematic and ecological approach. Diss., Univ. Athens, 354 pp.

Stewart, P. M., E. P. Smith & J. Cairns, Jr., 1987. Relationship of the physico-chemical environment to diatom and protozoa communities. A multivariate approach. Arch. Protistenkd. 134: 331–341.

Tafas, T. P., 1991. The microflora of Lake Trichonis (Aetoloakarnania, Western Greece). Quantitative and qualitative phytoplankton analysis. Seasonal succession. Diss., Univ. Athens, 363 pp.

Tafas, T. P. & A. Economou-Amilli, 1991. Evaluation of phytoplankton variation in lake Trichonis (Greece) by means of multivariate analysis. Mem. Ist. ital. Idrobiol. 48: 99–112.

Tafas, T. P., D. Danielidis, J. Overbeck & A. Economou-Amilli, 1997. Limnological survey of the warm monomictic lake Trichonis (central western Greece). I. The physical and chemical environment. Hydrobiologia 344: 129–139.

Thorrington-Smith, M., 1971. West Indian Ocean phytoplankton: a numerical investigation of phytohydrographic regions and their characteristic phytoplankton associations. Mar. Biol. 9: 115–137.

Tilman, D. & P. Kilham, 1976a. Sinking in freshwater phytoplankton: Some ecological implications of cell nutrient status and physical mixing processes. Limnol. Oceanogr. 21: 409–417.

Tilman, D. & S. S. Kilham, 1976b. Phosphate and silicate growth and uptake kinetics of the diatoms *Asterionella formosa* and *Cyclotella meneghiniana* in batch and semicontinuous culture. J. Phycol. 12: 375–383.

Tilman, D., S. S. Kilham & P. Kilham, 1976. Morphometric changes in *Asterionella formosa* colonies under phosphate and silicate limitation. Limnol. Oceanogr. 21: 883–886.

Tilman, D., R. Kiesling, R. Sterner, S. S. Kilham & F. A. Johnson, 1986. Green, blue-green and diatom algae. Taxonomic differences in competitive ability for phosphorus, silicon and nitrogen. Arch. Hydrobiol. 106: 473–485.

Tryfon, E., 1994. Structure and dynamics of phytoplankton assemblages in lake Mikri Prespa. Diss. Univ. Thessaloniki 238 pp + 16 pls. (in Greek).

Tryfon, E., M. Moustaka-Gouni, G. Nikolaidis & I. Tsekos, 1994. Phytoplankton and physical-chemical features of the shallow lake Mikri Prespa, Macedonia, Greece. Arch. Hydrobiol. 131: 477–494.

Utermöhl, H., 1958. Zur Vervollkommung der quantitativen Phytoplankton-Methodik. Mitt. int. Verh. theor. angew. Limnol. 9: 1–38.

Van Heusden, G. P. H., 1972. Estimation of the biomass of plankton. Hydrobiologia 39: 165–208.

Vollenweider, R. A., 1982. Eutrophisation des eaux. Méthodes de surveillance, d' évaluation et de Lutte. OCDE, Paris, Rapport technique, no 42078, 165 pp.

Vyverman, W., 1992. Multivariate analysis of periphytic and benthic diatom assemblages from Papua New Guinea. Hydrobiologia 234: 175–193.

Willen, E., 1976. A simplified method of phytoplankton counting. Br. Phycol. J. 11: 265–278.

Wyatt, T. & J. Horwood, 1973. Model which generates red tides. Nature 244: 238–249.